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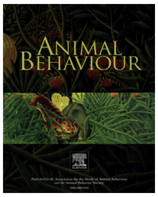

Partial honesty in a hummingbird polymorphism provides evidence for a hybrid equilibrium

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Animal signals, while informative, are unlikely to be entirely reliable. Models of such partially honest communication have traditionally taken the form of ‘honest-enough’ signalling, in which a subset of signallers can signal at lower cost and therefore exaggerate their perceived ability or condition. Although support for these models has been demonstrated, alternatives are rarely tested in nature. Recent theory has highlighted an alternative model that also results in partial reliability, yet functions through a different mechanism. In so-called hybrid equilibria, all signallers pay the same costs given their condition, yet low-quality signallers sometimes spoof the high-quality signal, which receivers sometimes heed and sometimes ignore. Although theoretically well established, documentation of hybrid equilibria in nature is rare. Here, using previously collected behavioural data from the field and literature, we detail a game-theoretic model based on the natural history of hummingbirds. We demonstrate that an unusual female plumage polymorphism found in these birds is best explained as a hybrid equilibrium. In addition to explaining the persistence of polymorphism, the model also offers testable parameters that may predict the wide range of sex variation in plumage found across hummingbirds and other taxa, including bright and dull monomorphism and sexual dimorphism. Ultimately, our findings show that intersexual mimicry can be modelled as a hybrid equilibrium, that hybrid signals likely exist in nature, and that there is the need for a greater diversity of models to explain stable communication.

The world reverberates with animal signals of every imaginable variety. Yet the pervasiveness of communication is perplexing: while signallers typically have at least some incentive to deceive, signals that are overly deceptive or not sufficiently informative should be ignored (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Seeking to solve this dilemma, the animal signalling literature has largely concentrated on the question of how honesty can be ensured. One prominent mechanism for ensuring honesty is differential costs or benefits to a signal, also known as handicap mechanisms (Grafen, 1990; Maynard Smith, 1991; Zahavi, 1975). Other mechanisms for honesty have been proposed as well (for a discussion of some of them, see Maynard Smith & Harper, 2003).

However, perfect honesty is not required to merit attention from signal receivers. In fact, perfectly honest signals are likely to be rare in nature (Johnstone & Grafen, 1993), and mathematical models have shown that some amount of error or deception may be tolerated at a game-theoretic equilibrium. For example, in systems where signal honesty results from differences in the cost of signalling, some undesirable signallers may be able to produce impressive signals at low cost without destabilizing signalling altogether (Hughes, 2000; Proulx, 2001).

Johnstone and Grafen (1993) developed a game-theoretic model of this partially honest scenario. Like other models that followed (e.g. Kokko, 1997; Proulx, 2001), signallers vary in terms of the property or status that the receiver aims to assess, but also in other ways that are not of concern to the signal–receiver but nevertheless influence the cost of signal production. In this way, ‘receiver-irrelevant’ costs influence the signal’s reliability. These models, which we refer to as ‘honest-enough’ models, parallel handicap models in their reliance on differential costs or benefits, but also

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predict a certain level of stable dishonesty. In honest-enough models, signallers play pure strategies in selecting their signals based either on external cues from the environment or on internal state. Individuals that display 'honestly' must differ from those said to signal 'dishonestly' due to payoff differences of some sort. Empirical studies have indeed found differences between honest and dishonest signallers in some species (e.g. Backwell et al., 2000; Barry, 2015; Candolin, 1999; Nielsen & Holman, 2012), but this is not always the case even when differences are explicitly investigated (Ghislandi et al., 2017). We note that for the purposes of this paper, we follow Searcy and Nowicki (2005) in equating 'honest' signals with those that benefit signal receivers when they respond to the signal and 'dishonest' signals with those that deviate from receivers' expectations in a way that is harmful to this receiver.

In contrast to honest-enough models, partially honest signalling systems may also evolve where signallers and receivers play mixed strategies, randomizing their signals and responses, respectively. These models typically assume that signallers differ only in the character being signalled.

The mixed strategy equilibrium with partially honest signalling is known as a 'hybrid equilibrium'. Although early theoretical examples were described in biology (Gardner & Morris, 1989; Viljugrein, 1997) and economics (Gibbons, 1992), hybrid equilibria found few empirical applications. Theoretical work two decades later illustrated the importance of hybrid equilibria for both evolutionary (Huttegger & Zollman, 2010, 2016; Zollman et al., 2013) and learning dynamics (Wagner, 2013). Although the hybrid equilibrium is in a sense weaker than an evolutionarily stable strategy, there is some theoretical evidence that it may be more likely to evolve than traditional handicap-style signalling (Kane & Zollman, 2015). This suggests that hybrid equilibria should be prevalent in natural systems, yet examples have not been previously documented, to our knowledge. Demonstrating a model's utility for explaining real-world situations is important for showing relevancy and grants the ability to test assumptions and predictions in nature.

Here we provide a game-theoretic model of hummingbird behaviour and, using previously published data in this system (Falk et al., 2021, 2022), demonstrate that a remarkable plumage polymorphism in females of the white-necked jacobin hummingbird, *Florisuga mellivora*, is best explained as a hybrid signalling equilibrium. We show that this model can explain the persistence of the stable polymorphism in female coloration that characterizes this and potentially other species of hummingbirds (Bleiweiss, 1985, 1992, 2001; Diamant et al., 2021; Ortiz-Pulido & Martínez-García, 2006). In white-necked jacobins, all males express the ornamented androchromic plumage type, with conspicuous blue heads and white tails. Most adult females express a nonornamented heterochromic plumage type, with a grey mottled throat and green-brown dorsum (Falk et al., 2021; Stiles et al., 2020). However, roughly ~20% of adult females are androchromic and practically indistinguishable from males by sight (Falk et al., 2021). Preliminary evidence indicates that the polymorphism is genetically heritable via a single locus of large effect (Falk et al., 2024). Previous studies have shown that males are more likely to be territorial than females, and they exhibit adaptations (e.g. wing shape, burst capacity) for agonistic flight manoeuvres. Although females differ from males, these traits, which increase the chance of winning aggressive interactions, do not differ between androchrome and heterochrome females (Falk et al., 2022). These studies support the hypothesis that androchrome females are mimicking males, resulting in reduced aggression from other hummingbirds and increased access to nectar resources (Falk et al., 2021). This intersexual social dominance mimicry has been proposed as a mechanism by which the female polymorphism could persist in white-necked jacobins and other hummingbird species (Falk et al., 2022).

We show that the intersexual social dominance mimicry hypothesis can be mathematically modelled as a hybrid equilibrium between a foraging hummingbird and an adversary that might seek to displace it from a nectar resource. We first develop the model, then discuss how previously published field observations support the model's assumptions and findings. We compare our hybrid equilibrium model with a traditional honest-enough signalling model to provide distinct empirical predictions of each. Lastly, we discuss applicability for this model in other taxa with sex-limited polymorphism (e.g. Bleiweiss, 2001; Diamant et al., 2021; Kunte, 2009; Oliveira et al., 2008; Ortiz-Pulido & Martínez-García, 2006), and the potential to predict other forms of sex colour diversity, including sexual dichromatism and bright and drab monochromatism (Beltrán et al., 2022; Dale et al., 2015).

MODEL

We model the interaction between a forager (player 1) and an adversary (player 2) as a discrete action–response game (Hurd, 1995; Számadó, 1999). 'Nature' moves first, choosing the sex of the forager to be male with probability k or female with probability $1 - k$. The forager chooses a signal: ornamented or nonornamented plumage. As the forager feeds from a nectar source, the adversary observes its signal but not its sex, then chooses to attack or avoid the forager. Adversaries may include any other individual that competes ecologically for similar resources, including conspecific and heterospecific individuals. The general intuition is that the forager would do well to avoid being attacked and the adversary would do well to attack females that have low resource-holding potential (RHP) but not to attack males that have higher RHP and could retaliate. Figure 1 shows this game in extensive form. We assume that sexual selection is the primary driver of extravagant male plumage and that males obtain a large fitness benefit b from

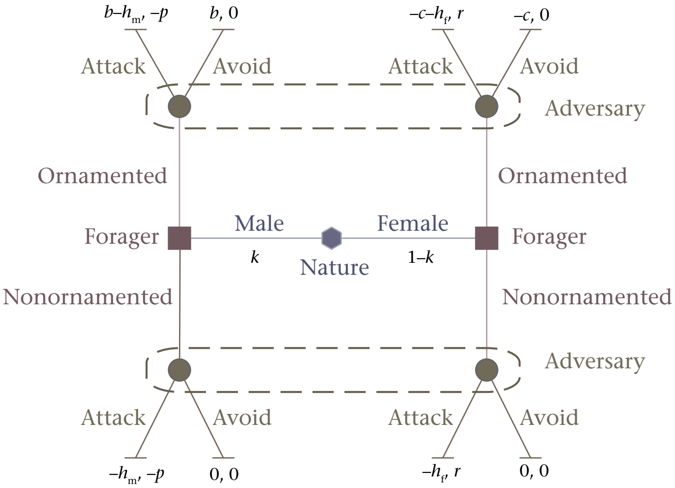

Figure 1. The jacobin signalling game. The game begins with 'Nature', represented by the hexagon at the centre, choosing the forager's sex at random. Next, the forager, represented by the squares, considers its sex and produces a signal, namely ornamented or nonornamented plumage. In the white-necked jacobin, this refers to androchromic and heterochromic plumage morphs, respectively. Finally, the adversary, represented by circles, chooses whether to attack or avoid the forager. The adversary observes the forager's signal but does not know the forager's sex, as implied by the dashed lines indicating information sets. Payoffs for forager and adversary, respectively, are as given at the terminal nodes.

developing ornamented plumage. Females, however, suffer a cost c from displaying ornamented plumage, most likely because of increased nest predation brought on by their conspicuous appearance. Only females suffer this cost because only female hummingbirds perform parental care.

Both males and females suffer a cost from being attacked by the adversary. Let h_m and h_f be the cost of being attacked to a male and a female, respectively, which likely differs between the sexes due to differences in RHP (Falk et al., 2022). The adversary reaps a reward r from attacking a female but receives a punishment p from attacking a male due to differences in RHP. Payoffs for forager and adversary are given at the terminal nodes in Fig. 1. See Table 1 for a summary of all variables.

Separating Equilibrium

Traditional honest signalling models of discrete action response games focus on separating equilibria. In this game, that would be an equilibrium with complete sexual dimorphism of foragers (Table 2), in which males always produce ornamented plumage and females always produce nonornamented plumage. Additionally, adversaries always attack nonornamented individuals but never attack ornamented individuals. These stand in contrast to pooling equilibria, where no information is communicated because, for example, males and females produce identical plumage.

Mathematically, a separating equilibrium requires the following conditions. First, at separating equilibrium, the adversary has perfect information about the sex of the forager, and thus the adversary must benefit from attacking females and suffer from attacking males.

$$r > 0 \tag{1}$$

$$p > 0 \tag{2}$$

Second, given that the adversary behaves in that way, male foragers must benefit from ornamented plumage and female foragers must benefit from nonornamented plumage. This requires that

$$b > -h_m \tag{3}$$

$$c > h_f \tag{4}$$

When these conditions are met, a stable separating equilibrium will exist in which the signaller will provide the adversary with complete information about its sex and the adversary will act on that information using a pure strategy (Table 2). Given that b, r, p and h_m are positive by assumption, the only binding condition is given by equation (4): $c > h_f$.

What happens when the above condition is not met? That is, what happens when the cost to a female of having ornamented plumage is less than the cost of being attacked by the adversary? In this case, no separating equilibrium exists. Instead, under appropriate conditions, there will be a hybrid equilibrium in which some but not all females produce ornamented plumage and some but not all adversaries attack ornamented foragers (Zollman et al., 2013).

Unlike with other signalling models, this game cannot have a pooling equilibrium, where there is no dimorphism and both types display the same plumage, that coexists with either the hybrid or separating equilibrium. When the payoffs do not meet the conditions for either the separating or hybrid equilibrium, then there will be a pooling equilibrium where both sexes display the same plumage and the adversary attacks with either probability 0 or 1 (Table 2).

Table 1
Summary of variables

Variable	Description
k	Probability that a forager is male
b	Benefit to males for ornamented androchrome plumage
c	Cost to females for ornamented androchrome plumage
h_f, h_m	Cost of being attacked to a foraging female or male, respectively
r	Benefit to adversaries for attacking females
p	Cost to adversaries for attacking males
x	Fraction of androchromes that are female
a	Fraction of females that are androchromes
y	Fraction of adversaries that attack androchromes

Hybrid Equilibrium

At a hybrid equilibrium, female foragers mix between two strategies: produce ornamented plumage and produce nonornamented plumage. Likewise, adversaries mix between two strategies: attack ornamented foragers and avoid ornamented foragers. At a mixed strategy Nash equilibrium, all pure strategies used at positive frequency must have the same payoff.

Let x be the fraction of ornamented females. Recall that a fraction $(1-k)$ of the foragers are female. If a fraction a of females are ornamented, then the fraction of ornamented foragers that are female is $x = a(1-k)/(k+(1-k)a)$. The payoff to an adversary of chasing an ornamented forager must be equal to the payoff of avoiding an ornamented forager:

$$x\,r-(1-x)p=0 \tag{5}$$

Simplifying,

$$x=\frac{p}{r+p} \tag{6}$$

Recall, x is the proportion of ornamented foragers that are female. To determine the percentage of females that are ornamented we solve for a:

$$x=\frac{p}{r+p}=\frac{a(1-k)}{k+(1-k)a} \tag{7}$$

Simplifying,

$$a=\frac{k}{1-k}\frac{p}{r} \tag{8}$$

In this expression, $k/(1-k)$ is the sex ratio of foragers (not necessarily of the entire population) and p/r is the ratio of the cost of attacking a male and the benefit of attacking a female. For the hybrid equilibrium to exist, $a < 1$. Combining that condition with the equation above, and multiplying both sides by $(1-k)/k$ yields,

$$\frac{1-k}{k}>\frac{p}{r} \tag{9}$$

Although this is technically a prediction of the model, measuring p and r would be quite difficult in practice and therefore we do not include it as a prediction in the sections that follow.

Now let y be the fraction of adversaries that attack ornamented foragers. The payoff to a female of being ornamented must be equal to the payoff to being nonornamented;

$$y\left(-c-h_f\right)-(1-y)c=-h_f \tag{10}$$

Simplifying,

Table 2
Model conditions for each equilibrium state, corresponding to differing forager and adversary strategies

Sexual phenotype (forager strategy)	Equilibrium type	Female conditions	Male conditions	Adversary conditions	Adversary strategy
Nonornamented monomorphism	Pooling	$c > 0$	$b < 0$	—	Adversary attacks all foragers when $r(1-k) > pk$ but never attacks foragers otherwise
Ornamented monomorphism	Pooling	$c < 0$	$b > 0$	—	Adversary attacks all foragers when $r(1-k) > pk$ but never attacks foragers otherwise
Ornamented monomorphism	Pooling/Separating	$c > 0$ $h_f > c$	$b > 0$	$r(1-k) < pk$	Adversary only attacks nonornamented foragers (which they never encounter) and never attacks ornamented foragers
Sexual dimorphism (male ornamented, female nonornamented)	Separating	$c > 0$ $c > h_f$	$b > 0$	—	Adversary attacks all nonornamented foragers (females) but never attacks ornamented foragers (males)
Polymorphism (male ornamented, female polymorphic)	Hybrid	$c > 0$ $h_f > c$	$b > 0$	$(1-k)/k > p/r$	y adversaries attack all foragers; $1-y$ adversaries attack only nonornamented foragers

h_m, h_f, p and r are all assumed to be positive. A dash (—) indicates no condition is necessary.

$$y = \frac{h_f - c}{h_f} \tag{11}$$

In order for the hybrid equilibrium to exist, $y > 0$, which requires that $h_f > c$. This demonstrates that the hybrid and separating equilibrium are incompatible.

Finally, we need to ensure that all males will choose to produce ornamented plumage. This requires that

$$b - y\,h_m > -h_m \tag{12}$$

Simplifying,

$$y < \frac{b + h_m}{h_m} \tag{13}$$

Since b and h_m are positive by assumption this inequality is trivially satisfied.

The values we have computed for x and y now give us the equilibrium strategies at the hybrid equilibrium. Male foragers will play the pure strategy (1, 0) where the first term 1 is the fraction of time producing ornamented plumage and the second term 0 is the fraction of time producing nonornamented plumage. Female foragers will play the mixed strategy $(a, (1-a))$. Adversaries confronted with a nonornamented forager will play the pure strategy (1, 0), where the first term is the fraction of the time that one attacks the forager and the second term is the fraction of the time that one avoids the forager. Adversaries confronted with an ornamented forager will play the mixed strategy $((h_f - c)/h_f, c/h_f)$.

This gives us a hybrid equilibrium with partially honest signalling that features polymorphism in plumage among females but not among males (Table 2). In addition, it features variable behaviour in response towards ornamented plumage but not in response towards nonornamented plumage. This equilibrium is evolutionarily stable in a slightly weaker sense than the separating equilibrium (sexual dimorphism), but in a way that nevertheless makes it a plausible end point for evolution (Huttegger & Zollman, 2010, 2016; Zollman et al., 2013).

Hybrid equilibria are not the only polymorphic equilibria predicted by models of signalling. In some models of bidirectional signalling in animal contests, polymorphism may be stable (Számadó, 2000). Because we are modelling a system where the signalling is one-way, we will restrict ourselves to the hybrid equilibrium in one-way signalling models.

EMPIRICAL EVIDENCE

Model Assumptions

The model we have outlined makes a number of assumptions about parameter values. Here we consider the evidentiary support for these assumptions.

(1) Males get a sexual selection benefit from ornamented plumage via mate choice ($b >> 0$): in hummingbirds, females provide all parental care to chicks, including nest construction, egg laying and incubation, feeding and fledging (Skutch, 1973; Stiles et al., 2020). Therefore, females are likely to have strong mating preferences and males likely experience very strong sexual selection. Evidence of this can be seen in prevalent body size sexual dimorphism (Colwell, 2000; Wilcox & Clark, 2022) and the wide diversity of bright iridescent ornamentation that is often unique to, or larger, in males (Beltrán et al., 2022; Parra, 2010; Simpson & McGraw, 2018; Skutch, 1973; Stiles et al., 2020). In addition, males often have long and/or ornate tails (Clark, 2010) and perform elaborate courtship displays to females that can involve the production of nonvocal feather sonations (Clark & Feo, 2008; Hogan & Stoddard, 2018; Rico-Guevara et al., 2022). In white-necked jacobins specifically, males perform courtship dives towards females that involve displaying their iridescent blue heads and fully spread, bright white tails while flying backwards (J. J. Falk, personal observation). In short, male ornamentation in this and other hummingbird species almost certainly provides a benefit to males through strong sexual selection, providing support for our assumption that $b >> 0$. In contrast, while bright ornamented coloration can be found in the females of many species, there is little evidence that these traits are intersexually selected. We note that $b < 0$ is possible when plumage is not sexually selected in males.

(2) Nesting with ornamented plumage is costly ($c > 0$): due to the small size of hummingbirds, their eggs and chicks may be an especially accessible prey item for many animals. Accordingly, studies of nesting success in hummingbirds have found very high rates of failure, up to 94% in one species, with the vast majority of these failures due to depredation during the egg stage (Baltosser, 1986). It follows that any female plumage that draws attention to the nest could lead to a nest failure (Caro, 2017). Ornamentation in males has evolved to increase conspicuousness towards females (Simpson & McGraw, 2018), so it is likely that the ornamented androchrome plumage in female hummingbirds incurs a nest

predation cost. Like most hummingbirds, white-necked jacobins exhibit female-only parental care and build open cup-shaped nests that leave females visible during incubation (Stiles et al., 2020).

(3) Being attacked by adversaries is costly ($h_m > 0$ and $h_f > 0$): for hummingbirds, aggressive chases and attacks make up the majority of social interactions. These battles carry the risk of physical damage (Rico-Guevara & Araya-Salas, 2015), and escaping can involve energetically costly flight (Sholtis et al., 2015). Hummingbirds have very high metabolic rate (Suarez, 1992), and therefore require nectar frequently and consistently to replace rapidly consumed energy. Displacement from a high-quality nectar resource may accumulate energetic costs because birds may lose a reliable source of food and would need to search for and locate a new nectar source (Groom et al., 2017; Rico-Guevara et al., 2021). Furthermore, given the high nest failure rates discussed above, even slight decreases in female efficiency may result in more time away from the nest and less ability to incubate and defend against predation.

(4) Attacking females results in a net reward for adversaries but attacking males has a net cost ($r > 0$ and $p > 0$): attacking a forager in order to access nectar will incur some degree of cost to adversaries, but if successful, access to a food reward. To adversaries, the net cost and reward is ultimately based on the RHP of the forager. Chasing and agonistic behaviour is common in hummingbirds (Sargent et al., 2021; Skutch, 1973; Stiles et al., 2020), and confronting an individual with higher RHP can result in physical injury, loss of a food resource or unnecessary energy expenditure while being chased (Evens & Harper, 2020; Rico-Guevara & Araya-Salas, 2015; Tobalske et al., 2010), all of which are especially costly for an animal with extremely high metabolic demands (Suarez, 1992). White-necked jacobin males tend to be both larger in overall body size and, on average, have higher muscle capacity than females (Falk et al., 2022), both of which are correlated with higher RHP (Bribiesca et al., 2019; Dakin et al., 2018; López-Segoviano et al., 2018; Segre et al., 2015). Therefore, attacking a male is more likely to be costly than attacking a female. While it is difficult to measure the total net cost and reward of these adversarial interactions, based on behavioural, morphological and muscle capacity differences between females and males, we simplify this interaction to a positive cost when attacking males and a positive reward when attacking females.

Note, however, that not all feedings involve direct interactions with adversaries as modelled here (Rico-Guevara et al., 2021; Sargent et al., 2021). Hummingbirds use both interference and exploitation competition, and in real-life situations, agonistic behaviour involves continuous assessment from potential adversaries. Approaching hummingbirds may assess the feeding hummingbird, then leave, which is accounted for in the model as 'avoid' behaviour from adversaries. However, adversarial behaviour in nature can vary from avoidance to simply signalling (e.g. displaying a spread tail), to threatening lunges and finally to a direct displacement chase, each of which affects the cost of the interaction. Nevertheless, our model is a reasonable representation of scenarios at either end of this spectrum. Another potential oversimplified assumption of our model is that ornamented androchrome males and females are indistinguishable to the adversary. Behavioural experiments with taxidermy mounts have shown that adversaries treat male and female androchromes similarly. However, colour analysis has found small yet statistically significant differences in their plumage coloration (Falk et al., 2021). Therefore, although contrary to behavioural experiments so far (Falk et al., 2021), it is plausible that other hummingbirds can distinguish sex in some contexts.

Model Predictions

Our hybrid signalling model makes testable predictions about coloration patterns and behaviour in this species. We describe empirical support for these predictions here.

(1) All males produce ornamented androchrome plumage and some but not all females do: as the model predicts, at a hybrid equilibrium, all white-necked jacobin males but only a fraction of females express androchrome plumage. A previous study (Falk et al., 2021) found that roughly a fifth (21/104) of adult females were androchromic while the rest were nonornamented heterochromic. All 195 males were ornamented.

(2) Adversaries attack heterochromes but only some androchromes: Falk et al. (2021) found that adversarial hummingbirds approaching feeders fitted with taxidermy mounts attacked heterochrome female mounts first in 76% of trials in which they were present. Androchromes (both male and female mounts) are therefore also the recipients of attacks but less than heterochromes. In the same study, out of 93 chases involving a heterochrome female, the heterochrome female was 12.4 times more likely to be chased rather than being the chasing individual. This demonstrates that heterochrome females are often on the receiving end of aggression. Androchromes show the opposite pattern and are more likely to chase others rather than be chased.

HYBRID EQUILIBRIUM OR 'HONEST-ENOUGH' SIGNALLING

What types of empirical evidence distinguish between hybrid and 'honest-enough' signalling models? To achieve stability with honest-enough signalling, Johnstone and Grafen (1993) modelled a scenario in which all signallers use pure strategies of either honesty or deception based on some aspect of their state (e.g. age, sex, size) or condition (e.g. parasite load, social status, health), whereby some individuals are able to subvert the typical cost differentials that enforce honesty and pay less of a cost to be dishonest. In other words, we expect individuals using honest or dishonest signals to have some consistent difference. A second expectation is that signal receivers also play a pure strategy and always heed or ignore the signal (Fig. 2).

In contrast, hybrid strategy models of partial honesty do not require honest versus deceptive signallers to differ in status or any other aspect, and in fact, expect the two strategies to appear 'randomly'. In addition, rather than always heeding the signal as in honest-enough models, partial signal honesty in hybrid equilibria is maintained by the behaviour of receivers sometimes 'probing' the honesty of the signal. Therefore, hybrid equilibrium models not only allow for variation in receiver behaviour, but require such variation. Lastly, hybrid equilibria can occur only when a 'class' of individuals uses a pure strategy of honestly signalling high condition or status, while another class uses a mixed honest/dishonest strategy in which the dishonest signal is indistinguishable from that used by the higher class.

By considering RHP as a measure of status or condition, we can compare the assumptions and predictions of these two models for describing white-necked jacobins. First, males can be considered a single class with higher RHP (Falk et al., 2022), and all males do indeed express the androchrome plumage signal (Falk et al., 2021). This prediction is consistent with all three models: fully honest handicap signalling, honest-enough signalling and the hybrid equilibrium. Second, some females also express androchrome plumage like males, but most express a distinct heterochrome plumage. This is inconsistent with the fully honest handicap model but consistent with both honest-enough and hybrid signalling. Third, the signal receivers (other hummingbirds) typically avoid

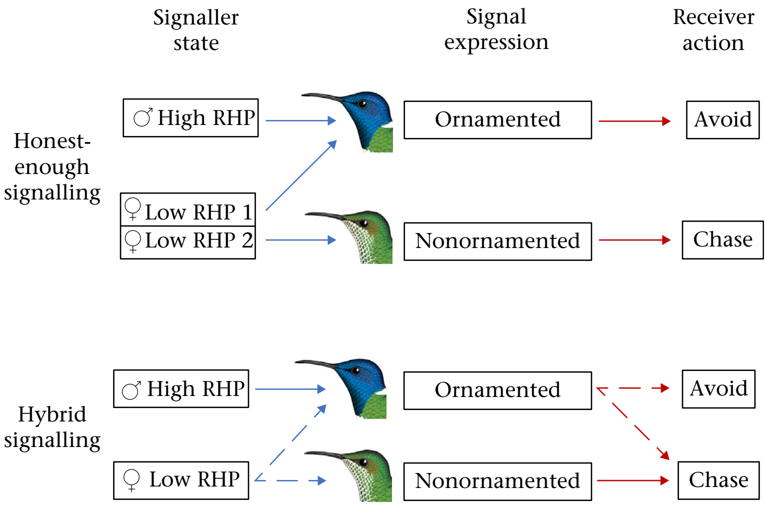

Figure 2. The expectations and predictions for partial female honesty in white-neck jacobins under an honest-enough handicap model versus a hybrid equilibrium model. Solid arrows indicate pure strategy options and dashed lines indicate mixed strategies. Signallers ‘choose’ a signal (blue) based on their status (e.g. age, sex, morphology, physiology), in this case their resource-holding potential (RHP), and signal receivers ‘choose’ a reaction (red) based on the signal. All males have high RHP and express androchromic plumage. Under honest-enough models, females choose their signal based on some aspect of their status, which determines the cost of dishonesty, and signal receivers heed the signal. In hybrid signalling models, females play a mixed strategy and occasionally express androchrome plumage, and receivers occasionally chase androchromes of either sex. Illustrations by Fernando Ayerbe. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

attacking androchromes, but do not always do so. This is consistent with the hybrid equilibrium but inconsistent with fully honest handicap signalling and honest-enough signalling. Finally, while clear differences have previously been shown between males and females, no within-sex differences have been found between female plumage types in terms of behaviour, nonplumage morphology or RHP (Falk et al., 2022). Both fully honest handicap signalling and honest-enough signalling predict that there should be differences (in RHP or in some other trait relevant to both parties), while the hybrid equilibrium is consistent with there being no differences. Because plumage type appears to be encoded by a single polymorphic locus (Falk et al., 2024), the androchromatic or heterochromatic plumage of adult females appears to be a mixed strategy expressed at the population level (Bergstrom & Godfrey-Smith, 1998). With phenotype being ‘randomized’ by the happenstance of genetic inheritance, female plumage is unlikely to be a condition-dependent response of the sort used in honest-enough models. However, even when variation is driven by a known genetic mechanism, we cannot rule out differences in condition entirely; the locus in question could have pleiotropic effects, and linkage disequilibrium could accumulate between the plumage locus and loci influencing other relevant phenotypes.

DISCUSSION

We have demonstrated that the plumage polymorphism in female white-necked jacobins is best described by a hybrid signalling model rather than an honest-enough signalling model. Two observations in particular deviate from the expectations of honest-enough models. First, no phenotypic differences have been found between androchrome and heterochrome females other than their plumage coloration, while clear distinctions between males and females in morphology, condition or resource-holding potential have been demonstrated (Falk et al., 2022). Honest-enough signalling models predict that such differences exist because the forager is deterministically conditioning on some underlying trait to determine its signal. Hybrid equilibrium predicts that there should be no difference. Second, adversaries that attack white-necked jacobins do not appear to play a pure strategy and occasionally attack androchrome individuals (of either sex). Honest-enough signalling models predict that the attacker should never attack an androchrome forager. The hybrid equilibrium predicts that they should attack with some probability.

Our model assumes no phenotypic differences between female morphs beyond plumage type. While this is supported by data, it is possible that differences may eventually be found. In this case, honest-enough models may also have theoretical value for this system. We posit that these two models may be ends of a continuum between condition-dependent and condition-independent partially honest signals. At the hybrid end of the spectrum, dishonesty is essentially a random occurrence among individuals with no underlying differences in their cost of signal display, and signal receivers vary in their propensity to ignore the signal. At the honest-enough end, dishonesty occurs in individuals that pay a lower relative cost of display, yet signal receivers always heed the signal even though the signal is imperfectly reliable.

A previous study (Falk et al., 2022) proposed that androchrome females engage in intersexual social dominance mimicry, which creates the conditions for maintaining the polymorphism because deceptive mimicry must be under negative frequency-dependent selection. The hybrid equilibrium model provides a mathematical basis to examine how frequency-dependent selection can occur: if the frequency of female androchromes were to increase, there would be a fitness advantage to adversaries who attack androchromes. The frequency of attacks on androchromes would increase and the fitness of female androchromes would decrease. The frequency of female androchromes would decrease in turn, reducing the benefit of attacking androchromes since they will more often be males.

It is intriguing to note that while a hybrid signalling model best explains adult female plumage, an honest-enough signalling model may be required to explain the plumage of juveniles of both sexes. Unlike most sexually dimorphic birds, juveniles of both sexes in this species have ornamented androchromic plumage (Falk et al., 2021). A previous study noted that juveniles of both sexes differ from adult males in that they have lower RHP (Falk et al., 2022). Also, first-year juvenile females differ systematically from adult females in that they do not make nests. Juvenile females are thus able to send the signal of androchrome plumage at lower cost than adults, setting up the possibility of an honest-enough signalling system. As the model predicts under these circumstances, the proportion of juvenile females that express ornamentation (100%) is higher than in female adults (~20%). However, juvenile plumage also contains markings that differ from adult males and female androchromes (Falk et al., 2021), so if juveniles are indeed mimics of adult males, their mimicry is less pristine and may be easier to recognize as bluff. Further field testing is required to verify the adaptive consequences and understand the full costs of ornamentation for juveniles versus adults.

We speculate that hybrid equilibrium models similar to the jacobin game may be useful in describing other mimicry systems, especially when mimicry has been implicated in a polymorphism. Sex-limited polymorphisms, where one sex is polymorphic and the other is not (Mank, 2023), naturally fulfil one of the predictions of a hybrid equilibrium: that individuals of one 'class' (either males or females) always signal one way, while the other uses the same signal partially. Both male mimicry of females and female mimicry of males have been found across taxa (Mank, 2023; Oliveira et al., 2008). We endorse closer examination of these intriguing systems as a valuable path for understanding the broader utility of this model.

Sex-limited polymorphisms in taxa other than hummingbirds could be modelled with a similar structure as the jacobin signalling game. For example, many damselfly species of the *Ischnura* genus have a female-limited polymorphism in which one of the morphs mimics males to avoid excessive mating attempts from males (Blow et al., 2021; Robertson, 1985). It should be possible to adapt the model we have described here to fit this context: rather than adversaries attacking and avoiding foragers, a damselfly game would involve males that either attempt a copulation or ignore other individuals. Similar mating avoidance strategies have been proposed to explain female-limited polymorphisms in several other animal taxa such as butterflies, bat bugs, anoles and cuckoo birds (Cook et al., 1994; Lee et al., 2019; Moon & Kamath, 2019; Reinhardt et al., 2007). Male-limited polymorphisms are also found extensively across taxa (Mank, 2023; Oliveira et al., 2008) and often involve mimicry of females to prevent territorial aggression from males and increase access to mating opportunities (Gross, 1996). Unlike the jacobin signalling game, mimics in this case deceptively offer a benefit to receivers rather than a bluff of higher RHP. Nevertheless, a similarly structured model may be able to provide testable predictions for such a system.

We have primarily focused on the conditions and implications of a hybrid equilibrium with female polymorphism, yet pure strategies are also possible in this model (Table 2). As noted previously, when the cost of androchrome plumage to females is greater than the cost of aggression from adversaries, our model predicts sexual dichromatism with ornamented males and nonornamented females. While sexual dichromatism is common in hummingbirds, sexual monochromatism, where both sexes are either highly ornamented or drab, also frequently occurs. In the jacobin signalling game we have assumed that males gain a positive benefit b due to sexual selection on ornamented androchrome plumage. This is likely true in white-necked jacobins, but it is not always the case across hummingbirds. While it can be difficult to distinguish what is ornamented versus nonornamented, the hermit clade consists of mostly sexually monochromatic species with cryptic brown and green plumage that do not express the vivid iridescence and elaborate display feathers famous in other hummingbirds (Beltrán et al., 2022; McGuire et al., 2014). Sexual selection is instead expressed in nonplumage modalities, with their lek mating strategies, elaborate dances, and in some cases, complex vocalizations (Araya-Salas et al., 2019; Araya-Salas & Wright, 2013; Stiles & Wolf, 1979; Trail, 1990). We suspect that perhaps the cost of ornamentation in the hermit clade exceeds the benefit b of ornamented plumage among male hermits and allows for complete adoption of drab coloration in both sexes (i.e. nonornamented 'heterochrome' plumage, Table 2).

Conversely, the jacobin signalling game also predicts monomorphically ornamented females and males (i.e. 'androchrome') under certain circumstances. As with the hybrid equilibrium, a lower nesting cost of ornamentation for females is still necessary ($c < h_f$), but rather than the condition found in equation (9), we expect to see ornamented monomorphism when

$$\frac{1-k}{k} < \frac{p}{r} \tag{14}$$

Such a condition could be met when the cost to an adversary for attacking a male far exceeds the reward for chasing a female. In this case, it would behove adversaries to never attack ornamented foragers, and all females should adopt ornamentation. This leaves an equilibrium where both sexes are purely androchrome (i.e. ornamented sexual monochromatism) and adversaries almost never attack, representing a case of strong intersexual mimicry (Table 2). We note that ornamented sexual monomorphism is also possible if $c < 0$, a case that we have not considered in depth, but one that would also be possible if the cost of nesting were low (Table 2) and females receive a benefit to ornamentation perhaps through signalling territoriality (Wolf, 1969), attracting mates (Hare & Simmons, 2019) or genomic linkage with male plumage (Clark & Rankin, 2020; Lande, 1980). Both females and males of many hummingbirds have similar degrees of bright iridescent plumage, yet the adaptive reasons for female ornamentation have only been considered in a few species (Wolf, 1969, 1975). Therefore, while not yet tested, our model offers an intriguing hypothesis for ornamented sexual monochromatism, as well as the predictions to test such a hypothesis across species. By combining these conditions for ornamented monochromatism with the conditions described previously, the model we derive not only predicts polymorphism, but also provides testable predictions for sexual coloration, including sexual dichromatism and bright and drab monochromatisms (Table 2) (Beltrán et al., 2022; Dale et al., 2015).

The handicap model for honest signalling has been remarkably influential in demonstrating how honest signalling can evolve, even when signals are only partially reliable. However, the jacobin signalling game demonstrates that an alternative nonhandicap mechanism better describes female polymorphism in white-necked jacobins given the current data. Comparing these two types of models demonstrates the pitfalls of relying solely on a single mechanism for understanding biological communication. The hybrid model provides a mathematical basis for unifying ecological competition with social and sexual signalling, ultimately predicting a wide range of real-world signalling outcomes including the existence of stable, partially honest signals.

Author Contributions

Jay J. Falk: Writing – review & editing, Writing – original draft, Visualization, Validation, Conceptualization. **Carl T. Bergstrom:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Conceptualization. **Kevin J.S. Zollman:** Writing – review & editing, Validation, Conceptualization. **Alejandro Rico-Guevara:** Writing – review & editing, Supervision, Resources, Conceptualization.

Data Availability

No data were used for the research described in the article.

Declaration of Interest

The authors declare no conflicts of interest.

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