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# Interspecific social dominance mimicry in birds

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Interspecific social dominance mimicry (ISDM) is a proposed form of social parasitism in which a subordinate species evolves to mimic and deceive a dominant ecological competitor in order to avoid attack by the dominant, model species. The evolutionary plausibility of ISDM has been established previously by the Hairy-Downy game (Prum & Samuelson). Psychophysical models of avian visual acuity support the plausibility of visual ISDM at distances ~>2–3 m for non-raptorial birds, and ~>20 m for raptors. Fifty phylogenetically independent examples of avian ISDM involving 60 model and 93 mimic species, subspecies, and morphs from 30 families are proposed and reviewed. Patterns of size differences, phylogeny, and coevolutionary radiation generally support the predictions of ISDM. Mimics average 56–58% of the body mass of the proposed model species. Mimics may achieve a large potential deceptive social advantage with <20% reduction in linear body size, which is well within the range of plausible, visual size confusion. Several, multispecies mimicry complexes are proposed (e.g. kiskadee-type flycatchers) which may coevolve through hierarchical variation in the deceptive benefits, similar to Müllerian mimicry. ISDM in birds should be tested further with phylogenetic, ecological, and experimental investigations of convergent similarity in appearance, ecological competition, and aggressive social interactions between sympatric species. Evolutionary explanations of mimicry must consider the possibility that mimics evolve to deceive model species themselves.

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ADDITIONAL KEYWORDS: avian mimicry – coevolutionary arms race – competition – convergent evolution – coral reef fishes – Hairy-Downy game – Müllerian mimicry – visual deception.

## INTRODUCTION

Interspecific mimicry frequently evolves through natural selection on appearance to avoid attack (Wickler, 1968; Ruxton, Sherrat & Speed, 2004). Classically, the evolution of interspecific mimicry is thought to involve three players– a model, a mimic, and a third-party observer/predator. In Müllerian mimicry, two or more toxic/noxious species converge in appearance on each other to share the benefits of a common aposematic warning signal. In Batesian mimicry, a harmless species evolves to mimic the aposematic signals of a toxic, venomous, or noxious model species, and benefits from deceiving predators or competitors about itself. In contrast, mimicry of host eggs and offspring by brood parasites is a well understood two-party mimicry mechanism in which the model species is also the deceived party (Rothstein, 1990; Langmore *et al*., 2011). However, the evolution of mimicry between ecological competitors in the absence of aposematic or noxious models, or third-party observers is poorly understood.

Hypotheses of non-brood parasitic mimicry in birds have persisted for 150 years, yet no satisfactory or broadly accepted general explanation has emerged. Alfred Russel Wallace (1863, 1869) proposed several examples of mimicry in non-toxic birds. Wallace hypothesized that smaller subordinate species may gain an evolutionary advantage from mimicking a larger dominant species by deceiving other small species, scaring them off, and thereby gaining access to resources with less competition. Alternatively, in discussing the convergent plumages of two species of

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Neotropical raptors– the Bicoloured Hawk *Accipiter bicolor* and the Rufous-thighed Kite *Harpagus diodon*– Osbert Salvin (cited in Newton & Gadow, 1893–96: 572–575) proposed that the larger species evolves to mimic a smaller species so that other small species will mistake it for the smaller species, allowing the larger species to sneak up and prey upon them.

Generations later, Martin Moynihan (1968) proposed that interspecific plumage coloration convergence evolves to facilitate social interactions within multispecies foraging flocks. Moynihan reasoned that species would communicate both intraspecific and interspecific social signals more efficiently by converging on similar plumages and social signals. Martin Cody (1969, 1973) later proposed that convergent similarity would evolve among ecological competitors to facilitate interspecific territoriality. Murray (1976) criticized Cody's hypothesis as conflicting with mechanisms of competitive exclusion, and evolutionary character displacement to reduce competition among sympatric species. Murray concluded that Cody had failed to explain when ecological competitors should be selected to converge or diverge from one another. Later, Barnard (1978) proposed that mimicry among flocking birds evolved as a mechanism of visual predator confusion. He proposed that selective predation upon individuals with outlying phenotypes would favour convergent evolution among interspecifically social birds. Ziegler (1971) and Baker & Parker (1979) also hypothesized that a type of Batesian mimicry could evolve in birds if some species evolve to mimic other unprofitable prey species or noxious species. However, none of these previous theories has been quantitatively modelled or theoretically confirmed. These previously proposed hypotheses for the evolution of avian mimicry have received little subsequent intellectual or empirical support.

In an analysis of Wallace's classic proposal of mimicry between clades of the larger bodied friarbirds (*Philemon*, Meliphagidae) and the smaller Old World orioles (*Oriolus*, Oriolidae) in Indonesia, New Guinea, and Australia, Diamond (1982) presented a new hypothesis for the evolution of mimicry in the absence of third-party observers. Diamond proposed that a smaller species may evolve to resemble a larger, socially dominant, model species in order to deceive the dominant species itself, and to reduce aggressive attack. Diamond presented behavioral evidence in support of mimicry between the *Oriolus-Philemon* clades, but he remained inconclusive about whether this example of mimicry evolved through deception of additional, third-party species (Wallace, 1863), or through deception of the dominant model species.

Spear & Ainley (1993) proposed that the Kermadec Petrel (*Pterodroma neglecta*) has evolved to mimic the plumage of species in two genera of related pelagic kleptoparasites– mainly South Polar Skua (*Catharacta maccormicki*), and Pomarine Jaegers (*Stercorarius pomarinus*)– which have a distinctive white patches on the bases of the outer primaries. Spear & Ainley documented that Kermadec Petrel avoids kleptoparasitic attacks from skuas and jaegers, and thus gains a direct benefit from mimicking these larger dominant species. However, they also proposed that Kermadec Petrel benefits from increased success of its own kleptoparasitic attacks by imitating the plumage of the larger species, indicating multiple potential evolutionary advantages to mimicry in this species.

Progress in phylogenetic reconstruction has recently revealed new examples of evolutionary convergence in appearance among bird species that were originally thought to be closely related. These discoveries have clearly established the need to understand the evolution of non-aposematic mimicry between ecological competitors in the absence of additional third-party participants. For example, a striking example of unexpected plumage convergence comes from the Hairy Woodpecker (*Picoides villosus*) and Downy Woodpecker (*Picoides pubescens*) – two common, broadly sympatric North American species that are strikingly similar in plumage (Fig. 1). However, the Downy Woodpecker has only 43% of the body mass of the Hairy (Dunning, 2008). Recent molecular phylogenetic research has demonstrated that these two species are not close relatives within the genus *Picoides*, and that their plumage similarities are convergently evolved (Weibel & Moore, 2002, 2005). However, Weibel & Moore (2005) abandoned attempts to explain this striking pattern of convergent evolution because of the lack of a coherent theory about how non-aposematic mimicry evolves. Thus, a detailed mechanism for the evolution of mimicry between socially dominant and subordinate ecological competitors is clearly required.

Rainey & Grether (2007) reviewed and classified types of mimicry between ecological competitors. Their brief discussion of mimicry of a dominant ecological competitor was restricted to song sharing between bird species (as hypothesized by Cody, 1969). They did not consider convergence in visual appearance. However, Rainey & Grether (2007) called for theoretical and empirical research on competitive mimicry.

Most recently, Prum & Samuelson (2012) proposed an explicit evolutionary mechanism for interspecific social dominance mimicry (ISDM) between ecological competitors in the form of an evolutionary game. The Hairy–Downy game documents the fitness consequences of mimicry by members of a subordinate species for both the mimic and model species. The results of the game provide a quantitative theoretical framework for the evolution of ISDM between ecological competitors.

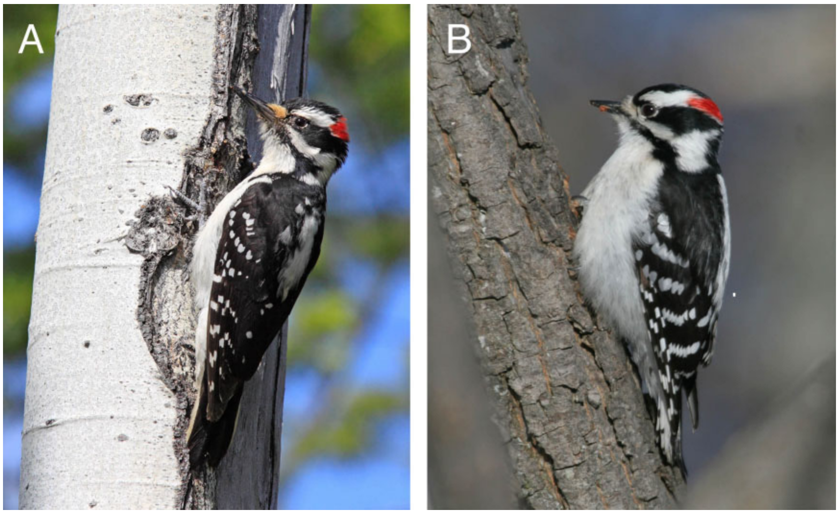

**Figure 1.** Evolutionary convergence in plumage between male (A) Hairy Woodpecker *Picoides villosus* and (B) Downy Woodpecker *Picoides pubescens*. Hairy and Downy Woodpeckers are sympatric, virtually identical in appearance, but they differ in size and are not closely related within the genus *Picoides* (Weibel & Moore, 2002, 2005). Photos reproduced with permission of Laurie Neish/VIREO (left) and A & J. Binns/VIREO (right).

ISDM is a mechanism of using social deception to regain ecological advantages from larger, dominant ecological competitors. Ecological competition can take the form of *interference* competition, in which individuals of different species directly compete for resources through social interactions, or *exploitative competition*, in which one species gains an ecological advantage through more efficient utilization of the contested resource (Schoener, 1983). Interference competition creates interspecific social conflict and the ecological advantages of social dominance. Body size, in particular, provides fundamental advantages in interference competition among bird species (Wolf, Stiles & Hainsworth, 1976; Ford, 1979; Mauer, 1984; Alatalo *et al*., 1985; Minot & Perrins, 1986; Alatalo & Moreno, 1987; Robinson & Terbourgh, 1995). Thus, ISDM involves deceptive manipulation of interspecific social interactions by smaller species to achieve ecological advantages.

In this paper, I will briefly review the results and predictions of the Hairy–Downy model of ISDM (Prum & Samuelson, 2012). I then examine the evidence of plumage and behavioral mimicry between ecological competitors in birds, and evaluate the plausibility of ISDM in birds generally. I examine the following predictions of the model of ISDM evolution:

1. Visual deception should be physiologically plausible at ecologically relevant visual distances between individuals.
2. Model species are larger in body mass than mimic species, and socially dominant over them.
3. Shared phenotypic similarities between model and mimic species are not homologous– i.e. not shared by descent from a common ancestor. Model and mimic species are not closest relatives, and are each more closely related to other species that differ in their appearance.
4. Model species are under natural selection to evolve distinctive visual appearances that will evade the cost of ISDM. Likewise, mimic species are under natural selection to maintain deceptive similarity. Consequently, ISDM can create a coevolutionary arms race in visual appearance. If geographic isolation or speciation occurs subsequent to the origin of mimicry, independent populations of models and mimics may produce coevolutionary radiations in visual appearance among clades. Differentiation among populations of the model species will precede adaptive coevolution by mimics.
5. Models may evolve distinct, persistent, non-courtship display behaviour that facilitates visual discrimination of conspecifics from mimics. These displays will also be subject to mimicry and coevolutionary elaboration between models and mimics.

Rather than generally review all evolutionary mechanisms of avian mimicry, I will focus on the proposal and analysis of potential avian examples of social dominance mimicry between two parties. The goal is to inspire future empirical work further testing this overlooked mimicry mechanism, which will necessarily include investigation of whether the deceived parties are model species, other species, or both (Rainey & Grether, 2007).

## EVOLUTIONARY DYNAMICS OF INTERSPECIFIC SOCIAL DOMINANCE MIMICRY

The Hairy–Downy game provides insights into the necessary and sufficient conditions for the evolution ISDM and a description of its evolutionary dynamics (for details, see Prum & Samuelson, 2012). The game models the coevolution of alternative strategies within two syntopic species that compete through intraspecific and interspecific social interactions over a common resource, or over resources with a common spatial distribution. The larger species is *socially* dominant over the smaller subordinate species by direct physical, interference competition (Schoener, 1983). By analogy to the convergently plumaged Hairy *Picoides villosus* and Downy Woodpeckers *P. pubescens* (Fig. 1), the larger species in the game is called Hairy and the smaller species is called Downy. Interactions between Hairys and Downys are modelled as a Hawk–Dove game expanded to four players (Prum & Samuelson, 2012).

The four classes of players are a Hairy hawk, a Hairy dove, a Downy mimic which resembles a Hairy, and a Downy non-mimic, which has some other distinctive appearance. Interactions between Hairy hawks and Hairy doves proceed as in a standard Hawk–Dove game. Hairy hawks always attack other Hairys. They defeat Hairy doves, but pay some cost to aggression in combat with other Hairy hawks. Hairy doves bluff and retreat from Hairy hawks; they lose the entire resource but pay no cost. Hairy doves split any contested resource with other Hairy doves. In interactions between species, both Hairy hawks and Hairy doves attack non-mimic Downys, and win the resource. Hairy doves treat Downy mimics as other Hairy doves and, split the resource, providing an advantage to mimicry. Hairy hawks attack Downy mimics and win, and Downy mimics may pay an additional cost of mimicry that Downy non-mimics avoid. Downys of both types always split resources with each other, though Prum & Samuelson (2012) explore some alternatives to equal payoffs between Downy strategies.

Competitive advantages of any strategy may yield fitness advantages over the other strategy within its own species, or over either strategy within the other species. This process creates complex coevolutionary dynamics among the four strategies within the two species (Prum & Samuelson, 2012). Assuming that the background fitness of Downy and Hairy are appropriate to support ecological coexistence (Prum & Samuelson, 2012), Downy mimics will evolve as long as the cost of mimicry is sufficiently low in comparison to the cost of aggression and the value of resources to Hairy and Downy. If these conditions hold, the result is a unique Nash equilibrium with all four strategies present in the community.

As the cost of mimicry increases, Downy mimics will disappear from the community, and Hairy hawks and Hairy doves will evolve to the predicted equilibrium proportions of the original Hawk–Dove game. As the cost of mimicry approaches zero, the frequency of Downy mimics will increase, the frequency of Hairy hawks will decline (but not to zero), the frequency of Hairy doves will become arbitrarily small, and the frequency of Hairy hawks to Downy mimics will evolve the equilibrium of the Hawk–Dove proportions. In other words, Downy mimics evolve to displace Hairy doves in social interactions with Hairy hawks. Interestingly, non-mimic Downys become more frequent too. The equilibrium approaches a limit consisting of Hairy hawks, Downy mimics, and Downy non-mimics. As the cost of combat for a Hairy hawk increases, the frequency of both Hairy hawks and Hairy doves declines. Depending on the relative values of the contested resources to Hairy and Downy, and the cost of mimicry, the decline of Hairys can result in either an increase in the frequency of Downy mimics or Downy non-mimics. Non-mimic Downys will be rare when: (1) the costs of mimicry is small, (2) the background fitness of Downy is near the lower limit for a Downy sustainability, (3) the value of resources to Downys is not too large, and (4) the cost of combat for Hairy hawks is high.

Prum & Samuelson (2012) show that there are no parameter conditions which will stably maintain Hairy in the presence of Downy mimics alone. If mimicry is costless ($c_m = 0$), then the coexistence of Hairy hawks and Downy mimics alone is a stable state, however the frequency of Downy non-mimics can drift in the population. However, if the basic game is altered to provide any intraspecific advantage to mimicry, then Hairy hawks and Downy mimics can coexist in the absence of Downy non-mimics. For example, this could occur if non-mimics mistakenly identify mimics as Hairys, and retreat at some non-zero frequency.

## AVIAN VISUAL PERCEPTION, ACUITY AND MIMICRY

### USE OF PICTORIAL CUES TO JUDGE DISTANCE TO AN OBJECT

The efficacy of mimicry frequently relies on visual deception (Wickler, 1968; Ruxton *et al.*, 2004). In particular, the efficacy of ISDM rests upon the probability that an individual mimic will be mistaken for an individual of a larger model species with a similar visual appearance. Evaluation of this possibility requires consideration of the psychophysical capabilities of avian visual systems. Here, before reviewing proposed cases of avian ISDM, I evaluate the plausibility of visual size deception with an analysis of avian vision acuity.

Humans and other vertebrates use multiple sources of information to estimate the distance to, and the size of, an object in the visual field. Distance cues can come from ocular information (e.g. accommodation, muscle stress, and ocular convergence), binocular information (or stereopsis), dynamic information (e.g. motion parallax, optical flow), and pictorial information (e.g. texture gradients, relative sizes, shadows, parallel lines, object recognition, familiar size, etc.) (Palmer, 1999: 199–253). In the absence of unambiguous non-pictorial cues, use of pictorial cues can dominate the cognitive mechanisms of the perception of object size and distance. Experimental data from humans show that object shape and colour pattern can contribute to the identification of an object in the visual field as a familiar item, which can then influence the perception of object size and distance (Palmer, 1999). For example, in the absence of non-pictorial information about distance to an object in the visual field, human observers will use their familiarity with the size of a golf ball, a baseball, a fire hydrant, or a human being to estimate the distance to objects that are recognized as one of these items.

Visual ISDM requires that model species use pictorial cues – i.e. shape, colour, and colour pattern information – to mistakenly identify a mimic as a conspecific. ISDM can occur when an individual of a model species uses its prior familiarity with conspecific size to overestimate the size of, and the distance to, a mimic individual of another smaller species, and then makes a social decision based on this erroneous conclusion.

Most non-raptorial birds have eyes placed toward the sides of their heads resulting in limited capacity for stereopsis (Martin, 1993). Furthermore, pigeons and possibly other birds have limited accommodation (or focus) capability in the narrow field of stereopsis, which is often specialized for focusing only at close distances on potential food items (Hodos, 1993). As a consequence of limited stereopsis, visual perception mechanisms in most non-raptorial birds are highly constrained. Most non-raptorial birds must rely on pictorial information from the separate left and right visual fields to identify objects in their visual fields. Consequently, they must estimate the sizes and the distances to these objects based on their familiarity with these classes of objects. Increased reliance on pictorial information is necessitated by the limited stereopsis. Thus, fundamental structure of most avian visual systems predisposes them to the class of visual illusions that contribute to ISDM.

## QUANTITATIVE ESTIMATE OF VISUAL PLAUSIBILITY OF ISDM

The size of any object projected from the visual field on to the retina is described by its visual angle. Visual angle, $a$, is given by $\tan a = s/d$, where $s$ is the linear size of the object and $d$ is the distance from the observer (Fig. 2) (Palmer, 1999). For example, Downy and Hairy Woodpeckers are 16 cm and 24 cm long, respectively (Peterson, 1980). At a distance of five metres away, a Downy Woodpecker will create a retinal image with a visual angle of 1.832° (Fig. 2). For quick reference, the width of one's thumb held at arms length subtends a visual angle of ~2° (Goldstein, 2007: 245). The difference in the distances to two objects that subtend the same visual angle scales linearly with the difference in size of the two objects. So, the visual angle of a 16 cm long Downy Woodpecker at 5 metres is the same as the visual angle of a 24 cm Hairy Woodpecker at a distance of 7.5 m (Fig. 2). Thus, an individual of a model species that has misidentified a mimic individual as a conspecific will overestimate the distance to that individual by the ratio of their linear sizes ($s_{model}/s_{mimic}$) times the actual distance. In other words, mistaking a Downy Woodpecker for a Hairy Woodpecker will result in overestimating the distance to that individual by 50% of the real distance: i.e. (24 cm/16 cm) = 3/2.

Avian visual acuity can be used to evaluate the plausibility of visual ISDM in birds. Visual acuity is measured in terms of spatial frequency in cycles/degree– i.e. the smallest periodic line or pixel pattern that can

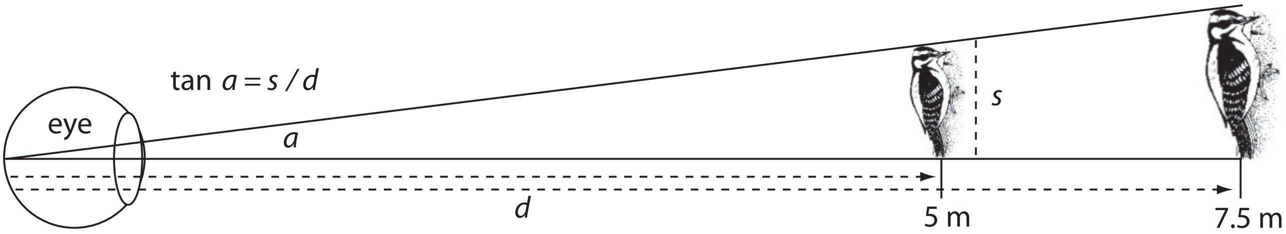

**Figure 2.** Visual angle, $a$, is given by $\tan a = s/d$ where $s$ is the linear size and $d$ is the distance to the object (Palmer, 1999). An identical visual angle can be created by two objects of different sizes at different distances from the observer. A 16 cm Downy Woodpecker at 5 m distance and a 24 cm Hairy Woodpecker at 7.5 m will both subtend a visual angle of 1.832° (illustration not to scale).

be visually resolved for a unit of visual angle. The minimum-sized pattern that a bird can visually resolve (e.g. either a food item or plumage pattern detail) can be calculated for a given distance and visual angle using data on avian visual acuity. Psychophysical data indicate that the visual acuity of birds varies over an order of magnitude from 12.7 cycles/degree in pigeons (Hodos, 1993) to 137–143 cycles/degree in eagles and other raptors (Reymond, 1985).

For a given visual system, the minimum-sized, resolvable visual pattern at a given distance (in mm/cycle) can be calculated from the linear size of the object divided by the product of the visual angle of the retinal image and the observer's visual acuity (in spatial frequency):

$$\mathrm{mm/cycle} = \mathrm{mm/(degrees\,(cycles/degree))} \qquad (1)$$

Accordingly, at five metres, a pigeon with a visual resolution of 12.7 cycles/degree can visually resolve a black-and-white checkered plumage pattern with a linear size greater than ~6.9 mm. The distinctive plumage differences of Hairy and Downy Woodpeckers are quite a bit smaller than this size. For example, the distinctive black spots on the white outer tail feathers of Downy Woodpeckers (which are absent from Hairy) are ~2 mm wide. Such features could only be visually resolved by a pigeon at a distance of less than 1.66 m away. Thus, this analysis implies that a pigeon would have difficulty distinguishing the distinctive features of the plumage pattern of a Downy Woodpecker at greater than 2–3 metres. In contrast, a raptor with an order of magnitude better acuity (~127 cycles/degree) could resolve plumage pattern details larger than a 0.69 mm at 5 m. With this extraordinary resolution, mimetic visual deception of raptors would require much greater visual distances and finer visual pattern matching.

This preliminary calculation of the spatial resolution of avian vision indicates that ISDM is psychophysically plausible in some non-raptorial birds at distances greater than 2–3 m. Psychophysical plausibility of any specific model/mimic system could be calculated with data on the visual acuity of the model and the size scale of the differences in shape and plumage pattern. In general, the effective distance threshold of visual size confusion will depend upon the size scale of the distinctive features of the model and mimic species (i.e. the quality of mimicry) and the visual acuity of the model species.

## REVIEW OF INTERSPECIFIC SOCIAL DOMINANCE MIMICRY IN BIRDS

To assess the plausibility, frequency, diversity and ecology of ISDM in a group of highly visual organisms – the birds – I surveyed the literature for previous examples of avian mimicry (Wallace, 1863, 1869; Newton & Gadow, 1893–96; Moynihan, 1968; Wickler, 1968; Cody, 1973; Diamond, 1982; Spear & Ainley, 1993; Komárek, 1998; Ruxton *et al.*, 2004; Witt, 2005; Negro, 2008; Sazima, 2010), and reviewed personal communications with other ornithologists (Miguel Marini, pers. comm.), and identified some new examples from my own museum observations and field experience. As in Hairy and Downy Woodpeckers, some hypotheses of mimicry emerged first from new data on phylogenetic relationships. I included only those species that have specific plumages patches, pattern elements, or details that indicate a communication function. For each species, I searched for data on body mass (Dunning, 2008), geographic distribution, habitat, natural history and ecology, and phylogenetic relationships (Table 1).

Because this is not a review of all forms of mimicry in birds, but rather an attempt to examine the plausibility and possible phylogenetic and ecological distribution of ISDM in birds, I have excluded from consideration proposed examples of third-party deceptive avian mimicry, e.g. the proposed mimicry of Turkey Vulture *Cathartes aura* flight mode by the Zone-tailed Hawk *Buteo albonotatus* (Willis, 1963) I have excluded the unique proposed case of Müllerian mimicry among toxic, aposematic plumages of pitohuis (Dumbacher & Fleischer, 2001). I have excluded egg and nestling mimicry of hosts by obligate brood parasites in which two-party deception has been long established (Rothstein, 1990).However, I have included several potentially ambiguous cases that may simultaneously involve two-party and three-party mimicry (e.g. cuckoo mimicry of *Accipiter* hawks, and Kermadec Petrel mimicry of skuas and jaegers). I have excluded other generalized forms of representational, objective mimicry, such as the 'eyespots' on the back of the heads of pygmy owls (*Glaucidium*). I also excluded convergent similarity between non-sympatric species with no direct social or ecological interactions, e.g. *Sturnella* meadowlarks (Icteridae) from North America and *Macronyx* longclaws (Motacillidae) from Africa (see below). With a single exception (*Buthraupis* and *Dubusia* tanagers, Thraupidae; Table 1), I rejected all examples of visual mimicry proposed by Moynihan (1968), Cody (1973), Béland (1977), and Witt (2005); based on visual inspection of study skins, and my familiarity with many of these species in the field, I have concluded that these examples – e.g. Loggerhead Shrike *Lanius ludovicianus* and Northern Mockingbird *Mimus polyglottos* – lacked sufficient detail to be confidently distinguishable from the null expectation of shared plumage similarity among sympatric species. I do not think that these examples warrant further consideration as instances of ISDM.

**Table 1.** Proposed examples Interspecific Social Dominance Mimicry (ISDM) in birds (Aves) with body masses and quality of mimicry. References listed cite relevant phylogenetic studies and any previous hypotheses of mimicry

| Models | | | Mimics | | | | |
|---|---|---|---|---|---|---|---|
| Genus species | Family | Mass (g) | Genus species | Family | Mass (g) | Mimicry quality | References |
| *Streptoprocne zonaris* | Apodidae | 98.1 | *Cypseloides lemosi* | Apodidae | 28.1 | Closely Similar | [1] |
| | | | *Panyptila cayennensis* | Apodidae | 21.1 | Closely Similar | |
| | | | *Aeronautes montivagus* | Apodidae | 20.1 | Closely Similar | |
| *Catharacta maccormacki* | Stercorariidae | 1277 (m) | *Pterodroma neglecta* | Procellariidae | 501 | Closely Similar | [2, 3] |
| | | 1421 (f) | | | | | |
| *Catharacta skua* | Stercorariidae | 1271 (m) | | | | | |
| | | 1409 (f) | | | | | |
| *Skua pomarinus* | Stercorariidae | 648 (m) | | | | | |
| | | 740 (f) | | | | | |
| *Puffinus bulleri* | Procellariidae | 407 | *Pterodroma inexpectata* | Procellariidae | 316 | Closely Similar | [4] |
| *Pterodroma inexpectata* | Procellariidae | 316 | *Halobaena caerulea* | Procellariidae | 202 | Closely Similar | |
| | | | *Pachyptila vittata* | Procellariidae | 196 | Closely Similar | |
| | | | *Pachyptila desolata* | Procellariidae | 147 | Closely Similar | |
| | | | *Pachyptila salvini* | Procellariidae | 159 | Closely Similar | |
| | | | *Pachyptila belcheri* | Procellariidae | 145 | Closely Similar | |
| | | | *Pachyptila turtur* | Procellariidae | 137 | Closely Similar | |
| | | | *Pachyptila crassirostris* | Procellariidae | 149 | Closely Similar | |
| | | | *Pterodroma cookii* | Procellariidae | 178 | Closely Similar | |
| | | | *Pterodroma pycrofti* | Procellariidae | 159 | Closely Similar | |
| | | | *Pterodroma defillipiana* | Procellariidae | 169 | Closely Similar | |
| | | | *Pterodroma axillaris* | Procellariidae | 165 | Closely Similar | |
| *Accipiter nisus* | Accitripidae | 150 (m) | *Cuculus* sp. | Cuculidae | 80–120 | Closely Similar | [2] |
| | | 325 (f) | *Hierococcyx* sp. | Cuculidae | 77–151 | Closely Similar | |
| *Accipiter bicolor* | Accitripidae | 212 (m) | *Harpagus diodon* | Accitripidae | 200 (f) | Virtually Identical | [5] |
| | | 390 (f) | | | | | |
| *Accipiter hentsii* | Accitripidae | 1050 | *Eutriorchis astur* | Accitripidae | 770* | Virtually Identical | [6, 7] |
| *Spizaetus ornatus* | Accitripidae | 1009 (m) | *Accipiter poliogaster* (juv.) | Accitripidae | 302 (m)* | Virtually Identical | [5] |
| | | 1429 (f) | | | | | |
| *Spizaetus africanus* | Accitripidae | 1047 | *Dryotriorchis spectabilis* | Accitripidae | ? | Virtually Identical | [6] |
| *Spizastur melanoleucus* | Accitripidae | 850 | *Leptodon cayanensis* (juv.) | Accitripidae | 474 | Closely Similar | [5, 7] |
| *Nisaetus cirrhatus* | Accitripidae | 1300–1600 | *Ictinaetus malayensis* | Accitripidae | 1000–1600 | Closely Similar | [5, 7] |
| *Nisaetus alboniger* | Accitripidae | 830 | *Nisaetus nanus* | Accitripidae | 510–610 | Closely Similar | [5, 7] |
| | | | *Accipiter trivirgatus* | Accitripidae | 199 (m) | Closely Similar | |
| | | | | | 353 (f) | | |
| | | | *Aviceda jerdoni* | Accitripidae | 363 | Closely Similar | |
| *Tringa melanoleuca* | Scolopacidae | 171 | *Tringa flavipes* | Scolopacidae | 77.5 | Virtually Identical | [8] |
| *Lorius chlorocercus* | Psittacidae | 174 | *Charmoysyna margarithae* | Psittacidae | 49.7 | Quite Similar | [9] |
| *Harpactes diardii* | Trogonidae | 95.4* | *Harpactes kasumba* | Trogonidae | 72.1* | Quite Similar | [10] |

**Table 1.** *Continued*

| Models | | | Mimics | | | | |
|---|---|---|---|---|---|---|---|
| Genus species | Family | Mass (g) | Genus species | Family | Mass (g) | Mimicry quality | References |
| *Ramphastos t. tucanus* | Ramphastidae | 595 | *Ramphastos v. vitellinus* | Ramphastidae | 363 (m)<br>324 (f) | Virtually Identical | [11] |
| *Ramphastos t. cuvieri* | Ramphastidae | 680–702 | *Ramphastos v. culminatus* | Ramphastidae | 395 (m)<br>363 (f) | Virtually Identical | |
| *Ramphastos swainsoni* | Ramphastidae | 709 | *Ramphastos v. ariel* | Ramphastidae | | Closely Similar | |
| | | | *Ramphastos brevis* | Ramphastidae | 412 | Virtually Identical | |
| | | | *Ramphastos sulfuratus* | Ramphastidae | 433 (m)<br>401 (f) | Closely Similar | |
| *Baryphthengus ruficapillus* | Momotidae | 158 | *Electron platyrhynchum* | Momotidae | 73 | Virtually Identical | [12] |
| *Baryphthengus r. martii* | Momotidae | 178 | *Electron p. pyrrholaemum* | Momotidae | 73 | Virtually Identical | |
| *Campephilus principalis* | Picidae | 516 | *Dryocopus pileatus* | Picidae | 287 | Closely Similar | [13] |
| *Campephilus guatemalensis* | Picidae | 242 | *Dryocopus lineatus* | Picidae | 183 | Closely Similar | |
| *Campephilus gayaquilensis* | Picidae | 240 | | | | Closely Similar | |
| *Campephilus melanoleucos* | Picidae | 256 | | | | Closely Similar | |
| *Picoides villosus* | Picidae | 60–70 | *Picoides pubescens* | Picidae | 27.7 | Virtually Identical | [14, 15] |
| *Picoides leucotos* | Picidae | 108 | *Picoides minor* | Picidae | 19.8 | Virtually Identical | [14, 15] |
| *Chrysophlegma mentalis* | Picidae | 101.5 | *Picus puniceus* | Picidae | 79.1 | Closely similar | [14–16] |
| *Chrysocolaptes lucidus* | Picidae | 142 | *Dinopium javanense* | Picidae | 72.8 | Closely similar | [14–16] |
| *Chrysocolaptes festivus* | Picidae | 213 | *Dinopium benghalense* | Picidae | 100 | Closely similar | |
| *Meiglyptes tristis* | Picidae | 31 | *Hemicircus concretus* | Picidae | 27 | Closely similar | [14–16] |
| *Meiglyptes jugularis* | Picidae | 53 | *Hemicircus canente* | Picidae | 43 | Closely similar | |
| *Cinclodes excelsior* | Furnariidae | 62–66 | *Cinclodes fuscus* | Furnariidae | 30 | Virtually Identical | [17] |
| *Philydor rufus* | Furnariidae | 25 | *Thamnistes anabatinus* | Thamnophilidae | 20 | Closely Similar | [18] |
| *Lipaugus vociferans* | Cotingidae | 82.2 | *Laniocera hypopyrrha* | Tityridae | 51 | Virtually Identical | [19] |
| | | | *Rhytipterna simplex* | Tyrannidae | 31.8 | Virtually Identical | |
| *Lipaugus unirufus* | Cotingidae | 82.1 | *Laniocera rufescens* | Tityridae | 48.1 | Virtually Identical | |
| | | | *Rhytipterna holerythra* | Tyrannidae | 36.8 | Virtually Identical | |
| *Leptopogon superciliaris* | Tyrannidae | 11.7 | *Pogonotriccus opthalmicus* | Tyrannidae | 10.5 | Closely Similar | [19] |
| *Leptopogon amaurocephalus* | Tyrannidae | 11.7 | *Pogonotriccus poecilotus* | Tyrannidae | 8 | Closely Similar | |
| | | | *Pogonotriccus orbitalis* | Tyrannidae | 6.6–7.6 | Closely Similar | |
| | | | *Pogonotriccus venezulensis* | Tyrannidae | 9 | Closely Similar | |
| | | | *Pogonotriccus chapmani* | Tyrannidae | 9 | Closely Similar | |
| | | | *Pogonotriccus eximius* | Tyrannidae | 7.5 | Closely Similar | |
| | | | *Phyllomyias cinericeps* | Tyrannidae | 9.5 | Closely Similar | |
| | | | *Phyllomyias plumbeiceps* | Tyrannidae | ? | Closely Similar | |
| | | | *Myiornis auricularis* | Tyrannidae | 5.3 | Closely Similar | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Megarhynchus pitangua* | Tyrannidae | 73 | *Myiozetetes similis* | Tyrannidae | 28 | Virtually Identical | [19] |
| *Pitangus sulphuratus* | Tyrannidae | 61 | *Myiozetetes cayanensis* | Tyrannidae | 25.9 | Virtually Identical | |
| | | | *Myiozetetes granadensis* | Tyrannidae | 29.3 | Closely Similar | |
| | | | *Philohydor lictor* | Tyrannidae | 25.5 | Virtually Identical | |
| | | | *Phelpsia inornata* | Tyrannidae | 29.4 | Virtually Identical | |
| | | | *Conopias parva* | Tyrannidae | 21 | Closely Similar | |
| | | | *Conopias albovittatus* | Tyrannidae | 24.4 | Closely Similar | |
| *Myiodynastes maculatus* | Tyrannidae | 43.2 | *Legatus leucophaius* | Tyrannidae | 22.2 | Closely Similar | [19] |
| | | | *Empidonomus varius* | Tyrannidae | 27.1 | Closely Similar | |
| *Philemon subcorniculatus* | Meliphagidae | 194 | *Oriolus forsteni* | Oriolidae | 109 | Virtually Identical | [20–24] |
| *Philemon fuscicapillus* | Meliphagidae | ? | *Oriolus phaeochromus* | Oriolidae | ? | Closely Similar | |
| *Philemon m. moluccensis* | Meliphagidae | ? | *Oriolus b. bouroensis* | Oriolidae | ? | Closely Similar | |
| *Philemon m. timorlaoensis* | Meliphagidae | ? | *Oriolus b. decipiens* | Oriolidae | ? | Closely Similar | |
| *Philemon b. buceroides* | Meliphagidae | ? | *Oriolus v. viridifuscus* | Oriolidae | ? | Quite Similar | |
| *Philemon b. pallidiceps* | Meliphagidae | ? | *Oriolus v. finschi* | Oriolidae | ? | Quite Similar | |
| *Philemon novaeguineae* ‘ ’ | Meliphagidae | 140 | *Oriolus szalayi* | Oriolidae | 95 | Quite Similar | |
| | | | *Pycnopygius stictocephalus* | Meliphagidae | 38.5 | Closely Similar | |
| *Coracina larvata* | Campephagidae | 60* | *Lalage fimbriata* | Campephagidae | 29.3 | Closely Similar | [25] |
| *Pericrocotus flammeus* | Campephagidae | 20 | *Pericrocotus igneus* | Campephagidae | 15 | Closely Similar | [25] |
| *Pericrocotus ethologus* | Campephagidae | 19 | *Pericrocotus brevirostris* | Campephagidae | 16.5 | Quite Similar | |
| | | | *Pericrocotus solaris* | Campephagidae | 14.5 | Closely Similar | |
| | | | *P. cinnamomeus* (male) | Campephagidae | 8.6 | Quite Similar | |
| *Xenopirostris polleni* | Vangidae | 61.5 | *Tylas eduardi* | Vangidae | 46.8 | Virtually Identical | [26] |
| *Dicrurus adsimilis* | Dicruridae | 40.3 | *Melaenornis pammelaina* | Muscicapidae | 30.2 | Virtually Identical | [24] |
| *Lanius collaris* | Laniidae | 40.8 | *Sigelus silens* | Muscicapidae | 25.7 | Virtually Identical | [24] |
| *Malaconotus cruentus* | Malaconotidae | 76.7 | *Chlorophoneus multicolor* (orange morph) | Malaconotidae | 50.9 | Closely Similar | [27] |
| *Malaconotus blanchotii* | Malaconotidae | 78.7 | *Chlorophoneus multicolor* (yellow morph) | Malaconotidae | 50.9 | Closely Similar | |
| | | | *Chlorophoneus sulfureopectus* | Malaconotidae | 27.1 | Closely Similar | |
| *Moho nobilis* | Mohoidae | 46 (f)<br>63 (m) | *Drepanis pacifica* | Fringillidae | 33* | Closely Similar | [28–30] |
| *Buthraupis montana* | Thraupidae | 96 | *Dubusia taeniata* | Thraupidae | 37 | Closely Similar | [31] |
| *Oreothlypis superciliosus* | Parulidae | 9 | *Parula americana* | Parulidae | 7.5 | Closely Similar | [32] |
| | | | *Parula pitiayumi* | Parulidae | 6.6 | Closely Similar | |

Body Mass data from Dunning (2008) except for *: *Eutriorchis astur* from Thorstrom *et al.* (1995); *Accipter poliogaster* from São Paulo University Museum of Zoology; *Harpactes* mass from Thompson (1966); *Pogonotriccus poecilotus*, *P. eximius* from del Hoyo, Elliot & Christie (2004); *Coracina larvata* from Delaware Museum of Natural History.; *Drepanis pacifica* estimated from *Telespiza cantans* (Dunning, 2008). References: 1- Chubb, 2004; 2- Hackett *et al.*, 2008; 3-Spear & Ainley, 1993; 4- Welch *et al.*, 2014; 5- Griffiths *et al.*, 2007; 6- Negro, 2008; 7- Lerner & Mindell, 2005; 8- Gibson & Baker, 2012; 9- Astuti *et al.* 2006; 10- Hosner *et al.* 2010; 11- Weckstein, 2005; 12- Sibley & Ahlquist, 1990; 13- Webb & Moore, 2005; 14- Weibel & Moore, 2002; 15- Weibel & Moore, 2005; 16- Cody, 1969; 17- Chesser, 2004; 18- Moyle *et al.*, 2009; 19- Tello *et al.*, 2009; 20- Wallace, 1863; 21- Diamond, 1982; 22- Driskell & Christidis, 2004; 23- Johannson, Pasquet & Irestedt, 2011; 24- Barker *et al.*, 2004; 25- Jønsson *et al.*, 2010; 26- Yamashigi *et al.*, 2001 27- Fuchs *et al.* 2004; 28- Ngeumbock *et al.*, 2009; 29- Fleischer, James & Olson, 2008; 30- Lerner *et al.*, 2011; 31- Barker *et al.*, 2012; 32- Lovette *et al.*, 2010.

Using human vision, each proposed model/mimic pair was classified by me as either *quite similar* (i.e. multiple broadly similar features in colour pattern), *closely similar* (i.e. numerous, detailed features shared across the plumage but some distinctive differences discernable at close range), or *virtually identical* (i.e. difficult to distinguish at close distances even under ideal circumstances, and often distinguishable only by trained observers) (Table 1). Avian colour vision is tetrachromatic and includes substantial sensitivity in the ultraviolet (Hart, 2001). Thus, it is possible that some species characterized as closely similar or virtually identical are actually more easily distinguishable to the birds themselves. This outcome could only result if some model species are successful at manipulating ultraviolet (UV) light reflectance by their plumages in ways that the mimics are not. However, convergent evolution among species in plumage coloration within the human visible spectrum is still visible to birds, and still requires an evolutionary explanation. Additional research will be required to analyze the similarity in spectral reflectance among convergent plumages of the different species involved.

## FREQUENCY OF OCCURRENCE AND BODY SIZE

I propose ~50 phylogenetically independent origins of visual ISDM in birds involving 60 model and 93 mimic species, subspecies, populations, age classes, or polymorphisms from 30 families of birds (Table 1) (Fig. 3). In 25 cases, the mimics were classified as virtually identical to the model species, whereas 65 examples were considered to be closely similar (Table 1). Five cases were classified as quite similar.

Both models and mimics varied over two orders of magnitude in body mass (Table 1). Mimics range in body mass from 18–90% of their model species with an average mass of 55.7% of their models (± 17.8% S.D.). A linear regression of subordinate species mass to dominant species mass has a slope of 0.5684 and an $R^2$ value of 0.83 (Fig. 4). The relationship is quite linear over two orders of magnitude. This regression was not corrected for the phylogenetic interrelationships among many of the samples. However, a linear regression using a reduced data set of phylogenetically independent observations –that is only a single data point from each hypothesized evolutionary origin of mimicry, e.g. only one *Ramphastos* comparison, etc. – produced a similar slope of 0.586 with an $R^2$ value of 0.81.

The slope of the regression provides a second generalized estimate of the ratio of the mass of mimics to models of ~56–58%. Based on a simplistic, cubic relationship between the linear size of an object and its mass, mimics can be estimated to be ~82% of the linear size, on average, of their model species – i.e. $(0.8242)^3 = 0.56$. A average linear size discrepancy between mimic and model of ~17–20% is in the highly plausible range for visual size confusion to occur. Furthermore, given that a small difference in linear dimensions scales with a much larger difference in body mass, any such visual confusion could confer a great competitive advantage to a smaller species in aggressive, interspecific social interactions.

Some of the most extreme outliers – both in similarity and dissimilarity in body mass ratios – are large raptors that mimic other raptors (Fig. 4). The very high visual acuity of raptors means that visual deception can function at great distances when other cues about object size are less relevant to visual perception. Furthermore, the real risk of attack by raptors will also make mimicry advantageous even at relatively small differences in body mass.

The frequency distribution for mimic/model body mass ratios for the proposed mimic/model species pairs shows a peak at ratios between 0.4–0.5, and no pairs with body mass ratios > 0.9 (Fig. 5A). In other words, the proposed sample of models and mimics does not include any examples of avian species pairs with convergent visual appearance that have very similar body sizes. [Other radiations of closely related, sympatric bird species with highly similar appearance were not included in the sample because there is no phylogenetic evidence that they have convergent plumages, e.g. *Empidonax* flycatchers, *Phylloscopus* warblers, *Collocalia* swiftlets, etc. Notably, these radiations include species with plain and poorly differentiated plumages. Apparently, these species have diverged in plumage colour only slightly since common ancestry, and do not appear to be examples of ISDM.]

Is the absence of very similarly sized birds in the sample of proposed mimic/model pairs unexpected by chance alone? In other words, what is the null expectation for a frequency distribution of body mass ratios among species that have not evolved as sympatric social mimics? We can examine this question by imagining a few different null distributions. The first null model is purely mathematical. The distribution of ratios produced from repeated random samples of two values from a normal distribution of body mass will be another normal distribution centered at one. To make this null model equivalent to the sample of body mass ratios of hypothesized models and mimics, all body mass ratios > 1 should be inverted so that the mass of the larger species is in the denominator. (This transformation is equivalent to folding the right hand side of a normal distribution over on to the left side, and adding them together.) The resulting null distribution will look like the left half of a normal distribution with a peak at 1.

We can also hypothesize a second, evolutionary, phylogenetic null distribution from an evolutionary

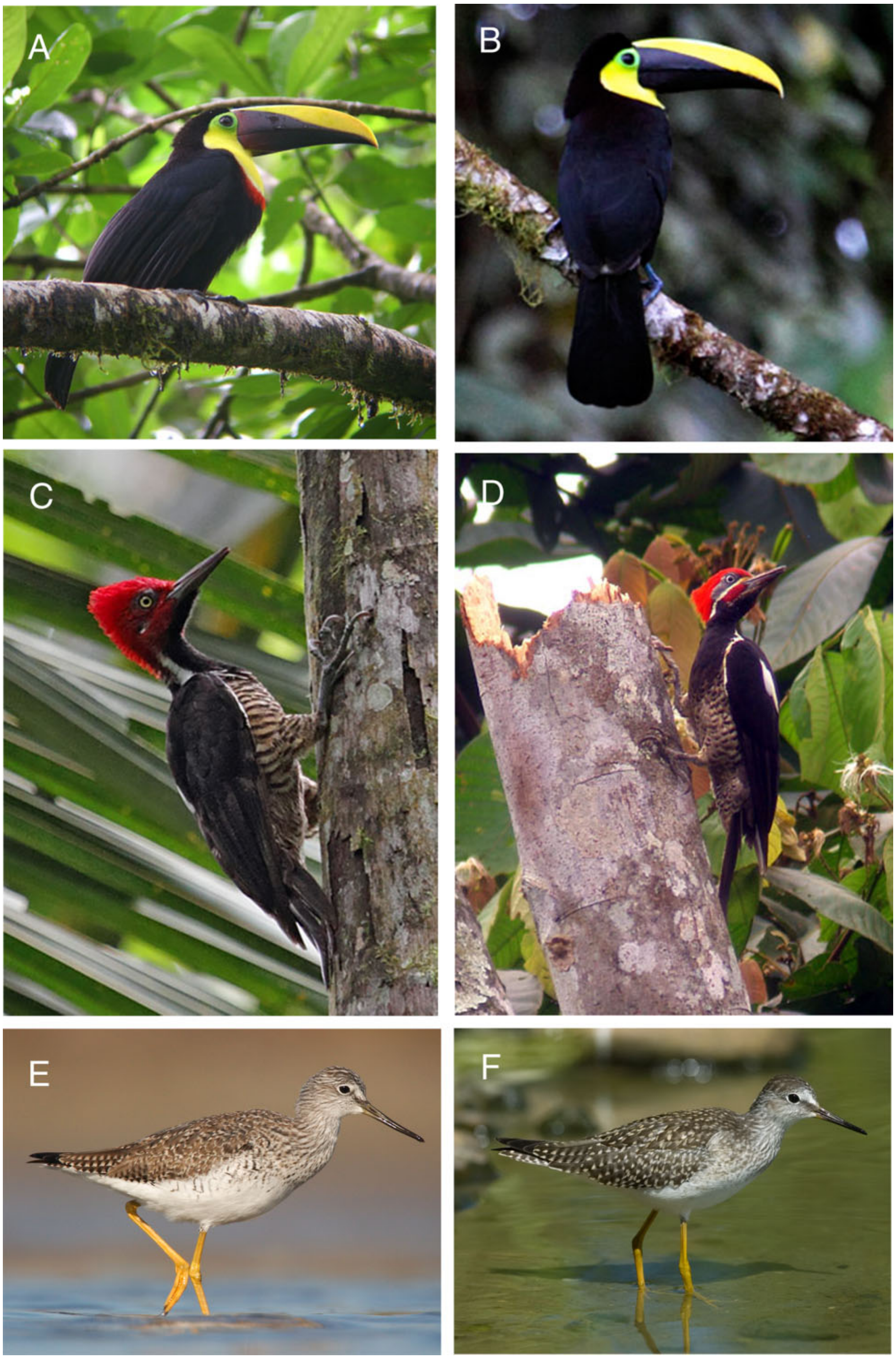

**Figure 3.** Five examples of interspecific social dominance mimicry (ISDM) in birds; model species on the left, and mimic species on the right. A, Chesnut-mandibled Toucan *Ramphastos swainsoni* model, and B, Choco Toucan *Ramphastos brevis* mimic. C, Guayaquil Woodpecker *Campephilus gayaquilensis* model, and D, Lineated Woodpecker *Dryocopus lineatus* mimic. E, Greater Yellowlegs *Tringa melanoleuca* model, and F, Lesser Yellowlegs *Tringa flavipes* mimic. G, Ornate Hawk Eagle *Spizaetus ornatus* model, and H, Immature plumage Pale-bellied Goshawk *Accipiter poliogaster* mimic. I, Rufous Motmot *Baryphthengus ruficapillum martii* model, and J, Broad-billed Motmot *Electron platyrhynchum pyrrholaemum* mimic. These pairs of species of toucans, yellowlegs, hawks and motmots were classified as virtually identical, and this pair of woodpecker species were classified as closely similar (Table 1). Photo credits: (A–D) Nick Athanas, (E) R. Crossley/VIREO, (F) J. Jantunen/VIREO, (G) Mateus Hidalgo, (H) J. McKean/VIREO, (I) D. Wechsler/VIREO, (J) T. Friedel/VIREO.

**Figure 3.** *Continued.*

random walk process. At common ancestry, any two related species/populations will have a mass ratio of 1. A ‘Brownian motion’ evolutionary process, in which evolution species mass evolves in a random walk, will result in a distribution of body mass ratio that have a mean of one but with increasing variance with time since common ancestry (Felsenstein, 1985). Again, when these ratios are transformed so that all values are $< 1$, the null distribution will again resemble the left half of a normal distribution with a peak at 1.

The evolutionary history of real clades would also include natural selection on body size that will produce

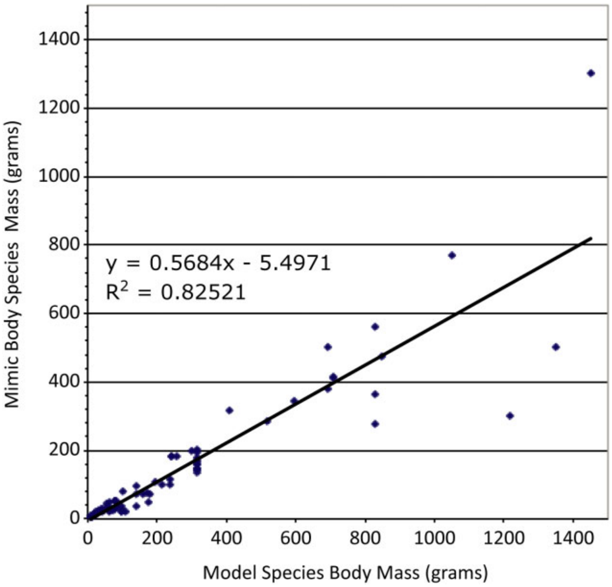

**Figure 4.** Linear regression of the hypothesized mimic species body mass (g) to the hypothesized model species body mass (g) from a sample of proposed avian species mimic and model pairs (Table 1): $y = 0.5684x - 5.49$; $R^2 = 0.83$. The larger species is hypothesized to be the model. Mass data from Dunning (2008), other references, and museum specimens (see Table 1). Regression is based on species averages, or averages of the average of each sex.

adaptive differences in body mass among species and clades. Body mass ratios of species from different clades with adaptive divergence body mass will yield values that are substantially < 1. However, comparisons among closely related species within subclades with similar ecologies and histories of selection will continue to have a tendency toward body mass ratios near 1. Thus, some adaptive divergence in body size will result in a multipeak frequency distribution in body mass ratios: one peak near 1 for closely related species within undifferentiated subclades, and another peak (or peaks) produced by comparisons among species from clades that have adaptively diverged in body size. This distribution will still retain one local peak at 1.

All three 'null' models– mathematical, evolutionary, and adaptive– predict a single or local peak in body mass ratios of 1. The adaptive divergence null model also predicts an additional peak at values related to the comparisons among species from 'large' and 'small' subclades. To test these null predictions, I produced body mass ratio frequency distributions for randomized pairs of 70 species each of woodpeckers (Picidae) and flycatchers (Tyrannidae) using data from Dunning (2008). These frequency distributions showed a peak at 0.6 for both woodpeckers and flycatchers (Fig. 5B, C), indicating some heterogeneity in body size within subclades of each family. But both exhibited a second peak in the body mass ratio distributions at body mass ratios between 0.9–1.

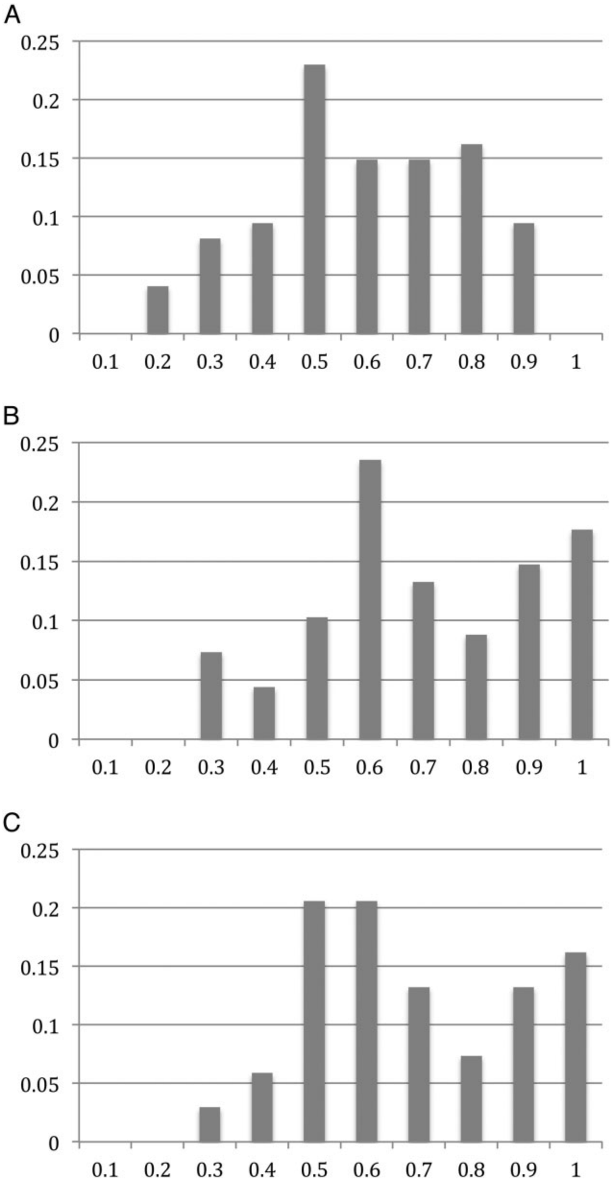

**Figure 5.** A, Frequency distribution of the mimic/model body mass ratios for the proposed avian examples of ISDM (Table 1). B, C, Null frequency distributions of body mass ratios of random pairs of species for 75 species of (B) woodpeckers (Picidae), and (C) tyrant flycatchers (Tyrannidae). The larger species has been placed in the denominator. The frequency distribution of the proposed model/mimic pairs has a single peak at 0.5, whereas the null distributions of random species pairs within clades show bimodal peaks with one peak between 0.9–1.0.

In conclusion, all three null models predict some tendency toward mass ratio values near 1. Randomly generated frequency distributions generated from body mass ratios of species from two avian families are congruent with these null predictions. In contrast, the observed distribution of mass ratios between the proposed mimic/model species pairs is unusual for the absence of species pairs with very similar body sizes (Fig. 5A). This result indicates that the phenomenon of convergent similarity in avian body plumage is strongly associated with asymmetry in body size. This observation further confirms the prediction that social advantages to interspecific social dominance (ISD) mimics are the result of being mistaken for another species with larger body size.

These findings suggest that mimic species are not merely evolving signals to facilitate simultaneous social interactions between conspecific and heterospecific individuals (i.e. Cody, 1969, 1973), but that mimetic species have evolved convergent visual signals in order to acquire deceptive interspecific social and ecological advantages in interference competition mediated by body size.

### Ecological diversity

The proposed examples of avian ISDM exhibit tremendous variation in ecology, foraging methods, and habitat preferences. Proposed avian examples of ISDM include: pelagic seabirds (Procellariidae, Stercorariidae), shorebirds (Scolopacidae), aerial insectivores (Apodidae), sallying canopy insectivores (Tyrannidae, Campephagidae), forest canopy frugivores (Psittacidae, Ramphastidae, Cotingidae Meliphagidae, Oriolidae), insectivores of open savannah woodlands (Dicruridae, Laniidae, Malaconotidae, Muscicapidae), dead wood excavating forest insectivores (Picidae), forest interior frugivores and insectivores (Momotidae, Picidae, Furnariidae, Thamnophilidae, Cotingidae, Tityridae, Tyrannidae, Vangidae), nectarivores (Mohoidae, Fringillidae), and high altitude grassland insectivores (Furnariidae). Common to many of these examples are habitats and foraging methods that afford long, open sight line distances to other potentially competing individuals within the habitat. Whether foraging in open air, in the top of forest canopy, in grasslands, open savannahs, on a mud flat, on the open ocean, or even sallying and sally gleaning within understory forest openings, such species are likely to first visually encounter one another at distances large enough to create ambiguity in the judgement of relative body size. Nocturnal birds (owls and nightjars) and diving birds (waterfowl, grebes, alcids, etc.) are absent from the sample.

In conflict with Moynihan (1968) and Barnard (1978), there does not appear to be a strong relationship between mimicry and interspecific foraging flock attendance. Of all the proposed examples, only a few pairs exhibit facultative multispecies flocking behaviour: *Tringa melanoleuca* and *T. flavipes*; *Philydor rufus* and *Thamnistes anabatinus*; *Xenopirostris polleni* and *Tylas eduardi*; *Dicrurus adsimilis* and *Melaenornis pammelaina*; and *Buthraupis montana* and *Dubusia taeniata* (Table 1).

### Geography and distribution

A detailed analysis of the geographic distribution of each of the proposed participants in avian ISDM is beyond the scope of this paper. However, at a regional scale, nearly all of the proposed examples of ISDM exhibit a close correlation between the geographic distribution of the models and the mimics. In some instances, the distributions of the mimics are more geographically restricted than those of their models. For example, the distribution of the model Hairy Woodpecker extends south into the Mesoamerican mountains, but the distribution of the model Downy Woodpecker does not. Likewise, the model species the White-collared Swift *Streptoprocne zonaris* is found broadly distributed throughout the Neotropics, whereas one of its three mimic species, the White-chested Swift *Cypseloides lemosi*, is restricted to the northern Andes only. These disjunctions are entirely consistent with the predictions of the Hairy–Downy game, which establish the threshold values of background fitness below which mimic populations will not be sustainable.

In a few instances, the range of the mimic is broader than the model. Perhaps most prominently, the mimetic Pileated Woodpecker *Dryocopus pileatus* has a broad distribution in the mature coniferous and deciduous forests of eastern North America, across Canada, and south again into the mountains of the Pacific Northwest, whereas the now extinct model species, the Ivory-billed Woodpecker *Campephilus principalis*, lived in old growth forests of the south-eastern North America. However, nearly the entire allopatric distribution of Pileated Woodpecker was covered with glaciers during the last glacial maximum ~18 000 years ago (Dyke & Prest, 1987). Thus, the entire distribution of the Pileated Woodpecker would likely have been sympatric with the Ivory-billed Woodpecker during glacial maxima providing ample opportunity and advantage for coevolution of appearance through ISDM. The major differences between the distributions of the two species may be the result of differential range expansion during glacial retreat.

Perhaps one of the weaker proposed examples of avian ISDM is the mimicry by two species of ranging *Parula* warblers of a Central American *Oreothlypis* warbler. Both proposed mimics are broadly distributed, but *P. pitiayumi* has a resident population sympatric with *O. superciliosus*, whereas *P. americana* breeds allopatrically but migrates and winters in sympatry with *O. superciliosus*. This case deserves further investigation.

### PHYLOGENETIC DIVERSITY AND PATTERNS

Minimum phylogenetic support for the hypothesis of ISDM consists of evidence that the model and mimic species are not sister taxa, and that either or both are more closely related to other species which lack the plumage colour and pattern similarities that the mimics and models share. More advanced phylogenetic support would consist of phylogenetic analyses of the events in plumage and colour character evolution that have resulted in convergent appearance between the model and mimic. The strongest phylogenetic support for ISDM would be documentation of coevolutionary radiation among multiple species from the model and mimic clades (see below).

In most examples, models and mimics are members of the same families, but eight cases involve models and mimics from different families such as: petrels and skuas; hawks and cuckoos; cotingas, mourners, and tyrant flycatchers; honeyeaters and orioles; drongos and flycatchers; shrikes and Old World flycatchers; mohos and Hawaiian honeycreepers (Table 1). In these instances, the evolutionary convergence in appearance is clearly supported by the distant phylogenetic relationships between proposed models and mimics (Table 1). In general, woodpeckers appear to exhibit the highest frequency of the evolution of ISDM of any avian family. Additional proposed examples of mimicry exist between south Asian species of *Chrysophlegma* and *Picus, Chrysocolaptes* and *Dinopium*, and *Meiglyptes* and *Hemicircus* (Table 1).

All proposed cases of avian mimicry are supported to some detail by molecular phylogenetic hypotheses (Table 1). Indeed, the proposal of various instances of ISDM has been motivated by phylogenetic discoveries that highly similar species are not closely related (Weibel & Moore, 2002, 2005; Chesser, 2004; Weckstein, 2005; Jønsson *et al*., 2010; Gibson & Baker, 2012).

Phylogenetic relationships can provide clear evidence of evolutionary plumage convergence. For example, recent phylogenetic analyses document that the Greater Yellowlegs *Tringa melanoleuca* is related to Greenshank *T. nebularia* and Redshank *T. totanus*, whereas the Lesser Yellowlegs *T. flavipes* is most closely related to Willet *Catoptrophorus semipalmatus* (Gibson & Baker, 2012). Yet, from these different lineages, Greater and Lesser Yellowlegs have convergently evolved to be virtually identical in every detail of plumage and coloration pattern (Fig. 3E–F).

Only a few of the proposed examples of avian ISDM have been previously analyzed in any phylogenetic detail. A recent phylogenetic analysis of plumage colour character evolution in *Picoides* woodpeckers supports two independent instances of convergence in appearance– between Hairy and Downy in North America, and between Middle Spotted and Lesser Spotted Woodpeckers (*Picoides leucotus*, and *P. minor* respectively; formerly *Dendrocopos*) in Eurasia (Weibel & Moore, 2002, 2005).

Although the two other woodpecker genera are not phylogenetically closely related (Webb & Moore, 2005; Fuchs *et al*., 2006), multiple species of *Campephilus* and New World *Dryocopus* woodpeckers have converged in plumage pattern including white pattern stripes on the back, neck, and face (Fig. 3C, D). Further, the North American Pileated Woodpecker (*Dryocopus pileatus*) and the Ivory-billed Woodpecker (*Campephilus principalis*) share additional white wing patches, whereas several Neotropical *Dryocopus* and *Campephilus* species share coarsely barred, black and buff under parts. Even though Neotropical *Campephilus* are smaller than the North American *Dryocopus pileatus*, all New World *Dryocopus* are smaller in body mass than sympatric *Campephilus* species (Table 1), supporting the hypothesis that *Dryocopus* are mimics of *Campephilus* models. In congruence with the predictions of the ISDM mechanism, the mimetic plumage of *Dryocopus* appears to be derived to resemble *Campephilus*. The genus *Dryocopus* is of Old World origin (Webb & Moore, 2005). Old World *Dryocopus* and their relatives entirely lack white scapular and neck markings, and mostly have black bellies. Thus, the white neck, back and facial markings of New World *Dryocopus* were phylogenetically derived in the common ancestor of the New World clade of *Dryocopus* in sympatry with *Campephilus* species. Indeed, the convergent white scapular markings of *Campephilus* and *Dryocopus* woodpeckers are produced by different tracts of feathers in each genus.

In several cases, multiple phylogenetically independent lineages have convergently evolved on the appearance of a single model species, providing clear evidence of the non-homology of these derived plumage similarities. For example, species of New World *Cypseloides, Panyptila*, and *Aeronautes* swifts have independently evolved to mimic the white collar of the larger *Streptoprocne zonaris* (Apodidae). Multiple species from within the unrelated tyrant flycatchers genera *Pogonotriccus, Phyllomyias*, and *Myiornis* have converged in appearance on *Leptopogon* species (Tyrannidae). Species of both *Oriolus* (Oriolidae) and *Pycnopygius* (Meliphagidae) have converged to resemble *Philemon* honeyeaters (Meliphagidae).

*Pericrocotus* minivets are tropical Asian canopy insectivores with a complex evolutionary history of transitions from mostly grey to brilliantly red and black plumages (Jønsson *et al*., 2010). Recent phylogenetic work has documented that the red-and-black patterned species are members of multiple distinct clades, and consist of two large bodied species (19–20 g) and four small bodied species (8.6–16.5 g) (Dunning, 2008; Jønsson *et al*., 2010). Although a detailed phylogenetic character analysis is required to reconstruct the history of the evolution of the boldly patterned red and black plumage, homology among all of these species is highly unlikely (Jønsson *et al*., 2010).

### COEVOLUTIONARY RADIATION

Because ISDM impacts the fitness of the model species (Prum & Samuelson, 2012), model species will come under natural selection to diverge in appearance from their socially parasitic mimics. Likewise, as models evolve to be more dissimilar in appearance, mimic species will come under natural selection to maintain deceptive similarity to the model. Thus, ISDM may result in the onset of antagonistic coevolution in appearance among models and mimics. If geographic isolation or speciation occurs among populations of sympatric models and mimics, then ISDM may foster coevolutionary radiation among multiple populations or species within model and mimic clades.

Alternatively, one could hypothesize multiple independent evolutionary origins of ISDM in each species pair. However, such a pattern would require that ISDM is even more likely to evolve *de novo*, but it would be highly unparsimonious. In every case in which multiple species or populations within one clade mimic species in another clade, I assume a single origin of mimicry with the most recent common ancestor of the mimic clade.

Several of the examples of avian ISDM exhibit substantial evidence of antagonistic coevolutionary radiation among model and mimic species. The strongest evidence comes from the clades of larger, dominant, yelping and smaller, subordinate, croaking *Ramphastos* toucans. The possibility of mimicry among species of *Ramphastos* toucans was first suggested by Haffer (1974). A molecular phylogeny and comparative analysis by Weckstein (2005) documents no fewer than four distinct models and five mimetic forms, several of which are virtually identical (e.g. Fig. 3A, B; Table 1). These nine total species and phenotypically distinct subspecies exhibit convergently correlated combinations of four throat colours (white, yellow, orange, and orange bordered by white), three over tail covert colours (red, yellow, and white), three facial skin colours (red, green, and blue), and five different bill colours and coloration patterns (Short & Horne, 2001; Weckstein, 2005) (Fig. 3A, B). Although Weckstein (2005) inferred that some plumage similarities shared among sympatric species may be retained, primitive character states (e.g. white upper tail coverts), this phylogenetic pattern provides clear evidence that multiple distinctive coloration traits (e.g. throat, facial skin, red and yellow over tail coverts, bill coloration, and bill colour patterning) have rapidly coevolved between multiple sympatric forms of these two clades.

As mentioned above, *Dryocopus* and *Campephilus* woodpeckers also present clear patterns of coevolved plumage patches in sympatric lineages of the two genera, including derived white scapular patches, white wing patches, barred belly, and white neck and facial markings. The broadly distributed Neotropical mimic *Dryocopus lineatus* is sympatric with three different model species of *Campephilus*. As predicted by coevolution by ISDM, the phenotypic diversification among populations of the model *Campephilus* appears to be proceeding in advance of the coevolutionary response by populations of mimetic *Dryocopus*.

Most of the Neotropical motmots (Momotidae) have distinct, ornamental racket-tipped central tail feathers. Tail rackets are featured in conspicuous tail wagging displays, and have no known ecological function (Murphy, 2007). West of the Andes, the South and Central American populations of Rufous Motmot *Baryphthengus ruficapillus* and the mimic Broad-billed Motmot *Electron platyrhynchum* have the conspicuous tail rackets shared commonly across the family, whereas east of the Andes, the sympatric subspecies *Baryphthengus ruficapillus martii* and *Electron platyrhynchum pyrrholaemum* lack tail rackets. By outgroup comparison to other motmots, the presence of tail rackets is primitive to both genera. Thus, the sympatric populations of both species east of the Andes exhibit correlated and derived evolutionary losses of tail rackets. Tail racquets are clearly social signals (Murphy, 2007), and it is highly unlikely that there could be ecological natural selection for the loss of these racquets in two virtually identical, sympatric species in the absence of a communication function. Given that these non-sister species are virtually identical and the lack any obvious ecological or environmental explanations for racket loss (e.g. a third sympatric *Momotus* motmot has tail rackets), the unique and correlated evolutionary losses of tail rackets provides substantial evidence of antagonistic coevolution in model and mimetic populations *Baryphthengus ruficapillus* and *Electron platyrhynchum* east of the Andes.

There is one documented example of the coevolution of a novel display behaviour between models and mimics. The yellow belly, wing bars, and eared facial pattern of the tyrannulet flycatchers *Leptopogon superciliaris* and *L. amaurocephalus* are mimicked by several species from three independent tyrannulet flycatcher genera – *Pogonotriccus, Phyllomyias*, and *Myiornis* (Table 1) (Tello *et al*., 2009). These *Leptopogon* species frequently flick open one wing and then the other when perched, like a nervous tic (Hilty & Brown, 1986; Ridgely & Tudor, 1994; R. O. Prum pers. observations). The wing flicks do not function in flushing insect prey, as in certain *Myiobius* redstarts (Jablonski, 1999; Mumme, 2002), and they are performed too frequently and continuously to function in courtship communication. Unlike their own non-mimetic congeners, several *Pogonotriccus* and *Phyllomyias* species that mimic *L. superciliaris* and *L. amaurocephalus* have also evolved to perform conspicuous nervous wing flicks while perched (Hilty & Brown, 1986; Ridgely & Tudor, 1994; R. O. Prum pers. observations). Mimetic *Myiornis auricularis*, however, do not flick their wings. This strong pattern of behavioral coevolution implies that the wing flick display of *Leptopogon* evolved as a derived behavioral novelty by the model species to distinguish itself from its mimics, and evade the ecological costs of interspecific social mimicry. As predicted by the ISDM mechanism, multiple mimic species have coevolved the same conspicuous behavioral trait to maintain effective deceptive similarity to the model, but others (i.e. *Myiornis auricularis*) have not yet done so.

A phenotypically less complex coevolutionary radiation occurs between the model *Philemon* friarbirds and mimics from two different avian families (Meliphagidae, Oriolidae) among different Australo-Papuan and Indonesian islands (Diamond, 1982). No detailed phylogenies are yet available for the friarbird and oriole species in this complex, but there is a clear pattern of autapomorphous interisland differentiation in plumage colour patterns among populations of model friarbirds and mimic orioles (Diamond, 1982), which is highly indicative of an antagonistic coevolutionary radiation.

## MIMICRY COMPLEXES

There are several examples in birds of multiple species mimicry complexes that exhibit a substantial range in body size. The evolution of ISDM has only been explicitly modelled between two species (Prum & Samuelson, 2012). However, the evolutionary mechanism appears to be generalizable to a more complex, multispecies interaction in which there is a hierarchy of benefits accruing simultaneously to multiple species with different body sizes. All models species will come under natural selection to evade mimicry by a socially subordinate ecological competitor. Thus, models will come under natural selection to differentiate from mimics. However, I hypothesize that an intermediate-sized mimic species will be constrained from evading mimicry by an even smaller species because the intermediate-sized mimic is under simultaneous natural selection to maintain the deceptive similarity to the larger model species. Because of this constraint, intermediately sized mimics will become vulnerable candidates for deceptive social mimicry by smaller species.

In this way, ISDM can create the opportunity for the evolution of convergent appearance among multiple species in a guild of sympatric, ecological competitors. This process will result is the coevolutionary entrainment of multiple species into a quasi-Müllerian mimicry complex of species with a broad range of body sizes. As in Müllerian mimicry, multiple species in a community will converge on a common appearance. Unlike the classic model Müllerian mimicry, in which each toxic species is equivalently toxic and pays similar toxicity costs, each species in an ISDM complex will still experience fitness costs from the mimicry of other species that are smaller than it is. However, it is now broadly appreciated that toxic Müllerian mimics may pay very different costs to toxicity, so that the hierarchy of costs and benefits among different species within a Müllerian mimicry complex can be highly asymmetrical (Mallet, 2001). So, an ISDM complex may be very similar in evolutionary dynamics to real examples of Müllerian mimicry among toxic species. Distinctively, however, in an ISDM complex, only the largest, dominant species is unconstrained to evolve in appearance; all others will be constrained to follow the leader, and will be unable to evade mimicry by yet smaller mimics.

The premier avian example of a mimicry complex is the coradiation of Neotropical kiskadee-type tyrant flycatchers (Tyrannidae) which consists of a network of canopy aerial insectivores from six different genera with extremely similar appearance– rufous wings and tail, light yellow belly, and white throat and face with a black facial mask. The complex is characterized by two large, potentially top, model species– the Boat-billed Flycatcher *Megarhynchus pitangua* (73 g) and *Pitangus sulfuratus* (61 g) (Fig. 6). These two larger bodied species are mimicked by an array of successively smaller species from at least four different genera: *Phelpsia inornata* (29.4 g), *Myiozetetes* sp. (29-25 g), *Philohydor lictor* (25 g), *Conopias* sp. (24-21 g) (Table 1). According to Tello *et al*. (2009), *Pitangus sulfuratus* and *Philohydor lictor* form a weakly supported clade, and thus may have homologous plumage similarities. However, these genera are both distantly related to *Megarhynchus, Phelpsia*, and *Conopias*. Thus, even without a detailed phylogenetic, comparative analysis, there must have been substantial convergence in appearance among multiple lineages to explain the extant broadly shared pattern of plumage elements.

Another potential ISDM complex involves multiple species from four genera of grey and white pelagic tubenoses (Procellariidae) that share a prominent dark M-pattern on their upper wings. These species are broadly sympatric in the Pacific, southern Indian, and southern Atlantic Oceans. The largest, proposed model species in the complex is the Bulller's Shearwater *Puffinus bulleri* (407 g). The complex also includes multiple species of 'cookilaria' *Pterodroma* petrels (Onley & Scofield, 2007) which range in size from the largest, Mottled Petrel *Pterodroma inexpectata* (316 g), to a series of five, smaller species from *P. cookii* (178 g) to *P. longirostris* (143 g) (Table 1). The other two genera

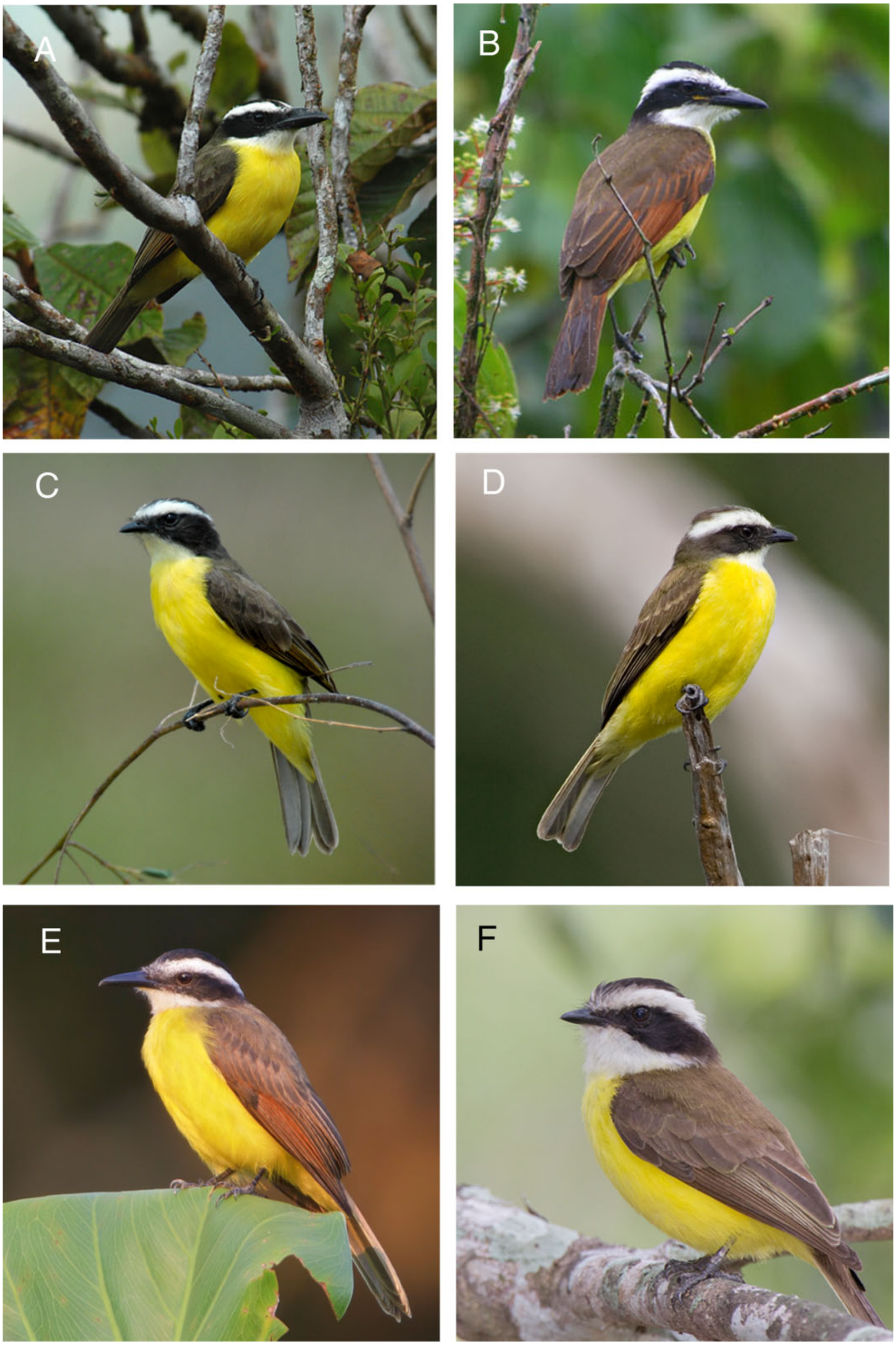

**Figure 6.** Multispecies mimicry complex of Neotropical kiskadee-type flycatchers (Tyrannidae). A, Boat-billed Flycatcher *Megarhynchus pitangua* (73 g). B, Great Kiskadee *Pitangus sulphuratus* (61 g). C, Rusty-margined Flycatcher *Myiozetetes cayanensis* (25.9 g). D, Social Flycatcher *Myiozetetes similis* (28 g). E, Lesser Kiskadee *Philohydor lictor* (25.5). F, White-throated Flycatcher *Phelpsia inornata* (29.4 g). Photo credits: (A) image in the public domain, (B) Nick Anthanas, (C) T. J. Ulrich/VIREO, (D) G. Lasley/VIREO, (E) G. Bartley/VIREO, and (F) T. Friedel/VIREO.

involved include the Blue Petrel *Halobaena caerulea* (202 g), and all species of *Pachyptila* prions, from the largest Broad-billed Prion *Pachyptila vittata* (196 g) to the smallest Fairy Prion *Pachyptila turtur* (137 g). (For the estimation of mimic/model body size ratios, I assumed that *Puffinus bulleri* is the model for *Pterodroma inexpectata*, and that *Pterodroma inexpectata* is the model for other *Pterodroma, Halobaena*, and *Pachyptila*. See Table 1.). A recent phylogeny that includes many of these species demonstrates that *Halobaena* and *Pachyptila* are sister taxa – i.e. *Halobaena* is the largest and most basal prion – but that *Halobaena-Pachyptila* clade is only distantly related to either *Puffinus bulleri* or the 'cookilaria' clade of *Pterodroma* petrels (Welch, Olson & Fleischer, 2014).

It appears that multiple members of *Halobaena* and *Pachyptila* may benefit from mimicking *Puffinus bulleri, Pterodroma inexpectata*, and other larger 'cookilaria'.

The situation is made more complex by the possibility that smaller *Pterodroma* may also benefit from their similarity to the larger *Pterodroma inexpectata*, despite the fact that their plumage similarities are homologous. Likewise, smaller *Pachyptila* may also benefit from their similarity to the larger *Halobaena caerulea* or *Pachyptila vittata*. In these instances, there is the intriguing possibility that the evolutionary origin of mimetic plumage could facilitate the subsequent evolution of variation in body size within a mimetic clade. In other words, species in a lineage of mimics that evolve smaller body sizes may be able to gain a new social advantages from their resemblance to other larger species of mimics within their own clade. Larger mimics are constrained from evolving away because they are mimicking a larger model in another clade. In this case, the retention of the mimetic M-pattern wing patches during the evolution of body size in *Pterodroma* and *Pachyptila* species could have allowed smaller species to gain social advantages from larger *Pterodroma, Halobaena*, and *Pachyptila* to whom they are closely related, and with whom they share homologous plumage elements. This hypothesis predicts that the ancestral body size in such clades should be large, and that the smaller species evolved within each clade after the origin of ISDM. This prediction is supported, at least preliminarily, by the observations that: (1) the smaller 'cookilaria' petrels are smaller than all other *Pterodroma*, (2) that the small prions are among the very smallest members of the family, and (3) that the larger-sized *Halobaena caerulea* is the sister group to *Pachyptila*. A similar mechanism could also apply to other clades, such as the lineages of kiskadee-type flycatchers that have diversified in body size while sharing homologous plumage elements, e.g. *Pitangus sulphuratus* and *Philohydor lictor*.

The radiation of 'eared' tyrannulets appears to constitute another ISDM complex that involves convergence in both visual plumage coloration patterns and visible behavioral displays. Model *Leptopogon* species (11.7 g) are mimicked by at least three lineages in two size classes: *Pogonotriccus* and *Phyllomyias* tyrannulets (7–9 g), and *Myiornis auricularis* (5.3 g). It is possible that the smaller *Myiornis auricularis* from south-eastern South American gains some additional benefit from mimicking the intermediately sized *Pogonotriccus eximius* as well as the larger *Leptopogon amaurocephalus*.

In New Guinea and nearby islands, large *Philemon* friarbirds (~194 g)(Meliphagidae) are mimicked by sympatric species of smaller *Oriolus* orioles (95–109 g)(Oriolidae). On New Guinea, an additional, even smaller mimic species has evolved from among the honeyeaters – the Streak-headed Honeyeater *Pycnopygius stictocephalus* (38.5 g) (Meliphagidae) (Diamond, 1982). The great disparity in size between the *P. stictocephalus* and the sympatric *Philemon* and *Oriolus* has raised the possibility that *P. stictocephalus* is mimicking *Oriolus*, or both *Philemon* and *Oriolus* (Diamond, 1982). This three species system constitutes a minimum case of a hierarchical mimicry complex. Likewise, a similar situation occurs in a mimetic assemblage of sympatric African bush-shrikes: *Malaconotus blanchottii* (78.7 g) > *Chlorophoneus multicolor* (yellow morph) (50.9 g) > *Chlorophoneus sulfureopectus* (27.1 g) (Table 1).

## MIMICRY POLYMORPHISM

In most proposed examples of ISDM, mimetic phenotypes appear to be fixed within a population. However, the Hairy–Downy game also predicts that polymorphisms in mimicry will be evolutionarily stable under a wide variety of conditions.

There are several instances where proposed mimetic plumages are not fixed in avian populations, implying the evolution of a stable, mixed equilibrium in mimicry. The most complex example is found in the Many-coloured Bush-shrike *Chlorophoneus multicolor*, which has two polymorphic forms that converge in appearance on two different sympatric model species of larger *Malaconotus* bush-shrikes (geographic variation in polymorphism frequency reviewed in Hall, Moreau & Galbraith, 1966; Fry, Keith & Urban, 2000). Apparently, these are genetic polymorphisms for plumage coloration in the population. This form of polymorphism is unusual because all members of the subordinate species are mimics, but the two morphs have each evolved to mimic a different, distinct model species. This is strong evidence that the variations in plumage colour of *C. multicolor* are under selection to maintain mimetic function. Unfortunately, there is no data on whether variation in the frequency of the mimetic colour morphs among populations of *C. multicolor* is correlated with the density of the proposed model species forms.

Another mechanism to create mimetic polymorphism is to have ontogenetic polymorphism. For example, the adult Ornate Hawk Eagle *Spizaetus ornatus* (Fig. 3G) and the Black-and-white Hawk Eagle *Spizaetus melanoleucus* are each mimicked by the juvenal plumages of the Grey-bellied Hawk *Accipiter poliogaster* (Fig. 3H) and the Grey-headed Kite *Leptodon cayanensis*, respectively. In these cases, the frequencies of the mimic and non-mimetic morphs are not free to evolve as modelled in the Hairy–Downy game since every individual in the population will be both a juvenile and an adult as it ages. The frequency of the two morphs could evolve by additional delay of maturation to adult plumage, however that could interfere with adult social and sexual communication. Consequently, the frequencies of the mimic and non-mimic morphs may diverge significantly from the quantitative predictions of the Hairy–Downy game equilibriums, and would have to be analyzed with a distinct evolutionary model.

A third mechanism that could maintain a lower frequency of mimicry within a species is sexual dimorphism in which only one sex mimics a dominant species. Sexual dimorphic ISDM is apparently uncommon in birds. For example, in *Pericrocotus* minivets, there is strong sexual dimorphism; in the mimetic species *P. igneus, brevirostris*, and *solaris*, the females strongly resemble the grey and white females of the model species *P. flammeus* and *ethologus*. But mimicry in *P. cinnamomeus* is restricted to the male only. Otherwise, several species of flycatcher have very minor variations in the colour of concealed central crown stripes of males, which probably play no role in mimicry. The evolution of sexual dimorphism in mimicry – i.e. mimicry restricted to one sex of the mimic species – could also be fostered by differential costs of mimicry to the two sexes.

### MULTIPLE SIMULTANEOUS MIMETIC MECHANISMS

Brood parasitic cuckoo mimicry of host egg and even host juvenile plumage coloration and patterning is well understood as a case of two-party deception (Rothstein, 1990; Langmore *et al*., 2011). However, some Old World brood parasitic cuckoos are simultaneously participating in another mimicry phenomenon. *Cuculus* cuckoos and *Hierococcyx* hawk-cuckoos have evolved to mimic the plumage coloration patterns, wing shape, and even flight style of *Accipiter* hawks (Payne, 2005). This mimicry has been hypothesized to function in deceiving host species about the identity of the adult female cuckoos during nest parasitism, and reducing aggression toward female cuckoos from their brood hosts (Davies & Welbergen, 2008; Welbergen & Davies, 2011). The host deception hypothesis has been supported by experimental presentations of taxidermy models to Great Tits *Parus major*, Blue Tits *Parus caeruleus*, and Reed Warblers *Acrocephalus scirpaceus*, which are hosts of the parasitic Common Cuckoo *Cuculus canorus* (Davies & Welbergen, 2008; Welbergen & Davies, 2011). However, many male cuckoos also strongly resemble accipiters even though they do not play any role in host deception. Male cuckoo mimicry of hawks is currently unexplained by the host deception mechanism.

It is possible that *Accipiter*-mimetic cuckoos could also be benefitting by protecting themselves from attack by accipiters through ISDM. The Eurasian Sparrowhawk *Accipiter nisus* regularly preys upon birds over 150 g (Cramp & Simmons, 1980), which exceeds the body mass of all *Cuculus* and *Hierococcyx* species. *A. nisus* is known to prey upon European Cuckoo *Cuculus canorus* at relatively low but consistent frequencies: 59 of 42 261 (or 0.14%) of prey items in Germany (Uttendörfer, 1938), 8 of 3654 (or 0.22%) of prey items in Holland (Tinbergen, 1948), and 0.06% of prey items across all habitats in Scotland (Newton, 1986). So, it is reasonable to hypothesize natural selection on cuckoos to avoid *Accipiter* predation. However, these low frequencies could reflect the effectiveness of deceptive plumage in discouraging accipiter predation. For example, in Scotland, predation by *A. nisus* was an order of magnitude higher – 4.22% of prey items – on Wood Pigeons (*Columba palumbus*; 590 g body mass) than on *C. canorus* (Newton, 1986). Although these prey frequencies are not controlled for the abundance of *C. canorus* and *Columba palumbus* in the wild, these data do indicate that predation on *C. canorus* is not limited because if its large body mass. Both sexes of cuckoos should be vulnerable to *Accipiter* predation, but male cuckoos may be more susceptible because of their behaviour of perching in the forest interior and calling for long periods of the day during the breeding season. Thus, this mechanism provides the first specific evolutionary explanation of male cuckoo mimicry of accipiters.

Cuckoos and accipiters cannot be considered to be ecological competitors in the usual sense, but the evolutionary dynamics of mimicking a predator to avoid predation by that predator is identical to ISDM. Predation is the most extreme form of ISD. Furthermore, like standard ecological competition, predation can be thought of as one species pursuing its self-interests at the (ultimate) expense to the fitness of the other species. Lastly, a potential prey item is always codistributed with the resources it utilizes, so the spatial distributions of the ecological resources utilized by the a predator and prey species still fit the requirements of the Hairy–Downy model. In summary, it is possible that mimetic appearance to provide multiple social advantages, and thus to be under simultaneous natural selection for multiple deceptive functions. Further research will be required to see whether *Accipiter* species are deceived by cuckoo mimicry.

Another example of the possibility of multiple, simultaneous mimetic mechanisms involves the mimicry of noxious, kleptoparasitic skuas and jaegers by the smaller Kermadec Petrel *Pterodroma neglecta*. Spear & Ainley (1993) document that the *P. neglecta* benefits directly from deceiving their models, as predicted by ISDM. Skuas and jaegers to not attack one another, and *P. neglecta* avoid all kleptoparasitic attack from skuas and jaegers as well. However, Spear & Ainley also propose that the white wing patches of skuas and jaegers have evolved to advertise their aggression and dominance to the birds that they attack. They further propose that *P. neglecta* also benefits from having this convergent plumage signals through a quasi-Müllerian mechanism that increases the efficiency of the petrels own kleptoparasitic attacks on other species. Spear & Ainley (1993) clearly document that *P. neglecta* mimics both the appearance and behaviour of skuas and jaegers supporting the existence of ISDM, but they do not present a clear, explicit mechanism for the evolution of their proposed '*Resistance is Futile!*' plumage signals by skuas and jaegers to the species they attack. Further, Spear & Ainley (1993) do not explain why the wing patches of skuas and jaegers are so obviously, observably size-graded. According to their hypothesis, small jaeger species should benefit from mimicking the larger, bolder wing patches of larger, more threatening, and socially dominant skuas, which they do not. Lastly, they did not report on the frequency and success rate of kleptoparasitism by other, similarly sized *Pterodroma* species that *lack* the mimetic white wing patches of *P. neglecta*. Such data would permit their hypothesis of an additional function of this plumage signal to be tested. In conclusion, Spear & Ainley (1993) provide direct evidence of ISDM in the interactions of these wild bird species, but this complex may have also evolved by additional selective forces involving mimetic deception of other, third parties.

Another potential case of avian ISDM was not included in this sample (Table 1), because available natural history information does not support it. *Surniculus* drongo-cuckoos (30–43 g; Cuculidae) have a strong resemblance to sympatric drongos (40–90 g; Dicruridae) with glossy black plumage and slightly forked tails. Payne (2005) was skeptical that these plumage similarities are mimetic because of a mismatch in geographic variation in the two clades. Further, drongos are aggressive generalists showing dominant social interactions with a wide range of other birds. So, as in *Cuculus* and *Hierococcyx* cuckoos, it is possible that *Surniculus* cuckoos could be deceiving their hosts for a reproductive advantage, and deceiving drongos through ISDM for an ecological advantage, or deceiving multiple, additional species about their noxious status and gaining an ecological advantage accordingly (as hypothesized by Wallace, 1863, 1869).

I have included the Southern Black Flycatcher *Melaenornis pammelaina* (Muscicapidae) as a proposed ISD mimic of the Forked-tailed Drongo (*Dicrurus adsimilis*). However, recent behaviour evidence indicates that *M. pammelaina* positively associates with *D. adsimilis*, and possibly also with multispecies foraging flocks (Morgan *et al*., 2012). Because this case includes a behaviorally noxious model species and the possibility of frequent interactions with additional species, it may be a good candidate for a classic third-party deception mimicry (Wallace, 1863, 1869).

## NON-MIMETIC PLUMAGE CONVERGENCE BY NATURAL AND SEXUAL SELECTION

Natural and sexual selection can produce convergence in plumage colour and pattern in the absence of any interspecific social interactions or mimicry. For example, the Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*; Icteridae) of open grasslands of North America and northern South America are strikingly similar in plumage colour and patterning to the Yellow-throated Longclaw *Macronyx croceus* (Motacillidae) of African grasslands and savannahs. Both species are striped dark and light brown above with a bright yellow belly and breast and a broad black collar. Obviously, given their evolution on different continents, the similar plumages of these species could not have evolved as a result of any natural selected on deceptive social interactions. Thus, it is possible that such extreme, convergent plumage similarity could evolve among sympatric species as well entirely without any deceptive advantages.

One way to estimate the possible frequency of sympatric convergence by natural selection in the absence of interspecific social interactions would be to identify all the examples of convergent appearance among allopatric species that are non-phylogenetically related. Such a list would include *Sturnella* and *Macronyx*, diving-petrels *Pelecanoides* sp. and the Dovekie *Alle alle*, Ivory Gull *Pagophila eburnea* and Snow Petrel *Pagodroma nivea*, etc. In these diving-petrels, alcids, gulls, and petrels, the plumage similarities are so closely related to adaptive hypotheses that these cases would be unlikely to be proposed as ISDM if they were sympatric. However, the similarities between *Sturnella* and *Macronyx* include highly detailed social signals, so these species would certainly attract attention as a possible example of mimicry if they were sympatric. The total frequency of this type of detailed false-mimetic convergence in social signals among all birds could be used to produce a null model of the general expectation of detailed plumage pattern convergence among sympatric species in the absence of any interspecific social function. This task is outside the scope of this paper, but I would predict that there are many more proposed examples of ISDM in birds than there are counter-examples like *Sturnella* and *Macronyx*. In conclusion, all proposed examples of ISDM should to be further tested for evidence of mimetic deception of the proposed socially dominant, model species.

Convergent plumage similarity may arise through parallel evolution if avian plumage patches are highly modular – i.e. controlled by sets of common regulatory genes that can evolve in the similar ways in response to independent sexual or natural selection. For example, *Icterus* orioles show a prominent pattern of parallel evolution of nearly identical wing bars, tail patches, hoods, and facial patterns among different species within the genus (Omland & Lanyon, 2000). However, these similarities have evolved among oriole species that are frequently allopatric without direct ecological interactions, undermining the likelihood that they evolved to function in interspecific communication and deception.

In an analysis of the convergent plumage similarity between male Black-and-white Tanager *Conothraupis speculigera* and male Black-and-white Seedeater *Sporophila luctuosa*, Witt (2005) proposed that the larger, rarer, and more locally distributed *C. speculigera* is a mimic of the smaller, more common, and broadly distributed *S. luctuosa*. However, given the rather course plumage details shared by *C. speculigera* and *S. luctuosa* and their differences in iris colour (red in male *C. speculigera*, and brown in *S. luctuosa*), I conclude that this is likely to be a case of non-mimetic, convergent evolution of similar plumage colour pattern modules – like *Icterus* orioles – between unrelated species that just happen to be sympatric. If this were a case of mimicry, it would be unlikely to be ISDM.

The plumages of all of the proposed examples of ISDM include some plumage patches, elements, or details that indicate a communication function. Consequently, I did not include several other groups of species that lacked compelling evidence that plumage colour patterns function in communication, such as the convergently black species of Andean thrushes: *Turdus fuscater, T. serranus*, and *T. leucops* (Turdidae). In these cases, it is difficult to argue convincingly that such featureless plumages are not the result of natural selection on other plumage functions. Some cases of proposed mimicry among raptors include largely black species (e.g. among Asian hawks-eagles), however each of these species has also evolved distinctive raised crests, and tail and wing stripes that clearly have a signaling function.

In sub-Saharan Africa, the two species of *Neocossyphus* ant-thrushes have a similar pattern of plumage appearance to the two species of *Stizorhina* flycatcher-thrushes. All four species have olive brown backs, grey crowns, and light rufous bellies. The west African and Central African *Neocossyphus poensis* and west African *Stizorhina finschi* have white outer tails, whereas the central African *N. rufus* and *S. fraseri* have rufous outer tails. I rejected the proposed hypothesis of mimicry between *Neocossyphus* and *Stizorhina* (Ziegler, 1971) because these two genera are sister taxa (Pasquet *et al.*, 1999). Thus, it is quite possible that their plumage similarities are homologs, and that there has been some slight convergent evolution in tail coloration due to natural selection. However, consistent with ISDM, *S. finschi* and *S. fraseri* are each substantially smaller in body mass (37 and 36 g, respectively) then are *N. poensis* and *N. rufus* (52 and 66 g, respectively). These body size differences could provide *Stizorhina* with an opportunity for interspecific, socially deceptive mimicry. Additional field work is required to establish whether interspecific interactions may have been important in the evolution of plumage coloration patterns in this clade.

The *Sturnella* meadowlarks and the *Macronyx* longclaws include multiple species that are *not* convergent in plumage coloration. However, multiple proposed examples of ISDM consist of clades with substantial, convergent plumage similarities among multiple sympatric species pairs – including the yelping and croaking clades of *Ramphastos* toucans; *Campephilus* and *Dryocopus* woodpeckers; racket-tailed and racketless subspecies of *Baryphthengus* and *Electron* motmots; friarbirds and orioles; and tyrant flycatchers (*Leptopogon, Pogonotriccus, Phyllomyias*, and *Myiornis*). Even in the absence of detailed data on interspecific social interactions among these clades, it is fair to say that there are no examples among all birds of the world of similarly detailed convergent radiations among *allopatric* species. This observation supports the conclusion that these radiations are unlikely to be caused by massively parallel natural selection on environmental functions of plumage coloration, and are likely to be coevolved radiations among socially interacting species.

Natural selection on environmental functions of plumage coloration can act simultaneously with natural selection on the interspecific social functions of plumage coloration. For example, one model-mimic pair shows correlated geographic variation in pigmentation that are congruent with Gloger's rule – the hypothesis that animal pigmentation tends to be darker in more humid regions of the distribution. Hairy (*Picoides villosus*) and Downy (*P. pubescens*) Woodpeckers show a strong pattern of congruence with Gloger's rule. Populations of both species from the humid, coastal Pacific Northwest of North America are conspicuously darker brown and less whitish. This geographic variation in plumage coloration is likely to be the result of convergent natural selection on plumage function, but it is important to note that Downy mimics would also be favored to coevolve these same plumage colours by natural selection to maintain deceptive similarity with the Hairy model. In this case, natural selection in Downy is likely to be acting simultaneously on plumage function in various environments and on the maintenance of deceptive interspecific social function. However, Gloger's Rule is still insufficient to explain the detailed plumage pattern shared between, and independently derived in, these two species; it is only relevant to the variation in whiteness vs. brownness of their belly coloration. Given the phylogenetic pattern of convergence across the entire plumage, Gloger's Rule does not make it more difficult to identify possible ISDM in these two species.

## DISCUSSION

Previous reviews of mimicry provide little insight into the question, 'Why should mimicry evolve between unrelated, non-aposematic, non-brood-parasitic species?' (Wickler, 1968; Ruxton *et al*., 2004). Rainey & Grether (2007) discussed mimicry between ecological competitors, and called for further research into the possible mechanisms for its evolution. Recently, Prum & Samuelson (2012) proposed an explicit mechanism of ISDM, and supported its evolutionary plausibility with the Hairy–Downy game. In ISDM, a subordinate species evolves to mimic and deceive a dominant species into misidentifying the mimic as an individual of the dominant species, and thus overestimate its size and the costs of aggression.

It has been clear for more than a century that some evolutionary explanation was required for the evolution of non-aposematic, non-brood parasitic avian mimicry. However, all previously proposed mechanisms are notably lacking detailed evolutionary mechanisms (Wallace, 1863, 1869; Newton & Gadow, 1893–96; Moynihan, 1968; Ziegler, 1971; Cody, 1973; Barnard, 1978; Diamond, 1982; Pough, 1988; Caro, 2005; Witt, 2005). None of these hypotheses has been strongly supported by evidence from any group of species. Many of these hypotheses are also particularly narrow in application. For example, Osbert Salvin's (Newton & Gadow, 1893–96) proposal of mimicry of a smaller species by a dominant one only applies to raptorial predators. Cody's (1969, 1973) proposal of adaptive interspecific territoriality neglected to consider that mutual interspecific territoriality is unlikely to be evolutionarily sustainable between competitive species pairs in which one species is *twice* the body mass of the other. Why should a species convergently evolve to tolerate a competitor species that it can easily dominate physically? In rejecting mimicry as an alternative to mutually beneficially, convergent similarity, Cody did not consider the possibility that mimics gain an advantage by deceiving their models. Thus, Cody's hypothesis remains weakly formulated.

In contrast, the Hairy–Downy game establishes the quantitative predictions for the ecological conditions favoring the evolution of mimicry of a socially dominant species by a subordinate species. ISDM also has the potential to explain a large number of examples of convergence in avian plumage coloration and patterning. The Hairy–Downy game establishes the conditions for evolutionarily stable equilibria between subordinate mimicry and dominant aggression in terms of the costs of aggression and mimicry, the value of the contested resources, and the relative density of the two species. Because mimics function like doves of the dominant species, the existence of mimics will create a coevolutionary feedback on the Hawk–Dove equilibrium within the dominant species, increasing the fitness of the aggressive hawk strategy, and lowering the fitness of both the dove and mimic strategies. It may seem that dominant species should be more aggressive to conspecifics, which are stronger direct competitors, than to smaller species which are weaker competitors and smaller ecological threats to fitness. However, the Hairy–Downy game demonstrates that intraspecific aggression within the dominant species will be constrained by the costs of aggression. Thus, the costs of aggression within the dominant species create the opportunity for social deception by smaller mimetic species.

Data on avian visual acuity support the sensory plausibility of visual ISDM in birds at ecologically relevant distances. Most bird species lack extensive stereopsis, especially at longer focal distances. Therefore, they must rely on pictorial information to assess the identity, size, and distance to objects within their visual fields, including other individual birds. Thus, several structural features of avian visual systems make the optical illusions necessary to achieve ISDM more likely. Birds vary in visual acuity by at least an order of magnitude, but visual modelling implies that ISDM would be effective in pigeons at distances greater than 2–3 metres.

Visual ISDM appears to be relatively common in birds, and encompasses a great variety of body sizes, habitats, diets, and foraging modes. The general relationship between body mass of mimics and their models is highly linear over three orders of magnitude. On average, mimics have 56–58% of the body mass of their models. Would such a result be expected from random pairs of bird species? Several null models analyzed above predict that the distributions of the body mass ratios of random pairs of species within a clade will have a general or local peak near one. The body mass ratios of the proposed mimic-model pairs show no such peak, whereas data sets generated from random pairs of species from two diverse families – woodpeckers and tyrant flycatchers – exhibited the predicted, null peaks near 1 (Fig. 5).

Body size is well understood to be a critical determinant of social dominance in interspecific interference competition in birds (Wolf *et al.*, 1976; Ford, 1979; Mauer, 1984; Alatalo *et al.*, 1985; Minot & Perrins, 1986; Alatalo & Moreno, 1987; Robinson & Terbourgh, 1995). The difference in body mass between the proposed ISD mimics and models is strikingly large. By comparison, human boxing weight classes, which are designed to insure a fair competition, differ by increments of only 2.5–4.5% of body mass. Like boxing weight classes, small differences in body mass between bird species provide a decisive physical advantage in direct, interference competition. For example, Milikan, Gaddis & Pulliam (1985) found that an average body mass difference of 8% between larger *Junco caniceps dorsalis* and smaller *J. c. caniceps* (Emberizidae) provided *dorsalis* with 98% success rate during in aggressive encounters in wintering flocks ($n = 111$ observations). Likewise, body mass differences of ~20% between Coal and Marsh Tits (Paridae) provide Marsh Tits with decisive social advantages during interspecific foraging interactions that have real impacts on Coal Tit foraging efficiency (Alatalo & Moreno, 1987). Thus, small body mass differences create overwhelming advantages in avian interference competition.

Clearly, all of the proposed avian ISD mimic species are vastly inferior physical competitors than their proposed model species. However, the observed differences between avian mimic and model species in body mass are consistent with a relatively modest reduction of ~18% in linear body dimensions: i.e. $(0.8242)^3 = 0.56$. Thus, a relatively small linear size discrepancy of ~18–20% is still small enough to plausibly create visual identity confusion, but it can simultaneously produce an enormous potential advantage to social deception by a smaller, physically subordinate, species. Thus, the opportunity for social deception by visual ISDM arises purely from the manner in which body mass scales with body size. This discrepancy can create a huge potential social advantage to those subordinate species that can exploit it through visual deception.

Why don't smaller species evolve to become larger so that they can win interference competition? One reason is that there can be energetic efficiencies to small size. In both tits (Alatalo & Moreno, 1987) and hummingbirds (Wolf *et al.*, 1976), smaller species expend less energy in foraging, and are able to forage more efficiently than their larger bodied competitors. Thus, there is a trade-off between the social advantages and energetic costs of large body size. ISDM is an evolutionary mechanism by which small species can deceptively expand the benefits of smaller body size without paying the additional energetic and physiological costs of being larger.

Given the fitness costs of mimicry to the socially dominant species, natural selection should act on models to differentiate from their mimics, and on the mimics to maintain deceptive similarity to their models. This process may create an antagonistic coevolutionary arms race in appearance between models and mimics. If the model and mimic are broadly distributed, the result may be a coevolutionary radiation among different isolated populations or species of models and mimics.

A pattern of antagonistic coevolutionary radiation through ISDM in birds is substantially supported by several, independent cases of phylogenetic coradiation among multiple species or populations of proposed mimics and models: including yelping and croaking clades of *Ramphastos* toucans; *Campephilus* and *Dryocopus* woodpeckers; racket-tailed and racketless subspecies of *Baryphthengus* and *Electron* motmots; friarbirds and orioles; and tyrant flycatchers (*Leptopogon, Pogonotriccus, Phyllomyias*, and *Myiornis*). There is also substantial evidence of coevolved, avian mimicry complexes: including kiskadee-type flycatchers from six genera, eared tyrannulets from four genera, and dark M-wing patterned petrels from four genera. These mimicry complexes appear to be the result of coevolutionary entanglement among multiple species mimicking the same models and each other. In addition to plumage similarities, avian ISDM may also involve behavioral mimicry. Model *Leptopogon* species perform nervous wing flicking behaviour, which is mimicked by several mimetic species of *Pogonotriccus* and *Phyllomyias* tyrannulets.

These proposed examples may underestimate the frequency of antagonistic coevolution by ISDM. In the absence of speciation or geographic differentiation in the model, or multiple independent lineages of mimics, it may be hard to identify a history of antagonistic coevolution in appearance between a single pair of model and mimic species. For example, the Hairy Woodpecker *P. villosus* has a distinct plumage pattern from other *Picoides*, but it is difficult to discern whether the Hairy's distinct plumage features evolved completely prior to the evolution of mimicry by Downy, or in coevolutionary response to it (Fig. 1). Likewise, it is unknown whether the Greater Yellowlegs *Tringa melanoleuca* evolved its plumage pattern and yellow leg colour prior to, or in response to, the evolution of mimetic coloration by the Lesser Yellowlegs *T. flavipes* (Fig. 3E–F). Thus, when a single mimic parasitizes a single model, and both species are distinct in appearance from their nearest relatives, it can be difficult to document evidence of coevolution.

The coevolutionary predictions of Hairy–Downy game provide an opportunity to test the alternative hypotheses of Wallace (Wallace, 1863, 1869; Diamond, 1982) and Salvin (Newton & Gadow, 1893–96: 572–575) about the evolution of non-aposematic mimicry for deception of third parties. If a smaller species mimics a larger species in order scare away other small ecological competitors (Wallace, 1863, 1869), there are no fitness costs to the model species, and therefore no prediction of coevolutionary differentiation between model and mimic. Similarly, no fitness costs to the model are expected if a larger species evolved to mimic a smaller species in order to sneak up on its prey undetected (Newton & Gadow, 1893–96). Thus, the substantial evidence of coevolutionary radiation in several clades of avian mimics and models falsifies the third-party hypotheses of avian mimicry.

An interesting prediction of ISDM is that coevolved phenotypic features are predicted to be essentially arbitrary – i.e. they are not likely to evolve to encode comparative, intraspecific information about variation in genotypic quality or condition, etc. (Prum, 2010). For a model species, derived phenotypic features that help evade mimicry will evolve through natural selection to distinguish itself from its mimics. Such traits will necessarily be arbitrary, because they will have to evolve away from any prior intraspecific signal of quality which has been duplicated by a mimic. For a mimic species, all phenotypic details that foster mimetic similarity are necessarily intraspecifically arbitrary, because they coevolve to match the details of the model species, and not to track intraspecific phenotypic or genetic quality variation. Although the antagonistic coevolutionary arms race in appearance is entirely adaptive, these specific changes in appearance are frequency dependent, interspecific, *social adaptations*, which are unlikely to correspond with any other extrinsic, environmental variables. Rather these features evolve through their function in the subjective sensory experiences and cognitive evaluations of other individuals (Prum, 2012). Consequently, such phenotypic traits are less constrained than other typical adaptations that have physical functional substrates. There is a finite set of ways in which a bird beak can crack open a seed, or haemoglobin can bind an oxygen molecule; but, the number of ways in which a model species can evolve to be visually distinguishable from a mimic is much greater and less constrained.

Thus, the phylogenetically rapid radiation in throat, rump, facial skin, beak coloration, and beak colour patterning among the yelping and croaking clades of *Ramphastos* toucans (Weckstein, 2005) likely constitutes an *arbitrary radiation* in phenotypic signals– i.e. an aesthetic arms race. Likewise, other coevolved mimicry systems are also likely to foster the evolution of arbitrary signals that lack information about individual condition or quality, whether they evolve in response to brood parasitism (e.g. egg colour and coloration pattern (Stoddard & Stevens, 2010) and nestling mouth patterns (Sorenson, Sefc & Payne, 2003; Langmore *et al*., 2011), Müllerian, or Batesian mimicry. By accelerating evolutionary change in the components of the phenotype that function in social interactions, coevolutionary radiation between mimics and models may ultimately foster a form of adaptive speciation in which model populations are driven to diverge from one another by natural selection to evade ISDM. It is interesting to note that *Ramphastos* toucans are evolving very rapidly in phenotype (Weckstein, 2005); it would be interesting to examine whether these phenotypic changes contribute to *Ramphastos* model species isolation (Haffer, 1974).

Examples of ISDM have likely gone unrecognized because the default explanation of close similarity in appearance is homology due to common ancestry. In the absence of aposematic function, explicit phylogenetic evidence of convergence, or the concept of ISDM, phenotypic similarity among ecological similar species that differ in body size has been parsimoniously ascribed to homology. Given our rudimentary progress on establishing the full, species-level phylogeny of life, striking convergence in appearance between non-aposematic organisms may be much more common than we currently realize.

Some examples of ISDM may have been overlooked because the animals themselves are so poorly known. For example, the Grey-bellied Goshawk *Accipiter poliogaster* is a very poorly known Neotropical bird, and its mimetic juvenal plumage is even less well appreciated. Even more poorly known is the proposed case of ISDM between two extinct species of the Hawaiian avifauna. The Hawaii Mamo *Drepanis pacifica* (Drepaninii, Fringillidae) appears to have been a very striking mimic of the Hawaii Oo *Moho nobilis* (Mohoidae). Both species are black with brilliant yellow patches on the undertails and on the sides of the breast. However, just like the convergent white back stripes of the New World *Campephilus* and *Dryocopus* woodpeckers, the feathers that contribute to the convergent yellow patches in the two Hawaiian species are produced by different feather tracts. The yellow side patches are made of elongate lateral breast feathers in *Moho* and axillary underwing and epaulette feathers in *Drepanis pacifica*. The species differ only in the presence of a yellow rump in *D. pacifica*, and a longer tail in *M. nobilis*. Similar plumage was shared by multiple *Moho* species on different islands, but the mimetic *D. pacifica* was only found on Hawaii. The feathers of both species were heavily exploited for native Hawaiian feather art, and are virtually identical in colour. Likely, the dearth of natural history information about these extinct species delayed the appreciation of their striking, convergent similarity in plumage.

Multiple communication functions of plumage coloration and coloration pattering may constrain the evolution of ISDM. In many species, intraspecific sexual and social selection on plumage coloration and patterning for intraspecific communication may be strong enough to completely prevent the evolution of mimic phenotypes (Prum & Samuelson, 2012). Any other naturally or sexually selected advantages to plumage coloration constitute potential costs to the evolution of mimicry. Thus, the origin of ISDM and any subsequent coevolution between model and mimic may be constrained if phenotypic appearance of either species is under pleiotropic selection for other intraspecific sexual or social signaling functions. This constraint may explain why ISDM is not even more common in birds. Furthermore, ISDM may be less likely to evolve among species that have elaborate intraspecific social or sexual signals, like lekking species. Following the evolutionary origin of ISDM, the rate of antagonistic coevolutionary morphological diversification may also be constrained by strong sexual or social selection in either the model or the mimic species. If the same signals that have evolved to be mimicked by the subordinate species are under strong sexual or social selection in the model, that will constrain the rate at which the model species can adaptively diverge from the mimic.

ISDM may also be less likely to provide social advantages when populations are in a stable 'social equilibrium' among a set of resident, heterospecific individuals with fixed territories, because consistent, repeated social interactions among specific individuals may result in an individual of the model species learning to recognize an individual in a specific territory as a mimic. This could lead to expanded aggression by the model, increase in the costs of mimicry, and to the loss of mimetic effectiveness. Thus, ISDM may be more common in non-territorial species, in species with seasonal variation in territoriality, or in species with high enough densities that most social interactions do not take place in predictable places between the same individuals.

## ADDITIONAL TESTS OF INTERSPECIFIC SOCIAL DOMINANCE MIMICRY

The data analyzed here provide initial proposals and preliminary tests of hypotheses of ISDM in birds. These proposals should be investigated further through natural historical, ecological, experimental, and phylogenetic analyses of the ecological, aggressive, and deceptive interactions among these species. The Hairy-Downy game provides explicit predictions for the conditions leading to the origin and stable maintenance of ISDM. Hypotheses of ISDM in birds should be tested with primary natural history observations confirming that: (1) the two species are syntopic, (2) utilize codistributed ecological resources, and (3) engage in interspecific social interactions. Because the ISDM hypothesis is novel, such data have not been specifically gathered or analyzed in this fashion for any of the proposed model-mimic species pairs. However, some current ecological data support the plausibility of the mechanism. For example Kisiel (1972) found substantial ecological overlap in feeding substrates between Hairy (*Dendrocopos* villosus) and Downy (*D. pubescens*) Woodpeckers, and documented aggressive displacement of Downys by Hairys on several occasions. Furthermore, Spear & Ainley (1993) document that the mimetic *Pterodroma neglecta* avoids kleptoparasitic attack from its models – skuas and jaegers.

Hypotheses of ISDM can be tested ecologically and behaviorally through comparative examination and experimental manipulations of the parameters incorporated in the Hairy-Downy game (Prum & Samuelson, 2012). These parameters include: (1) the relative background fitness of the subordinate and dominant species in absence of interspecific social interactions, (2) the values to each species of the spatially codistributed resources that are subject to interspecific competition or competitive exclusion, (3) the costs and frequency of aggression in the dominant species, (4) the costs and frequency of mimicry in the subordinate species, and (5) any social advantage of mimetic phenotypes over an non-mimetic phenotype within the subordinate species. I will discuss these alternatives in sequence.

Relative background fitness excluding interspecific social interactions could be examined through natural or manipulated exclusion experiments. The fitness values of the codistributed resources used by each species could be estimated from descriptions of diet and space use of both species. In some species, these parameter values could be experimentally manipulated with the use of feeders that differentially exclude one species or the other. However, significant dietary differentiation between species is not evidence of a lack of spatio-ecological competition. For example, social dominance may allow a species to exclude a subordinate species based on competition for a resource that is a small component of the subordinate species diet, but is of high value to the dominant species. Likewise, social exclusion may have a large impact on the fitness of the subordinate species even if the most critical resource to the subordinate is not specifically utilized by the dominant species. At its most extreme, the resources pursued by a model species could include the model species itself. In other words, species that mimic raptors may evolve mimicry in order to avoid predation on themselves. (This situation fits the definition of codistributed resources because a prey species is always codistributed with the resources it pursues.) Thus, there may be substantial or even complete dietary differentiation between two species, but there may still be selection on subordinate species to mimic a dominant species.

The cost of intraspecific aggression within the dominant species will be difficult to measure directly. Low frequency of aggression could indicate a lack of competitive conflict, but low frequency of aggression may also indicate high costs of aggression. Interestingly, ISDM will raise the fitness benefits of aggression and increase its frequency beyond the standard threshold of the traditional intraspecific Hawk–Dove equilibrium. This prediction gives rise to some opportunities to test the ISDM mechanism by comparisons of frequencies of intraspecific aggression within the dominant, model species between locations where it exists with and without a sympatric mimic. Interestingly, it is important to realize that under some of the conditions that favour mimicry, we should also expect aggression to be rare. For example, increases in the cost of aggression within the dominant species will lower the frequency of aggression and raise the fitness advantages of mimicry. Given that wild populations may be in equilibrium, the low frequency of social aggression is not necessarily evidence against the possible existence of interspecific social conflict and ISDM. Likewise, the costs of mimicry are also difficult to measure, but are expected to be quite low under many circumstances (Prum & Samuelson, 2012).

Some previous observations of dominance interactions between models, mimics, and other species in the wild provide some data on the impact of mimicry on interspecific social interactions. For example, Diamond (1982) reported observations of the frequencies of physical displacement of mimetic orioles and other frugivores by socially dominant friarbirds that support ISDM. However, aggressive interactions do not have to be frequent for them to have a decisive ecological and evolutionary impact. For example, in Marsh Tits and Coal Tits, aggressive attacks were rare even though Marsh Tit dominance due to body size strongly structured the ecology of the smaller, subordinate Coal Tit (Alatalo & Moreno, 1987). The important impacts of relatively rare social events on organismal niches may make tests of the role of aggressive encounters more challenging.

Rainey & Grether (2007) suggest that the main challenge for interspecific mimicry between ecological competitors is confirming that model species are deceived. Behavioral experiments to test mimetic deception specifically by creating experimentally altered, distinguishable non-mimetic forms and mimetic controls, and following whether these experimental phenotypes suffer a greater frequency of aggression or displacement by the socially dominant model species.

Lastly, data on visual acuity of proposed model species, observations of the distribution of the distances of first social encounters, measurements of visual sight line distances in natural habitats, and measurements of the detailed similarities between models and mimics would permit further evaluation of the psychophysical efficacy of visual deception between specific pairs of model and mimic species. An implication of this analysis is that ISDM is predicted to evolve more frequently in species that occupy open habitats that afford longer open sight lines. In more open habitats, social encounters are more likely to be initiated at distances large enough for the visual system to rely more on visual pattern information and object identification to evaluate size and distance. However, ISDM remains plausible for smaller species in more closed habitats in which social encounters are more likely at closer distances.

With detailed measurements of all parameter values, one could also compare the frequencies of dominant and mimetic strategies to the quantitative predictions of the Hairy–Downy game (Prum & Samuelson, 2012). It is important to note that unlike many examples of deception of third-party predators which learn about an aposematic signal through experience, higher frequencies of ISD mimics than models in a community *can* be evolutionary stable under many realistic conditions (Prum & Samuelson, 2012). There is no simple prediction about relative frequency of the mimics and models in ISDM.

## THE POSSIBILITY OF ACOUSTIC ISDM

Birds are highly vocal, and vocal cues are often used in intraspecific and interspecific social interactions [In this context, I am not referring to the well known cases of vocal mimicry by mockingbirds (Mimidae), mynahs (Sturnidae), lyrebirds (Menuridae), Lawrence's Thrush (*Turdus lawrencei*, Turdidae), etc., in which vocal mimics incorporate songs and calls of ecologically completely unrelated species into their complex, and diverse vocal repertoires. In such species, vocal mimicry is immediately identifiable as a heterospecific acoustic collage of many unrelated social signals. These species are more likely to have evolved their vocal mimicry through: (1) female choice for larger repertoires, and (2) evolutionary truncation of the development of vocal song learning to a stage of open-ended social learning (i.e. vocal learning neoteny) (Irwin, 1988)]. In principle, vocal ISDM between species with big differences in social dominance could evolve to function in an equivalent manner to visual ISDM with perhaps a few distinctive constraints. Two of these constraints would be individual vocal complexity, and consistent territorial residency (see above). In many species of birds, particularly oscine passerines, vocal variation is so extensive that each individual is distinctive and vocally recognizable. In such species, any single social interaction that allows the dominant model to detect the size discrepancy and subordinate social status of the mimic will lead to a permanent loss of social effectiveness of mimicry between these two individuals.

Therefore, vocal ISDM may not highly effective in species in which there is substantial capacity for individual vocal recognition. In contrast, ISD mimics will not be individually recognizable by their plumage appearance at the distances over which there is a likelihood of size confusion. So, one encounter between a visual mimic and its model will lead to permanent loss of mimetic function between those individuals. This constraint on the evolution of vocal ISDM should be particularly acute in mimic and model species that maintain consistent territories which give rise to repeated social interactions among stable neighbours. Territorial mimics would soon be identified as known subordinate individuals by their dominant species neighbours, and vocal mimicry would again loose its deceptive effectiveness.

Identifying, proposing, and testing examples of vocal ISDM would require an entirely different study, but I will present several plausible cases. For example, in the Neotropics, the Little Tinamou (*Crypturellus soui*) has evolved to be vocally very similar to the Great Tinamou (*Tinamus major*), even though it is approximately one-fifth of the body mass of its model. Given the phylogenetic distance between the species, the vocal diversity of their many close relatives, and the extreme similarity of their vocalizations in frequency, structure, and temporal pattern, this appears to be a good example of vocal convergence and possible vocal mimicry. Although these species are vocally distinguishable by trained observers from their acoustic quality (e.g. the smaller *C. soui* sounds sweeter and less resonant), vocal identity confusion between the species may be quite likely at greater distances with signal attenuation in the forest.

Alternatively, the primary (i.e. mate attraction) songs of Blackburnian (*Setophaga fusca*), Cape May (*S. tigrina*), and Bay-breasted Warbler (*S. castanea*) are quite distinct, but the secondary (i.e. territorial) songs of these three species are extremely similar and very difficult to differentiate (R. O. Prum, pers. observations). Since all three species breed microsympatrically in boreal forests of North America, it is plausible that the intrasexual, territorial functions of their secondary songs has converged on a similar acoustic structure to achieve interspecific territoriality. Blackburnian and Bay-breasted Warblers have been identified as sister taxa, but Cape May Warbler is only distantly related to them (Lovette *et al*., 2010). Thus, vocal similarity between Blackburnian and Bay-breasted Warblers may be homology, but the similarity of Cape May Warbler to the other two is a clear instance of vocal convergence. These three species are essentially identical in size, so this case appears to be more similar to the conditions for the convergent evolution of intra-interspecific communication efficiency, as hypothesized by Cody (1969), than a mechanism of vocal ISDM.

However, the possibility of vocal ISDM or other mechanisms vocal mimicry in birds cannot explain the existence of the extremely detailed and frequently coevolved examples of convergent similarity in *visual* appearance that are analyzed here.

## ISDM IN FISHES

It would be interesting to look for ISDM in other animals with high visual acuity, complex visual-social signaling, and long open sight line distances during social and ecological interactions. Prime possibilities for ISDM include coral reef fishes, some fresh water fishes, and desert lizards. As in birds, body size in fishes is known to play a decisive role in determining dominance interspecific interference competition (Nakano, 1995). Furthermore, the absence of extensive stereopsis in fishes requires that they use pictorial information to assess the size and distance to any particular object in their visual fields. This predisposes them to be deceived by visual colour pattern mimicry.

There is ample evidence of interspecific mimicry in fishes, but little consensus on the evolutionary mechanisms that support it. For example, Eagle & Jones (2004) report nineteen different cases of intergeneric and interfamilial colour pattern mimicry in coral reef fishes. Eagle and Jones classify five of these examples as non-toxic Batesian mimics of toxic model species, but the majority were classified as ‘aggressive’ mimics that attempt to deceive prey or host species about their identity to increase feeding opportunities. Eagle and Jones presented observations of ecological association between a model pygmy angelfish *Centropyge vroliki* and mimetic juvenile individuals of the surgeonfish *Acanthurus pyroferus*. They concluded that juvenile *Acanthurus* mimic *Centropyge* in order to reduce aggression from a third, larger, territorial species of damselfish, *Plectroglyphidodon lacrymatus*. Thus, Eagle and Jones propose that mimicry has evolved to deceive an ecological competitor rather than a predator, but they still hypothesize that this competitor is a third party, and not the model species itself. Interestingly, Rainey (2009) was unable to confirm this third-party deception mechanism for a population of *Acanthurus pyroferus* in French Polynesia, in which juveniles mimic a different species of pygmy angelfish, *Centropyge flavissima*. Rainey concluded that there may be geographic variation in mimicry mechanism. However, the possibility of ISDM has not yet been examined in any fishes; smaller juvenile *Acanthurus* surgeonfish may be mimicking various species of larger *Centropyge* pygmy angelfishes to avoid aggression. The fact that mimicry is restricted to smaller, juvenile individuals of *Acanthurus*, and that larger adults have their own distinct appearance, is congruent with the predictions of ISDM.

Like Diamond (1982), Eagle & Jones (2004) briefly raise the possibility that smaller *Acanthurus* are mimicking larger *Centropyge* to avoid attack by them, but Eagle and Jones conclude that 'this mechanism does not fall within the traditional framework of mimicry theory, and requires further investigation'. The Hairy–Downy game has confirmed the efficacy of this evolutionary mechanism, and future investigations should test the predictions of ISDM in coral reef fishes. Unfortunately, because ISDM has not been considered seriously, previous analyses of coral reef mimicry system have not yet reported the relative body size and aggressive interactions between the mimics and models themselves (e.g. the relative body sizes of sympatric *Centropyge* and *Acanthurus* species when *Acanthurus* switch away from mimicry to develop their own species specific coloration pattern). In addition, just as yelping and croaking *Ramphastos* have coevolved in appearance across the Neotropics, this fish system indicates the possibility of coevolution among mimic and model populations. *Centropyge* models and *Acanthurus* mimics may have radiated in appearance among various islands because of natural selection on the model to evade the fitness costs of mimicry and on the mimics to maintain the advantages of mimicry. The differentiated mimetic populations of *Acanthurus pyroferus* may not be recognized as separate species because the non-mimetic adults are not under adaptive natural selection to coevolve their appearance with populations of *Centropyge*, as the juveniles are. Thus, there may be an interaction between ISDM, speciation, and coral reef fish taxonomy. The ISDM hypothesis in coral reef fishes could be tested experimentally in the same manner as suggested above for birds.

In Neotropical freshwater river systems, Alexandrou *et al*. (2011) documented a diverse mimicry complex involving multiple lineages of Neotropical corydoradine catfishes, in which 2 or 3 sympatric species converge on one or a few very similar body pigmentation patterns in different river drainages. Alexandrou *et al*. propose this radiation as a Müllerian mimicry complex because corydoradine catfishes have spiny armour and produce an axillary gland toxin. However, many of the catfish colour patterns are quite subtle– arrays of simple black dots or bars– and lack bright, classically aposematic colours. So, it is not clear that these colour patterns function in aposematic communication to their predators. Further, Alexandrou *et al*. (2011) document that the coevolved mimicry groups always include fishes with substantial variation in body size, which is not explicitly predicted among Müllerian mimics. They interpret this diversity as ecological character displacement which stabilizes Müllerian mimicry.

Alternatively, the possibility exists that these colour patterns are not communicating toxicity to predators, but that these fishes constitute an ISDM complex within a guild of ecological competitors – like the kiskadee-type flycatchers. Alexandrou *et al*. (2011) document substantial differentiation between sympatric mimic pairs in ecomorphology and trophic level. As discussed above, however, substantial niche differentiation between species does not exclude the possibility of ecological interference competition that can foster the evolution of ISDM. Thus, the current data are entirely consistent with an ISDM complex. As in coral reef fishes, the ecology, body size, and social interactions among corydoradine catfishes need to be investigated; ISDM should be tested and rejected before corydoradine catfishes can be confidently described as classic Müllerian mimics.

In summary, future research on mimicry in fishes should expand the hypotheses entertained to include the hypothesis of two-party mimicry between ecological competitors with asymmetrical social dominance relationships.

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