VOL. 187, NO. 6 THE AMERICAN NATURALIST JUNE 2016

Mimicry Cycles, Traps, and Chains: The Coevolution of Toucan and Kiskadee Mimicry

Richard O. Prum[1,*] **and Larry Samuelson**[2]

1. Department of Ecology and Evolutionary Biology, Yale University, 21 Sachem Street, New Haven, Connecticut 06520; 2. Department of Economics, Yale University, 30 Hillhouse Avenue, New Haven, Connecticut 06520

Submitted May 31, 2015; Accepted October 6, 2015; Electronically published April 6, 2016

Online enhancements: appendix.

ABSTRACT: Interspecific social dominance mimicry (ISDM) is a form of social parasitism in which a subordinate species evolves to mimic and deceive a dominant interference competitor in order to avoid attack by the dominant species. ISDM has been proposed to result in (1) antagonistic coevolutionary arms races in appearance between the model and the mimic (e.g., *Ramphastos* toucans) and (2) the evolution of complexes of multiple species converging on a common visual appearance (e.g., kiskadee flycatchers). We present evolutionary games of antagonistic coevolution in appearance between pairs and triplets of sympatric species under interference competition. We identify conditions for the existence and stability of (1) coevolutionary mimicry cycles in appearance between evader and pursuer strategies of models and mimics, (2) mimicry chains in which three or more species are coevolutionarily entrained to evolve a single common appearance despite differences in their costs and benefits, and (3) mimicry traps in which a subdominant species is evolutionarily constrained from evading mimicry by a third, subordinate mimic species. Mimicry cycles will result in the evolutionary divergence of models and mimics from their ancestral phenotypes. The hierarchical evolutionary dynamics of ISDM traps and chains resemble Müllerian mimicry with variable costs to toxicity.

Keywords: mimicry, social dominance mimicry, interspecific social dominance mimicry (ISDM).

Introduction

Interspecific mimicry can evolve through natural selection as a means for mimics to avoid attack (Wickler 1968; Ruxton et al. 2004). Commonly, interspecific mimicry functions as a form of communication to a third, nonmodel species, such as a predator. In recent articles, we have proposed a form of interspecific social dominance mimicry (ISDM) in which a subordinate species evolves to mimic the visual appearance of a dominant species in order to fare better in interactions with the dominant species (Prum and Samuelson 2012; Prum 2014). Specifically, Prum and Samuelson (2012) analyzed a new two-species, four-strategy variation of the classic hawk-dove game to explore the evolutionary dynamics of ISDM. Named after the proposed example of ISDM between the dominant hairy and subordinate downy woodpeckers (*Picoides villosus* and *Picoides pubescens*, respectively), the hairy-downy game explored the evolutionary equilibria and dynamics of ISDM between species involved in interference competition for codistributed resources. The game established the evolutionary plausibility of this mimicry mechanism and made both quantitative and qualitative predictions about the process.

Subsequently, Prum (2014) surveyed likely examples of ISDM in birds. Prum proposed 50 phylogenetically independent examples involving 60 model and 93 mimic species from all across the diversity of birds. On the basis of the unusual phylogenetic patterns of covariation in appearance between clades of model and mimic species, Prum (2014) made several distinct coevolutionary predictions.

First, because ISDM produces negative effects on the fitness of the model species, models should come under natural selection to diverge in appearance from their socially parasitic mimics (Prum 2014). 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 is predicted to result in antagonistic coevolution in appearance among models and mimics (Prum 2014). This process will lead to codivergence in appearance of both species from their ancestral phenotypes. Furthermore, 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. Prum (2014) proposed multiple examples of this coevolutionary phenomenon, including the yelping model and croaking mimetic clades of *Ramphastos* toucans (Ramphastidae; fig. 1) and others.

Second, Prum (2014) proposed that an intermediate-sized mimic of a larger, dominant model species may be con-

---

[*] Corresponding author; e-mail: richard.prum@yale.edu.

Am. Nat. 2016. Vol. 187, pp. 753–764. © 2016 by The University of Chicago. 0003-0147/2016/18706-56293$15.00. All rights reserved.
DOI: 10.1086/686093

Figure 1: Examples of coevolutionary radiation between mimic and model clades of *Ramphastos* toucans (Ramphastidae). Larger model species from the yelping clade are on the left, and smaller mimic species from the croaking clade are on the right. *A*, *B*, Chestnut-mandibled toucan *Ramphastos swainsoni* model (*A*) and choco toucan *Ramphastos brevis* mimic (*B*). *C*, *D*, Red-billed toucan *Ramphastos tucanus tucanus* model (*C*) and channel-billed toucan *Ramphastos vitellinus culminatus* mimic (*D*). Mimic species are 55%–58% of the body mass of their sympatric models (Prum 2014). Photo credits: *A*–*C*, Nick Athanas (Prum 2014); *D*, Flickr users Roy and Danielle (CC BY 2.0; https://creativecommons.org/licenses/by/2.0/).

strained from evading mimicry by a third, even smaller, socially subordinate species because the intermediate-sized mimic may be under simultaneous natural selection to maintain the deceptive similarity to their larger, dominant model species. Because of this evolutionary constraint, mimics may be especially vulnerable candidates for deceptive social mimicry by even smaller species. Accordingly, ISDM may create mimetic convergence among multiple sympatric species in a guild of ecological competitors. The result would be the coevolutionary entrainment of multiple species into a quasi-Müllerian mimicry complex of species with a broad range of body sizes. Prum (2014) proposed several dramatic examples of mimicry complexes, for example, the rampant convergence in plumage among nine or more species from five genera of the kiskadee-type flycatchers (Tyrannidae; fig. 2).

Recently, Benz et al. (2015) established a new and unexpected mimicry complex in Neotropical woodpeckers. In southeastern South America live three species of black, white, and red woodpeckers—the robust woodpecker (*Campephilus robustus*), the lineated woodpecker (*Dryocopus lineatus*), and the helmeted woodpecker (*Dryocopus galeatus*). Benz and colleagues discovered that the species *galeatus* is not related to other *Dryocopus* but is embedded within the Neotropical woodpecker genus *Celeus* (i.e., it is *Celeus galeatus*). Although Prum (2014) proposed a *Ramphastos*-like mimicry radiation between model *Campephilus* and mimic

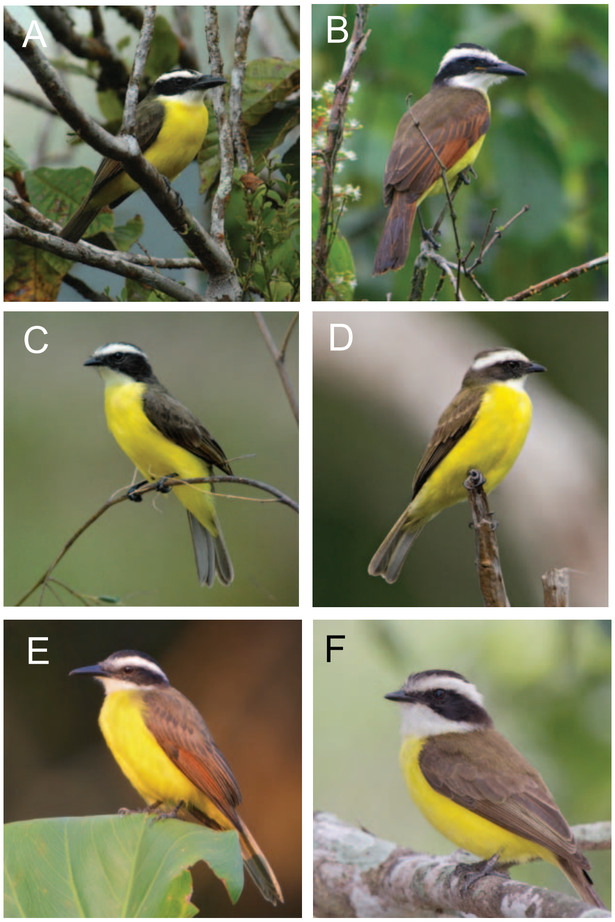


Figure 2: Examples of a mimicry complex among Neotropical kiskadee-type flycatchers (Tyrannidae). *A*, Boat-billed flycatcher *Megarhynchus pitangua* (73 g). *B*, Great kiskadee *Pitangus sulphuratus* (61 g). *C*, Rusty-margined flycatcher *Myiozetetes cayannensis* (25.9 g). *D*, Social flycatcher *Myiozetetes similis* (28 g). *E*, Lesser kiskadee *Philohydor lictor* (25.5 g). *F*, White-throated flycatcher *Phelpsia inornata* (29.4 g). Photo credits: *A*, http://www.1000birds.com/reports_CR_Boat-billed-Flycatcher.htm, by Nick Kontonicolas/www.1000birds.com; *B*, Nick Anthanas (Prum 2014); *C*, © T. J. Ulrich/VIREO; *D*, © G. Lasley/VIREO; *E*, © G. Bartley/VIREO; *F*, © T. Friedel/VIREO.

Dryocopus species, Benz and colleagues discovered that these southeastern South American species constitute a new example of a mimicry complex involving convergent similarity among three unrelated lineages of woodpeckers. Congruent with the predictions of Prum (2014), these three species are hierarchically arrayed in body size: *C. robustus*, 270 g; *D. lineatus*, 210 g; and *C. galeatus*, 128 g (Lammertink et al. 2016).

This article explores Prum's (2014) predictions about the evolutionary dynamics of ISDM. We examine the evolution of antagonistic coevolution in appearance through ISDM between pairs and triplets of sympatric species under interference competition. We identify the evolutionary conditions for the existence and stability of (1) antagonistic coevolutionary mimicry cycles in appearance between model and mimic species, (2) mimicry chains in which three or more species are coevolutionarily entrained to evolve a single common appearance despite their interspecific differences in costs and benefits, and (3) mimicry traps in which a subdominant mimic species is evolutionarily constrained from evading mimicry by a third, subordinate mimic species. We conclude with a discussion of how to test the assumptions and predictions of these ISDM models in the wild.

When introducing the idea of ISDM, Prum and Samuelson (2012) studied the contest for resources in the dominant species as a hawk/dove game while assuming that members of the subordinate species split the resource equally in any encounter. Here, we simplify the analysis by assuming that members of the dominant species also simply split the resource equally.

A Two-Species Community without Mimicry

Our point of departure is a study of an ecological and evolutionary interaction between two species, a dominant species 1 and a subordinate species 2, that engage in direct interference competition for codistributed ecological resources. Pairs of individuals engage in interactions that determine how a resource is to be split between them. The fitness outcomes of such an interaction depend on whether both individuals are from species 1, both are from species 2, or one is from each species, and they are given in table 1. Variables z_1 and z_2 are the background fitnesses of the two species. Background fitness refers to the fitness implications of all activities other than interactions with the other species. When two individuals of species 1 interact, they split the resource in question, which confers an additional fitness of $x_1 > 0$ on each of them. When two individuals of species 2 interact, they also split the resource, which confers an additional fitness of $x_2 > 0$ on each of them. Species 1 is socially dominant. Hence, when an individual of species 1 encounters an individual of species 2, the former takes all of the resource, resulting in a fitness increment of $2x_1$ for the individual of species 1 and a fitness increment of 0 for the individual of species 2.

Table 1: Fitness payoffs in a two-species community without mimicry

	1, dominant	2, subordinate
1, dominant	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1, z_2$
2, subordinate	$z_2, z_1 + 2x_1$	$z_2 + x_2, z_2 + x_2$

We assume that an individual from species 2 fares better than does an individual from species 1 when encountering an individual from species 1, and that an individual from species 1 fares better than does an individual from species 2 when encountering an individual from species 2, or

$$z_2 > z_1 + x_1, \tag{1}$$

$$z_1 + 2x_1 > z_2 + x_2. \tag{2}$$

If these inequalities do not hold, then the two species will not coexist—either one species will strictly (barring knife-edge ties) dominate the other (and hence only one will survive), or there will be two possible asymptotically stable states (under the replicator dynamics), each featuring only one of the two species (plus a mixed configuration that is unstable).

To gain some insight into these conditions, we note that inequalities (1) and (2) imply

$$z_2 > z_1, \tag{3}$$

$$x_1 > x_2, \tag{4}$$

(recall that $x_1, x_2 > 0$). The socially dominant species thus has a lower background fitness but has more to gain from winning the resources. In the "Evidence of Mimicry Chains, Cycles, and Traps" subsection of "Discussion," we explain why we may expect socially dominant species to have lower background fitnesses.

We refer to the population of species 1, to the population of species 2, and to the community that includes both species. We let p_i denote the proportion of the community composed of species *i*. Inequalities (1) and (2) imply that a unique Nash equilibrium and evolutionarily stable strategy exists, with the proportion of population 2 given by $p_2^* = [z_2 - (z_1 + x_1)]/(x_1 - x_2)$ (fig. 3), which is asymptotically stable under the replicator dynamics (see Hofbauer and Sigmund 1988, pp. 127–128).

A Two-Species Community with Mimicry

We now allow for mimics in the subordinate species population that resemble the dominant species 1. We refer to an individual in species 1 as a model and an individual in species 2 as either a mimic or a nonmimic. Fitnesses are given in table 2.

Once again, nonmimics from species 2 surrender the resource in encounters with species 1. Two members of species 2 split the resource, whether mimics or nonmimics. We assume that when a species 2 mimic meets an individual from species 1, the mimic is able to capture enough of the resource to enable a fitness gain of k_{21}, while the fitness of the individual from species 1 increases by $2x_1 - k_{21}$ over its background fitness.[1]

If k_{21} is sufficiently large (satisfying $z_1 + 2x_1 - k_{21} < z_2 + x_2$), then species 1 will be driven out of the community altogether. To see why this occurs, notice that mimics earn at least as high a fitness as nonmimics against every opponent, with mimics obtaining a strict fitness advantage against species 1. Hence, if species 1 were to survive, then nonmimics would be driven out of the community. Once nonmimics are gone, however, the inequalities $z_1 + 2x_1 - k_{21} < z_2 + x_2$, (1), and $k_{21} > 0$ ensure that mimics in species 2 earn a higher fitness than do individuals from species 1, both when encountering individuals from species 1 and when encountering individuals from species 2; hence, species 1 will be eliminated.

We accordingly assume that k_{21} is sufficiently small that both species survive. Thus, $z_1 + 2x_1 - k_{21} > z_2 + x_2$. The interpretation of this condition is that mimics cannot extract such a large share of the resource from models that models fare worse against mimics than do other mimics.

Given that species 1 survives, then mimics have a higher fitness than nonmimics in population 2; hence, the nonmimics will be eliminated from the community, leaving species 1 and mimics in species 2. As a result of mimicry, the proportion of the community that is composed of species 2 increases, and the fitness of both species increases (fig. 4).

How can being deceived by mimics be good for species 1? The average fitness of species 1 has increased, but the proportion of the community consisting of species 1 has decreased. This decrease in proportion is the key to the increase in species 1's fitness. Relatively more of species 1's interactions are now with species 2. While species 1 does not fare as well against mimics from species 2 as against nonmimics, species 1 still fares better against species 2 than against other individuals from species 1 (from the inequalities $z_1 + 2x_1 - k_{21} > z_2 + x_2 > z_1 + x_1$). Meeting species 2 more often (increasing p_2), even if gaining somewhat less each time, pushes the fitness of species 1 upward (increases $(1 - p_2)(x_1 + z_1) + p_2(z_1 + 2x_1 - k_{21})$).

Mimicry Cycles

We now consider a mutant in population 1 that captures all of the resource when interacting with members of population 2 while continuing to split the resource with existing members of population 1. Hence, this mutant has a different appearance from the model, thus inducing mimics to surrender the resource, and can distinguish itself and other mutants as well as the model and the mimic. (In reality, the

---

[1] We might more realistically assume that the mimic captures proportion q of the resource, for a fitness gain to the mimic of $q2x_2$ and a fitness gain to the model of $(1 - q)2x_1$. Doing so alters some of the calculations but leaves the conclusions of our analysis unchanged.

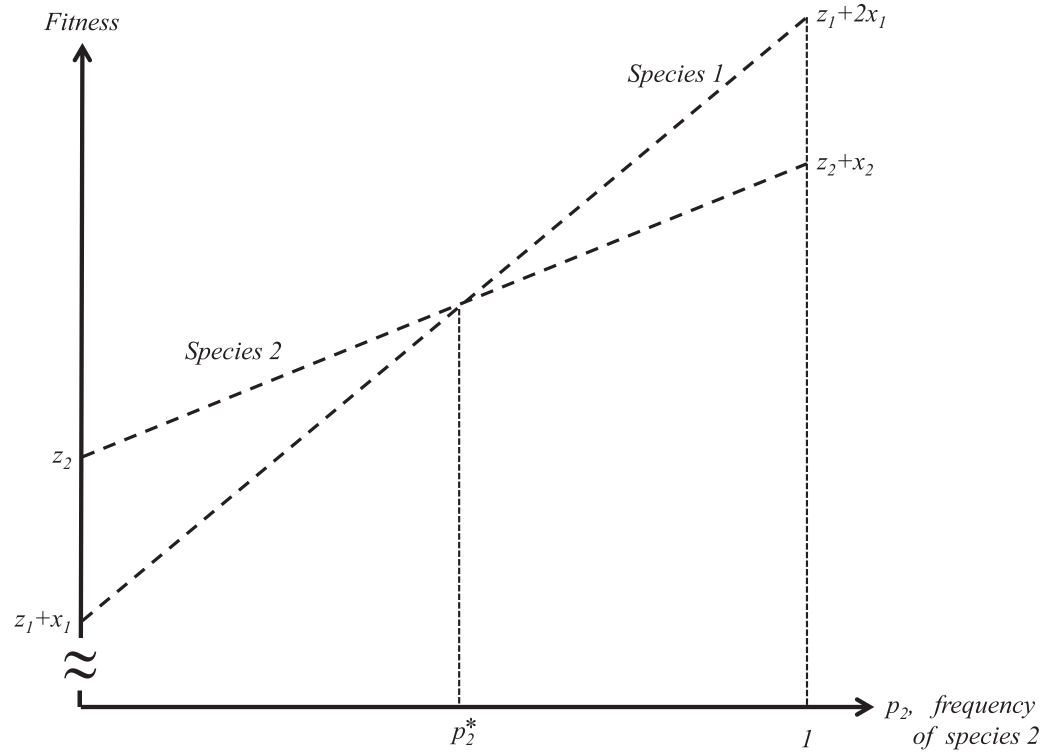


Figure 3: Fitnesses for a two-species interference competition interaction with no mimicry. The functions show the fitnesses of species 1 and species 2 as a function of the proportion of species 2 in the community. The asymptotically stable proportion is $p_2^* = [z_2 - (z_1 + x_1)]/(x_1 - x_2)$.

distinctive appearance and the capacity to recognize that distinctive appearance and distinguish mimics would have to coevolve, and the advantages of the distinctive appearance would be frequency dependent. But that model would require another level of complexity not included in this analysis.) We refer to such mutants as "evaders," since their fitness advantage comes from their ability to evade the fitness loss when encountering a mimic, k_{21}. Fitnesses are given in table 3.

Species 1 evaders will fare better than the original model as long as there are representatives of species 2. The result will thus be the evolution of a community consisting of species 1 evaders and (now ineffectual) species 2 mimics. The fitness matrix for such a community is identical to the first matrix presented in this article, describing a community of dominant species 1 and subordinate species 2. Population 1 once again consists entirely of dominant (evader) individuals, and population 2 consists entirely of (now ineffective mimic) subordinate individuals. For the same reasons that there was an opportunity for a species 2 mimic to invade that community, there is now an opportunity for an invasion by a species 2 pursuer strategy, which mimics the species 1 evader. We can then repeat the analysis of the preceding section to conclude that the result will be a community composed of species 1 evaders and species 2 pursuers, with the latter effectively mimicking the former. But, of course, this gives rise to an opportunity for an invasion in population 1 by a new evader, and so on.

As a result, we can expect coevolutionary "mimicry cycles." We start in the two-species setting without mim-

Table 2: Fitness payoffs in a two-species community with mimicry

	1, model	2, nonmimic	2, mimic
1, model	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1, z_2$	$z_1 + 2x_1 - k_{21}, z_2 + k_{21}$
2, nonmimic	$z_2, z_1 + 2x_1$	$z_2 + x_2, z_2 + x_2$	$z_2 + x_2, z_2 + x_2$
2, mimic	$z_2 + k_{21}, z_1 + 2x_1 - k_{21}$	$z_2 + x_2, z_2 + x_2$	$z_2 + x_2, z_2 + x_2$

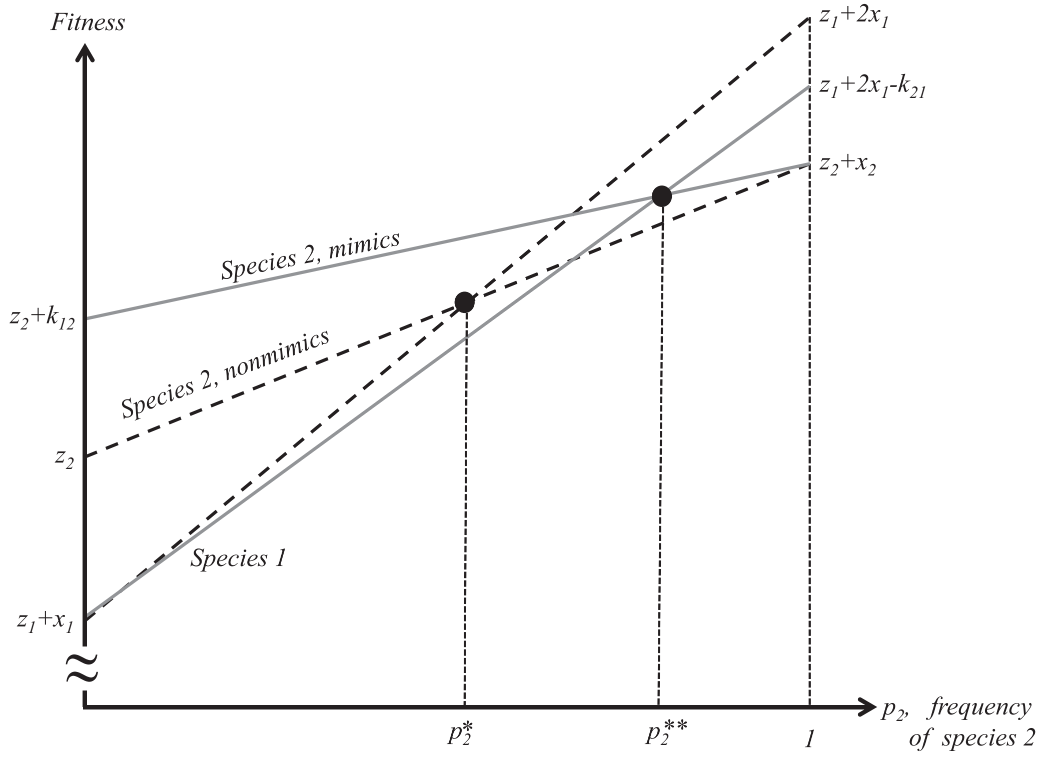


Figure 4: Fitnesses for two-species interference competition interaction with mimicry. The dashed black lines reproduce the fitness functions for the case in which species 2 is composed of nonmimics (fig. 3). The solid gray lines are the corresponding fitnesses when species 2 is composed of mimics. The intersection, identifying the asymptotically stable population proportions and the corresponding fitnesses, shifts upward and to the right, indicating that mimicry causes a larger share of the community to consist of species 2 ($p_2^{**} = [z_2 + k_{21} - (z_1 + x_1)]/(x_1 - x_2)$ as opposed to $p_2^* = [z_2 - (z_1 + x_1)]/(x_1 - x_2)$), and increases the equilibrium fitness of both species.

icry. Then a mutant mimic appears in species 2, driving out the nonmimics. Then a mutant evader appears in species 1, driving out the original individuals in species 1 and effectively converting species 2 back to nonmimics. Then a new mutant pursuer appears in species 2, this time mimicking the evader that now comprises species 1, and the cycle begins anew. The result will be an antagonistic coevolutionary arms race between model and mimic, with the successive evolution of new distinctive badges of dominant model species identity, and cycles of coevolved matching of those features by the mimic. Over time, both the model and the mimic species will diverge in appearance from their ancestral phenotypes prior to the evolution of mimicry. If speciation or geographic variation occurs within the models through isolation by distance, vicariance, or peripatric isolation, then this process will lead to divergence among model populations/species and to arbitrary coevolutionary radiation among populations.

A Three-Species Community without Mimicry

We now consider a community of three species with hierarchical social dominance relationships, which captures the intuition of an analysis with many species. As before, we begin by considering the community without mimics. The fitness matrix is given in table 4.

Table 3: Fitness payoffs in a two-species community with mimicry and population 1 evader

	1, evader	1, model	2, mimic
1, evader	$z_1 + x_1, z_1 + x_1$	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1, z_2$
1, model	$z_1 + x_1, z_1 + x_1$	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1 - k_{21}, z_2 + k_{21}$
2, mimic	$z_2, z_1 + 2x_1$	$z_2 + k_{21}, z_1 + 2x_1 - k_{21}$	$z_2 + x_2, z_2 + x_2$

Table 4: Fitness payoffs in a three-species community without mimicry

	1, dominant	2, subdominant	3, subordinate
1, dominant	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1, z_2$	$z_1 + 2x_1, z_3$
2, subdominant	$z_2, z_1 + 2x_1$	$z_2 + x_2, z_2 + x_2$	$z_2 + 2x_2, z_3$
3, subordinate	$z_3, z_1 + 2x_1$	$z_3, z_2 + 2x_2$	$z_3 + x_3, z_3 + x_3$

We assume a hierarchy, or chain, of social dominance, with species 1 (dominant) dominating both species 2 and species 3, species 2 (subdominant) being subordinate to species 1 but dominating species 3, and species 3 (subordinate) being subordinate to both species 1 and species 2. Any interaction between two individuals from the same species leads to a split of the resource (i.e., all strategies are assumed to be intraspecific doves), while any interaction between different species leads to the dominant species for that pair capturing all of the resource. As in the analysis of two species, the background fitnesses and the values of the contested resource vary among the species.

We assume that for any pair of species, the fitnesses involved in their interaction satisfy the coexistence conditions (1) and (2). The resulting inequalities are shown in table 5.

We make one further assumption, that

$$z_2 + 2x_2 > z_1 + 2x_1. \tag{5}$$

This implies that of the two species that socially dominate species 3, species 2 secures a larger fitness increment from interacting with species 3 than does species 1.

This three-species community then has a unique Nash equilibrium and evolutionary stable strategy that is asymptotically stable under the replicator dynamics and that is completely mixed, featuring all three species. (This need not be the case if inequality [5] fails.) In particular, that each species earns a lower fitness against itself than do the two other species ensures that any monomorphic population is subject to invasion. Similarly, a population consisting of only species 1 and 2 is liable to invasion by species 3 (because species 3 then earns a higher fitness than species 2 against both species 1 and species 2, from inequalities [10c] and $x_2 > 0$), a population consisting only of species 1 and 3 is liable to invasion by species 2 (which earns a higher fitness than species 1 against both species 1 and species 3, by inequalities [10a] and [5]), and a population consisting of species 2 and 3 is liable to invasion by species 1 (which earns a higher fitness than species 3 against both species 2 and species 3, from inequalities [11c] and $x_3 > 0$).

As before, these inequalities impose some restrictions, namely that

$$z_1 < z_2 < z_3, \tag{6}$$

so that species higher on the dominance chain have lower background fitness, and that

$$x_1 > x_2 > x_3, \tag{7}$$

so that species higher on the dominance chain have more at stake in the resource competition. Once again, it is explained in "Discussion" why we may expect higher background fitnesses lower on the dominance chain.

Mimicry Cycles and Mimicry Traps

Now suppose that mimics can appear in both species 2 and species 3. Mimics in species 2 gain an increase in fitness when confronting individuals from species 1. Mimics in species 3 gain an increase in fitness when confronting both species 2 and species 1. It is obvious that such mimics in species 2 will vanquish nonmimics in that population and that (conditional on species 2 being composed of mimics) mimics in species 3 will vanquish nonmimics in that population. Accordingly, we move immediately to the most interesting case in which species 2 and 3 are composed of mimics. Hence, species 1 is a model for species 2 and 3. Species 2 is a mimic of species 1 and a model for species 3. Species 3 is a mimic of species 1 and 2.

The fitnesses are given in table 6. Here, k_{21} identifies the fitness gain a species 2 mimic can secure when facing an individual from species 1. Similarly, k_{31} identifies the fitness gain a species 3 mimic can acquire when facing an individual from species 1, and k_{32} identifies the fitness gain a species 3 mimic can acquire when facing an individual from

Table 5: Coexistence conditions in a three-species community without mimicry

Inequalities (10)	$z_2 > z_1 + x_1$	(a)	$z_3 > z_1 + x_1$	(b)	$z_3 > z_2 + x_2$	(c)
Inequalities (11)	$z_1 + 2x_1 > z_2 + x_2$	(a)	$z_1 + 2x_1 > z_3 + x_3$	(b)	$z_2 + 2x_2 > z_3 + x_3$	(c)

Table 6: Fitness payoffs in a three-species community with mimics in populations 2 and 3

	Species 1, model for 2 and 3	Species 2, mimic of 1 and model for 3	Species 3, mimic of 1 and 2
1	$z_1 + x_1, z_1 + x_1$	$z_1 + 2x_1 - k_{21}, z_2 + k_{21}$	$z_1 + 2x_1 - k_{31}, z_3 + k_{31}$
2	$z_2 + k_{21}, z_1 + 2x_1 - k_{21}$	$z_2 + x_2, z_2 + x_2$	$z_2 + 2x_2 - k_{32}, z_3 + k_{32}$
3	$z_3 + k_{31}, z_1 + 2x_1 - k_{31}$	$z_3 + k_{32}, z_2 + 2x_2 - k_{32}$	$z_3 + x_3, z_3 + x_3$

species 2. If k_{21} and k_{31} are sufficiently large, mimicry will drive species 1 out of the community altogether. Similarly, if k_{31} and k_{32} are sufficiently large, then mimicry will drive species 2 out of the community. We assume the advantages of mimicry are sufficiently small, ensuring that all three species remain in the community and that a unique Nash equilibrium and evolutionarily stable strategy exist.

As in the two-species case, there is always pressure for an evader mutant to enter species 1 as long as this mutant can escape the mimicry by species 2 and 3. The advent of a species 1 evader will give rise to a coevolutionary race by mimic species 2 and 3 and a multispecies mimicry cycle. Would an analogous evader mutant be profitable in species 2, allowing species 2 to escape mimicry by species 3? If yes, then mimicry is more fragile in the three-species than in the two-species community, since evaders can profitably enter both species 1 and species 2. However, it is not obvious that an evader will be profitable in species 2. If a species 2 evader avoids the mimicry of species 3, it will (we assume) sacrifice the ability to mimic species 1. If the benefit of mimicking the dominant species 1 is greater than the gain of evading mimicry by the subordinate species 3, then an evader will not be profitable in species 2. In this case, we say we have a "mimicry trap." Species 2 is trapped into enduring the mimicry of species 3 because species 2 cannot afford to give up the ability to mimic species 1.

A mimicry trap will exist if

$$p_1 k_{21} > p_3 k_{32}, \tag{8}$$

where p_1 and p_3 are the equilibrium proportions of species 1 and 3, respectively. This characterization is intuitive (and hence a precise derivation is relegated to the appendix, available online): the left side, $p_1 k_{21}$, is the fitness that an evader mutant in species 2 would sacrifice from not being able to mimic species 1, while $p_3 k_{32}$ is the gain from evading mimicry by species 3. A mimicry trap exists if the loss to an evader in species 2 from no longer mimicking species 1 is larger than the gain from escaping mimicry by species 2. We can rewrite the mimicry trap condition (8) as

$$\frac{p_1}{p_3} > \frac{k_{32}}{k_{21}}. \tag{9}$$

Focusing on the right side of this condition, a mimicry trap requires that k_{32}/k_{21} be sufficiently small, that is, that species 2 gains sufficiently more from mimicking species 1 than it loses from being mimicked by species 3. Given the implication (7) of the conditions (10) and (11), which are necessary for evolutionary coexistence, we can reasonably expect $k_{32} < k_{21}$, since the value $2x_1$ at stake when species 2 mimics species 1 is larger than the $2x_2$ at stake when species 3 mimics species 2. Turning to the left side, a mimicry trap requires that p_1/p_3 be sufficiently large, that is, that species 1 be a relatively large share of the community compared with species 3.

To gain some insight into the conditions governing p_1/p_3, we focus on the case in which k_{21}, k_{31}, and k_{32} are small (recalling that if these values are too large, the models in the mimicry chain will not survive) relative to the various values $z_i + x_i$. The appendix shows that in this case p_1/p_3 will be less than 1. Inequality (9) will be more likely to hold—and hence a mimicry trap more likely to exist—when p_1/p_3 is large (though necessarily smaller than 1; fig. 5). The appendix shows that p_1/p_3 will be relatively large when (i) x_3 is relatively small, (ii) z_3 is relatively small, (iii) x_2 is relatively large, (iv) z_2 is relatively large, (v) z_1 is relatively large, and (vi) x_1 is relatively large. To summarize, the ratio of the proportion of species 1 in the community to that of species 3 will be relatively large—and hence the conditions conducive to the formation of a mimicry trap—when the background fitness and resource value to species 3 are relatively small and when the background fitness and resource values to the other two species are relatively large.

Discussion

Our analysis provides new theoretical support to the plausibility of the proposed mechanisms for antagonistic coevolution by ISDM (Prum 2014). In combination with population isolation by distance or vicariance, these coevolutionary processes could give rise to codivergence in appearance between sympatric clades of ISDM models and mimics. A similar process was examined for Müllerian and Batesian mimics by Gavrilets and Hastings (1998) using haploid genetics, constant population sizes for both species, and a limit of two alternative appearances. Here, we emphasize that subsequent mimicry cycles will likely involve the evolution of novel appearances and give rise to the coevolutionary divergence of both mimic and model species from their ancestral phenotypes.

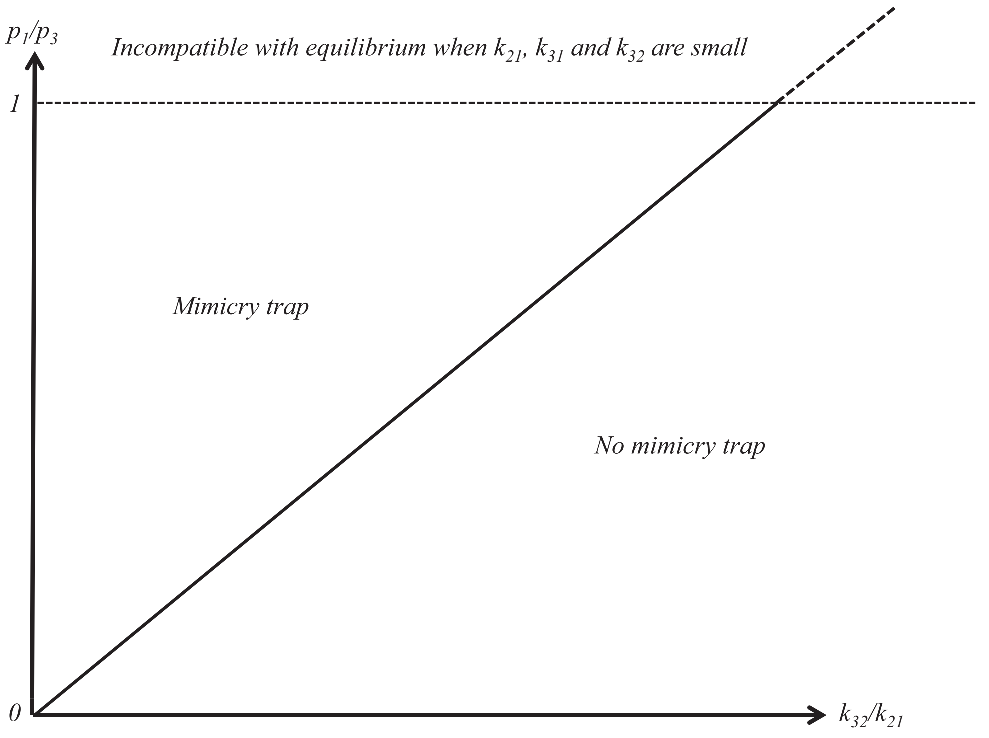


Figure 5: Quantitative conditions for a mimicry trap for the case in which k_{21}, k_{31}, and k_{32} are small. The vertical axis measures the ratio p_1/p_3 of the equilibrium sizes of populations 1 and 3, which in equilibrium is less than 1. The horizontal axis measures the ratio k_{32}/k_{21}, where k_{32} is the loss species 2 suffers from being mimicked in an encounter with species 3 and k_{21} is the gain species 2 attains from mimicry in an encounter with species 1. A mimicry trap exists when $p_1/p_3 > k_{32}/k_{21}$ (see inequality [9]), which corresponds to the region of the figure above the diagonal.

Our three-species ISDM analysis provides mechanistic support for the evolution of a mimicry complex composed of multiple species under interference competition that exhibit (i) a hierarchical distribution in dominance, so that species 1 dominates species 2 and 3 while species 2 dominates species 3; (ii) an inverse trend in background fitness, $z_1 < z_2 < z_3$ (i.e., fitness independent of all social interactions); and (iii) dominant species having more at stake in competition, $x_1 > x_2 > x_3$. The intermediate, subdominant species in this system will be in a mimicry trap if the fitness loss from no longer mimicking a larger, dominant species is greater than the gain from escaping mimicry by a smaller, subordinate species. The result will be a relatively stable mimicry chain of multiple species within a community that have converged on a similar appearance.

As in Müllerian mimicry (Ruxton et al. 2004), this multispecies ISDM process can give rise to convergence in appearance between multiple species in a community. Unlike the classic concept of Müllerian mimicry, in which each toxic species is equivalently toxic and pays the same toxicity costs, each species in an ISDM complex will still experience fitness costs from the mimicry of other, smaller species. Interestingly, however, it is now broadly appreciated that toxic Müllerian mimics vary in toxicity and can pay very different toxicity costs (Mallet 2001). Thus, an ISDM complex may be very similar in evolutionary dynamics to Müllerian mimicry among toxic species in which species vary in costs of toxicity. Distinctively, however, in an ISDM chain the largest, dominant species is unconstrained to evolve in appearance; all other species will be constrained to follow the leader and will be unable to evade mimicry by yet-smaller mimics.

Communication is often conceived of as the evolution of honest indicators of individual genetic quality and condition (Searcy and Nowicki 2005). However, ISDM fosters the evolution of visual communication signals that are not under selection for honest correlation with intraspecific variations in genetic quality or condition. Although novel model appearances will evolve by natural selection, they are frequency-dependent, interspecific, social adaptations that evolve because they provide a mechanism to avoid the cost of interspecific social deception. The advantages of novel model appearances "correlate" with species identity. Thus, novel appearances evolve in model species because they provide information about variation in species identity within the community. (Species identity does not vary within species like genetic quality or condition may.) Mimetic appearance will coevolve in mimics precisely because it undermines the social advantages of being able to distinguish dominant species identity. In this case, the coevolution in appearance among models and mimics is entirely arbitrary with respect to variation within species in genetic quality or condition.

Prum (2012) defined aesthetic selection as a process that involves (1) sensory perception of a signal, (2) cognitive evaluation, and (3) choice. Aesthetic evolution will result when variation among signals is heritable. Aesthetic evolution frequently will lead to aesthetic coevolution of the signal and its evaluation. As examples of aesthetic evolution, Prum (2012) proposed mate choice, pollination, frugivory, aposematism, and the coevolution of offspring begging/cuteness with parental care behavior. Antagonistic coevolution by ISDM provides another rich example of aesthetic evolution. In particular, evolutionary diversification of model and mimic clades, such as the yelping-model and croaking-mimic *Ramphastos* toucans, provides vivid examples of arbitrary aesthetic radiations in appearance. The specific evolution of yellow, red, or blue facial skin or of white, yellow, or orange throat coloration (and so on) occurs because they provide arbitrarily distinctive means to distinguish the model species from their coevolving social parasites. A similar aesthetic view should apply equally well to the arbitrary frequency-dependent, interspecific, social communication adaptations found in Müllerian and Batesian mimics.

Evidence of Mimicry Chains, Cycles, and Traps

Evidence of antagonistic coevolution in appearance between models and mimics appears to be quite widespread in birds. All 50 of Prum's proposed examples of avian ISDM featured some distinctive, derived plumage feature(s) that are shared between mimics and models (Prum 2014). With only a single model and mimic species, it can be difficult to differentiate whether model species have evolved their distinctive features prior to mimicry (i.e., whether ISDM occurs without mimicry cycles). However, there are numerous avian examples of coevolutionary radiation in appearance between models and mimics, including toucans, motmots, woodpeckers, friarbirds, and honeyeaters (Prum 2014). Assuming a single origin of mimicry in each clade, these cases provide excellent evidence of antagonistic coevolution in appearance (fig. 1). Likewise, there are several cases of mimicry complexes composed of unrelated sympatric species with convergent appearance, including kiskadee flycatchers, Andean tyrannulets, and shearwaters, petrels, and prions (Prum 2014); large Neotropical woodpeckers (Benz et al. 2015); and *Corydoras* catfishes (Alexandrou et al. 2011).

Our models assume that subordinate species have higher background fitness but that dominant species have more at stake. In general, there is strong support for the generalization that larger species are socially dominant and thus have competitive advantages in interference competition (Wolf et al. 1976; Alatalo et al. 1985; Milikan et al. 1985; Persson 1985; Freshwater et al. 2014). Although it is not universal, there is also a strong tendency for smaller, socially subordinate animals to be physiologically more efficient and thus superior to larger animals at exploitative competition (especially when resource levels are low), resulting in higher background fitness (Persson 1985). Smaller body species may have lower food requirements, lower transportation costs, and lower predation risks (Persson 1985). Thus, larger animals are frequently better interference competitors, whereas smaller animals are frequently superior exploitative competitors (Wilson 1975; Persson 1985). These are exactly the appropriate conditions for the evolution of ISDM. The patterns of conflicting advantages of exploitative and interference competition with body size are well documented in specific "model species" pairs of birds, such as marsh tits (*Parus montanus*) and coal tits (*Parus ater*; Alatalo and Moreno 1987), but these issues have not yet been investigated for any proposed examples of ISDM, including the *Ramphastos* toucans or kiskadee flycatchers (Prum 2014).

Tests of Assumptions and Predictions of the Theory

Prum (2014) proposes a series of experimental and comparative tests of ISDM theory. The models presented in the current article provide additional opportunities to test the proposed mechanisms for antagonistic coevolution by ISDM and mimicry chains. Because this is a new hypothesis, little or no relevant ecological and physiological data are available for any of our proposed examples of ISDM, antagonistic coevolutionary radiation, mimicry chains, or traps. However, we can describe various observations, data sets, and experiments that would be relevant to testing these models and their predictions.

Our coevolutionary models assume that (1) these species are interference competitors, and (2) larger species are social dominant. The conditions for species coexistence within the models further require that (3) subordinate species have higher background fitness, and (4) dominate species have more at stake in ecological competition.

The assumption of interference competition could be tested by descriptive investigation of the foraging ecology of these species, the quantification of the amount of dietary overlap between species, and the nature of their competitive social interactions. Classically, interference competition can be documented by observations that subordinate species suffer fitness-reducing diet shifts in sympatry with the competitor, avoid social interactions with dominant species, or suffer higher mortality and lower fitness in syntopy with dominant species. The assumptions of interference competition could be tested experimentally through model/mimic exclusion experiments.

Observations of social interactions between two nonmimicking, sympatric species of *Ramphastos* toucans at fruiting trees supports the assumption of larger species dominance and interference competition in toucans. At fruiting *Virola* nutmeg trees in Costa Rica, the larger chestnut-mandibled toucan *Ramphastos swainsoni* (639 ± 45 g) arrived within 15 min of dawn, when there are more ripe fruits available, whereas the smaller keel-billed toucan *Ramphastos sufluratus* (399 ± 45 g) tended to avoid the peak visitation times of its larger congener (Howe 1981). Furthermore, 28% of foraging visits to the tree by the smaller *R. sufluratus* were disrupted by attacks from the larger *R. swainsoni*, whereas none of the visits of the larger *R. swainsoni* were disrupted by *R. sulfuratus* (Howe 1981). These observations provide evidence of interference competition among *Ramphastos* toucans and indicate that body size is associated with social dominance in this genus.

Although hypotheses about social dominance could be explored with natural history observations of social interactions between species, the function of mimicry itself will make it challenging to simply test these assumptions. Mimics are hypothesized to have coevolved deceptive signals that make it more difficult for individuals of model species to differentiate between intraspecific and interspecific competitors. Thus, the absence of direct evidence of interference competition between models and mimics may be interpreted either as evidence that the ISDM mechanism is inapplicable (no social interference) or that ISDM is effective in moderating interspecific interference competition. In general, it is possible that rare social interactions function by establishing an atmosphere of social intimidation; for example, Alatalo and Moreno (1987) found clear evidence of interference competition and social dominance between *P. montanus* and *P. ater* despite the fact that social displacement interactions were rare.

Variation among species in background fitness and the relative gain from obtaining contested resources could be investigated through research on the physiological efficiency of foraging of model and mimic species in sympatry and allopatry or experimental exclusions. Furthermore, evidence about connections between foraging success, survival, reproductive investment, and lifetime reproductive success could be used to evaluate the relative fitness value of resources to different species. In general, if larger body sizes are less efficient at foraging and more energetically costly to maintain, then a larger individual may have more at stake in competition for a given resource.

Under most of the conditions that favor the coexistence of multiple species of mimics (fig. 5), our analysis predicts that subordinate species should exist at higher frequency in the community than model species (i.e., $p_1/p_3 < 1$). This prediction is testable with unbiased estimates of population density of models and mimics in multispecies mimicry complexes. Such data do not exist yet for species of kiskadee-type flycatchers.

Although there are few data to test these models of coevolution by ISDM at this time, we hope that the development of a detailed evolutionary model of this process will lead to fieldwork and experiments to test hypotheses of ISDM cycles, traps, and chains in birds, fishes, and other organisms.

Extensions of the Analysis

Our analysis provides a simple but versatile framework for the study of the evolution of mimicry between interference competitors. The analysis can be extended in many possible ways that are more specific or realistic to particular biology: perhaps the total value of the resource when a dominant species meets a subordinate species differs from that when two individuals of the dominant species meet, perhaps an individual of the dominant species does not capture all of the resource when meeting an individual of a subordinate species, perhaps the fitness gained by a mimic falls short (or exceeds) that lost by a model, and so on. These extensions would alter the calculations, but we expect them to add nothing conceptually new to the analysis. The appendix presents a generalization of the analysis in which background fitness adjusts, as does the size of the community, allowing the analysis to determine the size of the community as well as the proportion of dominant and subordinate species in the community. The appendix also describes how the analysis could be expanded to accommodate longer mimicry chains involving more than three species.

In our analysis of coevolutionary mimicry cycles, we assume that the novel model trait of having a distinctive appearance as well as the ability to recognize that distinctive appearance and to distinguish mimics are a single complex character. In the process, we ignore the frequency-dependent advantages of a novel evader appearance. A more complex analysis could separate these features and analyze their coevolution in more detail. For example, André (2015) recently analyzed the evolution of reciprocal altruism as the coevolution of two distinct traits: the ability to provide fitness benefits to another individual and the capacity to evaluate fitness benefits provided by other individuals.

Acknowledgments

We thank an editor, associate editor, and two referees for helpful comments and suggestions. R.O.P. acknowledges the support of the W. R. Coe Fund of Yale University. L.S. thanks the National Science Foundation (SES-1459158) for financial support. We thank S. Moroni for research assistance. For permission to reproduce their photos, we thank N. Athanas, G. Bartley, T. Friedel, G. Lasley, T. J. Ulrich, Flickr users Roy and Danielle, and the Visual Resources in Ornithology (VIREO) photo library.

Literature Cited

Alatalo, R. V., L. Gustafsson, M. Linden, and A. Lundberg. 1985. Interspecific competition and niche shifts in tits and goldcrest: an experiment. Journal of Animal Ecology 54:977–984.

Alatalo, R. V., and J. Moreno. 1987. Interspecific interactions, and use of foraging sites in tits (Paridae). Ecology 68:1773–1777.

Alexandrou, M. A., C. Oliveira, M. Maillard, R. A. R. McGill, J. Newton, S. Creer, and M. I. Taylor. 2011. Competition and phylogeny determine community structure in Müllerian co-mimics. Nature 469:84–89.

André, J.-B. 2015. Contingency in the evolutionary emergence of reciprocal cooperation. American Naturalist 185:303–316.

Benz, B. W., M. B. Robbins, and K. J. Zimmer. 2015. Phylogenetic relationships of the helmeted woodpecker (*Dryocopus galeatus*): a case of interspecific mimicry? Auk 132:938–950.

Freshwater, C., C. K. Ghalambor, and P. R. Martin. 2014. Repeated patterns of trait divergence between closely related dominant and subordinate bird species. Ecology 95:2234–2345.

Gavrilets, S., and A. Hastings. 1998. Coevolutionary chase in two-species systems with applications to mimicry. Journal of Theoretical Biology 191:415–427.

Hofbauer, J., and K. Sigmund. 1988. The theory of evolution and dynamical systems. Cambridge University Press, Cambridge.

Howe, H. F. 1981. Dispersal of a Neotropical nutmeg (*Virola sebifera*) by birds. Auk 98:88–98.

Lammertink, M., C. Kopuchian, H. A. Brandl, P. L. Tubaro, and H. Winkler. 2016. A striking case of deceptive woodpecker colouration: the threatened helmeted woodpecker *Dryocopus galeatus* belongs in the genus *Celeus*. Journal of Ornithology 157:109–116. doi:10.1007/s10336-015-1254-x.

Mallet, J. 2001. Causes and consequences of a lack of coevolution in Müllerian mimicry. Evolutionary Ecology 13:777–806.

Milikan, G. C., P. Gaddis, and R. Pulliam. 1985. Interspecific dominance and the foraging behaviour of juncos. Animal Behaviour 33:428–435.

Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? American Naturalist 126:261–266.

Prum, R. O. 2012. Aesthetic evolution by mate choice: Darwin's really dangerous idea. Philosophical Transactions of the Royal Society B: Biological Sciences 367:2253–2265.

———. 2014. Interspecific social dominance mimicry in birds. Zoological Journal of the Linnean Society 172:910–941.

Prum, R. O., and L. Samuelson. 2012. Evolution of interspecific social dominance mimicry modeled by the "hairy-downy" game. Journal of Theoretical Biology 313:42–60.

Ruxton, G. D., J. A. Sherrat, and M. P. Speed. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry. Oxford University Press, Oxford.

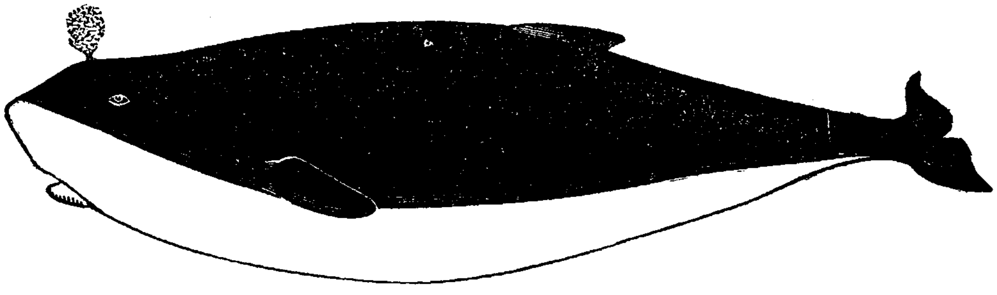
Searcy, W. A., and S. Nowicki. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton.

Wickler, W. 1968. Mimicry in plants and animals. McGraw Hill, New York.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. American Naturalist 109:769–784.

Wolf, L. L., F. G. Stiles, and F. R. Hainsworth. 1976. Organization of a tropical, highland hummingbird community. Journal of Animal Ecology 45:349–379.

Associate Editor: Vlastimil Křivan
Editor: Yannis Michalakis



"In all the typical Kogiæ, the lower jaw, for each ramus, has a more or less truncated oar-shaped posterior margin, and from its upper and lower angles, the respective margins converge, describing nearly straight or little convex outlines, to the alveolar area, the lower margin ascending upwards to the symphysis, where the rami are parallel or nearly so, and which project downwards into a longitudinally convex carina." From "The Sperm Whales, Giant and Pygmy" by Theodore Gill (*The American Naturalist*, 1871, 4:725–743).