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The Hairy–Downy Game: A model of interspecific social dominance mimicry

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HIGHLIGHTS

- We study the interaction between a socially dominant species and a potential mimic.
- This is the first investigation of mimicry between ecological competitors in the absence of third-party observers.
- We characterize the evolutionary dynamics, equilibrium, and comparative statics.
- This analysis should lay the foundations for empirical work in a number of areas.

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ABSTRACT

The evolution of many forms of mimicry are well understood, but the evolution of mimicry in the absence of aposematic models or third party participants remains poorly understood. This paper presents a model of the evolution of interspecific social dominance mimicry (ISDM), that does not rely on third-party observers, in the context of the *Hairy–Downy* game. Members of a socially dominant species contest a resource by playing the hawk–dove game. Nonmimic members of a subordinate species surrender the resource whenever encountering a member of the dominant species, and split the resource whenever interacting among themselves. Mimicry allows members of the subordinate species to pose as members of the dominant species who play dove, splitting the resource when facing other dominant doves while continuing to surrender the resource to dominant hawks. We characterize the evolutionary dynamics and equilibrium behavior of this game, developing conditions under which evolution will select for mimicry, and under which the subordinate species will consist (almost or even literally) entirely of mimics.

1. Introduction

1.1. Interspecific mimicry

Interspecific mimicry is known to evolve through natural selection on appearance to avoid attack (Ruxton et al., 2004; Wickler, 1968). Classically, mimicry includes three players: a model, a mimic, and a third party predator/observer. 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 about itself.

Progress in phylogenetic reconstruction has recently revealed new examples of evolutionary convergence in appearance among species which were originally thought to be closely related to one another. 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 observer/participants. However, the evolution of mimicry in the absence of aposematic models or third party participants remains poorly understood.

Wallace (1863, 1869) proposed several examples of mimicry in non-toxic birds. He hypothesized that smaller subordinate species may gain an evolutionary advantage from mimicking a larger dominant species in order to deceive other small species, frightening them away and thereby gaining access to resources with less competition. Alternatively, Osbert Salvin (cited in Newton and Gadow (1893–1896, pp. 572–575)) proposed that a larger species may evolve to mimic a smaller species so that other small species will mistake it for the smaller species, allowing the larger species to more readily prey upon them. Both of these proposals relied on third-party observer/participants.

Moynihan (1968) and Cody (1973) proposed that interspecific plumage coloration convergence may evolve to facilitate efficiency

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of social interactions within multi-species foraging flocks and among interspecifically territorial ecological competitors, respectively, but these proposals have not received much empirical support or intellectual enthusiasm. In a re-analysis of Wallace's classic example 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 and reduce aggressive attack. Diamond presented evidence in support of mimicry between the *Oriolus–Philemon* clades, but he remained inconclusive as to whether deception of additional, third-party species, or deception of the dominant model was more important in its evolution. More recently, Rainey and Grether (2007) reviewed and classified types of mimicry between ecological competitors. They identified competitive mimicry by a subordinate competitor of a dominant ecological competitor as a form of bipolar, antergic, defensive mimicry (following the classification of Vane-Wright, 1976). Their brief discussion of this phenomenon was restricted to song sharing between bird species, and did not consider convergence in visual appearance. Rainey and Grether (2007) called for theoretical and empirical research on competitive mimicry.

A striking example of unexpected plumage convergence comes from the Hairy Woodpecker (*Picoides villosus*) and Downy Woodpecker (*Picoides pubescens*), two broadly sympatric North American species that are strikingly similar in plumage. Although the two species can be distinguished by bill proportions and very subtle plumage characters, they are virtually identical in appearance (Fig. 1). However, the Downy Woodpecker has only 43% of the body mass of the Hairy (Dunning, 2008). Recently, 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 and Moore, 2002, 2005). Attempts to explain such striking patterns of convergent evolution have remained inconclusive because of the lack of a coherent theory about how non-aposematic mimicry evolves (Weibel and Moore, 2005).

There is also a rich literature on interspecific mimicry in coral reef fishes (reviewed in Eagle and Jones, 2004; Randall, 2005). Eagle and Jones (2004) raised the possibility that smaller subordinate species are mimicking larger, dominant ecological competitors, but conclude that "this mechanism does not fall within the traditional framework of mimicry theory, and requires further investigation." Clearly, a detailed mechanism for the evolution of mimicry between socially dominant and subordinate ecological competitors is required.

Fig. 1. Hairy Woodpecker (*Picoides villosus*, left) and Downy Woodpecker (*Picoides pubescens*, right). The two species are virtually identical in appearance, but Downy Woodpeckers have somewhat less than half the body mass of Hairy Woodpeckers. Photos reproduced with permission of Laurie Neish/VIREO (left) and A & J. Binns/VIREO (right).

1.2. Interspecific social dominance mimicry

This paper presents a model of the evolution of interspecific social dominance mimicry (ISDM). Our analysis explores the fitness consequences of mimicry by members of a subordinate species, within the subordinate species as well as within a dominant species. Inspired by the example of Hairy and Downy Woodpeckers, we refer throughout to the species in our model as woodpeckers, though the analysis could just as well apply to the interaction between any dominant and subordinate species incorporating the possibility of mimicry.

The analysis is centered around the *Hairy–Downy game*. The game is played by a dominant species, Hairy Woodpeckers, and a subordinate species, Downy Woodpeckers. The members of these populations interact in contests for the control of a resource. The interaction between two Hairies takes the form of the familiar hawk–dove game, and we thus think of the Hairy population as being composed of Hairy hawks and Hairy doves.

A Downy Woodpecker who is not a mimic surrenders the resource to a Hairy, whether the latter is a Hairy hawk or Hairy dove. To keep the analysis simple, we assume that two interacting Downies simply split the resource with one another.

We then consider the possibility of a Downy mimic. A Downy mimic resembles a Hairy sufficiently closely as to obtain a split of the resource when encountering a Hairy dove, just as would another Hairy dove. The Downy mimic surrenders the resource to a Hairy hawk, again just as would a Hairy dove, but may pay a cost (dubbed the "cost of mimicry") in doing so, arising out of Downy's smaller size. A Downy mimic thus incurs some (perhaps small) costs of mimicry, in return for being able to act as a dove (rather than surrendering the resource altogether) when encountering Hairy doves.

We develop our main results in Section 4:

- We establish sufficient conditions for the existence of an equilibrium in which Hairy hawks, Hairy doves, Downy mimics and Downy nonmimics coexist. Intuitively, these conditions include that the cost of mimicry be sufficiently small, that the resource not be too valuable to Downies, and that the Downy background fitness be neither too large nor too small. The latter two requirements ensure that Hairies and Downies coexist, though the latter may be nonmimics, with the key requirement for mimicry then being that it not be too costly.
- We characterize the evolutionary dynamics under these conditions, showing that there is a unique interior equilibrium.
- We calculate the equilibrium and derive comparative static results. For example:
  - As the cost of mimicry gets small, the equilibrium frequency of Hairy doves decreases to zero. Hairy hawks decrease in frequency but not to zero. The frequencies of both Downy mimics and Downy nonmimics increase.
  - As the cost to a Hairy hawk of fighting with other Hairy hawks increases, the equilibrium frequencies of Hairy hawks and Hairy doves decrease, while the ratio of Downy mimics to Downy nonmimics may either increase or decrease, depending on other parameter values.
  - The Downy population (and indeed the entire community of woodpeckers) will be composed almost exclusively of mimics when the cost of mimicry is relatively small, the value of the resource and the background fitness of Downies is