



# The hairy–downy game revisited: an empirical test of the interspecific social dominance mimicry hypothesis

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Understanding the emergence and persistence of convergent phenotypes is the subject of considerable debate. Species may converge on nearly identical phenotypes for a variety of reasons, including occupying similar environments, exhibiting similar foraging ecologies, and for signalling reasons such as mimicry. Interspecific social dominance mimicry (ISDM) is a hypothesis that states that socially subordinate species evolve a phenotype mimicking a dominant species so as to accrue resources and avoid aggression. A recently proposed test case for this phenomenon asserts that downy woodpeckers, *Picoides pubescens*, evolved mimetic plumage to avoid attacks from hairy woodpeckers, *Picoides villosus*. We examined this claim with a large behavioural data set collected by citizen scientists. We employed phylogenetic methods and simulations to test whether downy woodpeckers avoid aggression, and whether downy woodpeckers are more dominant than expected based on body mass. Contrary to the expectations of ISDM, we found that downy woodpeckers were markedly more often the target of hairy woodpecker attacks than expected based on their relative abundances. Our empirical data thus offers no support for the strict ISDM hypothesis as an explanation for downy–hairy woodpecker plumage convergence. However, downy woodpeckers are slightly more dominant than expected based on their body mass, albeit not significantly so. Our data therefore lend weight to previous suggestions that the benefits of mimicry potentially accrue from third-party species mistaking the mimic for the model, rather than the model mistaking the mimic for another model.

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Explaining the dynamics that influence phenotypic diversity is an ongoing challenge for evolutionary biologists seeking to decipher variation in and evolution of phenotypes (Cook, Grant, Saccheri, & Mallet, 2012; Darwin & Wallace, 1858; Darwin, 1859; Jiggins, Naisbit, & Mallet, 2001; Mallet & Joron, 1999; Toews et al., 2016). While many clades of animals show impressive phenotypic diversity, some exhibit very similar phenotypes. Accordingly, considerable research has concentrated on understanding how and why two or more species might converge on a single, shared phenotype (Consortium, 2012; Gianoli & Carrasco-Urra, 2014; Payne, 1982). One explanation for shared phenotypes is shared ecology (e.g. repeated evolution of melanism in several species of salt-marsh sparrows: Greenberg, Danner, Olsen, & Luther, 2012; Greenberg & Olsen, 2010). Convergence in phenotype may also be driven by shared biotic factors of two or more species. For example, convergence on a single phenotype is an oft-

used strategy to avoid predation (Ruxton, Sherratt, & Speed, 2005), and there are several reasons why antipredator mimicry may evolve. In the cases of antipredator phenotypic convergence, the mimicry complexes rely on the presence of well-defended (e.g. noxious or poisonous) species. These include multiple dangerous species converging on a single phenotype (Müller, 1879), or one or more harmless species tracking the phenotype of a dangerous species (Bates, 1862). Antipredation mimicry is a well-studied phenomenon with evidence from multiple taxonomic groups (e.g. Lepidoptera: Brower, 1958; Consortium, 2012; fish: Cheney, 2010; frogs: Darst & Cummings, 2006).

There are several well-described cases of plumage convergence in nonsister taxa in birds. While some of these cases are thought to function as antipredatory adaptations (Dumbacher, Deiner, Thompson, & Fleischer, 2008; Londono, Garcia, & Sanchez Martinez, 2015), there are many cases where nonsister taxa have converged on similar appearance with no tested explanation (Prum, 2014; Wallace, 1863). For instance, relatively distantly related, co-occurring species of *Ramphastos* toucans tend to have very similar plumages (Weckstein, 2005), but currently there is no

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evidence that members of these mimicry complexes avoid predation due to convergent phenotypes. Thus, there ought to be benefits to mimicry aside from predation avoidance. For example, competitive mimicry may drive one species to converge on the signals (vocal or plumage) of another species (Rainey & Grether, 2007). Wallace (1863) was one of the first to mention a possible process driving plumage mimicry in birds. Wallace suggested that less aggressive Papua New Guinean *Oriolus* orioles might mimic more aggressive *Philemon* friarbirds to gain access to preferred resources at the expense of subordinate third-party species. Although these ideas received some attention in the mid late-20th century (e.g. Cody, 1969, 1973; Diamond, 1982; Moynihan, 1968), the subject has received little attention since Murray (1976) dismissed such potential cases of avian mimicry as convergence in plumage characters due to similar selective pressures from the physical environment. Since then, research on competitive mimicry in other groups has continued, and a review by Rainey and Grether (2007) classifies different cases of competitive mimicry depending upon dominance relationships between the model, mimic and receivers. Recent work on competitive mimicry in birds by Jönsson, Delhey, Sangster, Ericson, and Irestedt (2016) has provided renewed support of Wallace's hypothesis that *Oriolus* species may obtain preferential access to resources due to mimicry. The existence of such candidate avian mimicry complexes suggest that competition may drive plumage evolution in these species.

A series of compelling papers (Prum, 2014; Prum & Samuelson, 2012, 2016) argued that many cases of avian mimicry are driven by the selective benefits of reduced aggression from syntopic, socially dominant species. The authors labelled this idea the interspecific social dominance mimicry (ISDM) hypothesis (Prum & Samuelson, 2012). The ISDM hypothesis was explored in a theoretical context by Prum and Samuelson (2012). The 'hairy-downy' game was named after the two species in the model: the hairy woodpecker, *Picoides villosus* (dominant species) and the downy woodpecker, *Picoides pubescens* (subordinate species). The 'hairy-downy' model is based on the hawk-dove game (Maynard Smith, 1982) with an expanded number of categories of individuals. Specifically, members of the dominant species can play either hawk or dove, while subordinate species can behave as mimetic or nonmimetic individuals. The benefit of mimicry in this model is that a dominant dove will split a contested resource with a subordinate mimic, resulting in a fitness benefit for the mimic. According to the model, mimicry could evolve if doing so incurred few costs (Prum & Samuelson, 2012); for example, the costs of changes to plumage colouration are assumed to be low, although individuals may suffer a cost if they are not recognized by the opposite sex. These theoretical exercises suggest that mimicry may evolve to fool model species by providing selective benefits to mimics. ISDM is a type of competitive mimicry and would be considered a type-D, bipolar (signal transmitter (S1) + signal receiver (R)), defensive antergic mimicry (Rainey & Grether, 2007; Vane-Wright, 1976) as the model and receiver are the same species.

We investigated one fundamental assumption established by Prum and Samuelson (2012); specifically, that the subordinate species experiences reduced aggression from the dominant model as a result of mimetic plumage. If dominant species do not reduce their aggression towards mimics, then the selective force driving phenotypic convergence proposed by the original ISDM hypothesis would not appear to exist. Although Prum (2014) listed 50 potential mimicry complexes, there has been no thorough investigation of aggression between model and mimic species. We examined ISDM in hairy woodpeckers and their putative mimic, the downy woodpecker. Given the dietary overlap between these two species there may be considerable fitness benefits for downy woodpeckers to deceive hairy woodpeckers (Beal, 1911). We test the prediction of

Prum and Samuelson (2012) that downy woodpeckers avoid high levels of aggression from hairy woodpeckers by using data from an extensive citizen science initiative. We compare aggression between these woodpecker species and the other species they interact with, to provide context for the rates of interspecific interactions we might expect to see between downy and hairy woodpeckers in the absence of plumage mimicry. We also use these same data to test an alternative hypothesis that mimicry prevents attacks from 'third-party' species other than the model. If third-party deception is occurring, then we predicted that downy woodpeckers would hold a more dominant position in an avian dominance hierarchy than expected based on their mass and phylogenetic position alone (Miller et al., 2017a).

## METHODS

### Data

We partnered with the citizen scientists of Project FeederWatch (Bonter & Cooper, 2012; <http://feederwatch.org/>) to gather behavioural interaction data at bird feeders around North America from February to April 2016 (time period 1) and November to December 2016 (time period 2). This is largely the nonbreeding season for almost all species included in the data set, although some of these species do start breeding in April. During this time, in addition to their standard feeder counts, which include information on species composition and abundance of birds at feeders, some participants submitted information on aggressive displacement events. Further details about collection and curation of the data set are described in (Miller et al., 2017a). For the purpose of this paper, we focused on the region of highest data density (locations east of the 100th meridian), and on species for which participants submitted at least 10 interactions in total from the study period.

### Estimating Probability of Interaction

To test whether downy woodpeckers receive less aggression from hairy woodpeckers than expected based on their abundance, we focused on FeederWatch checklists for which participants had also collected interaction data. A FeederWatch checklist is a list of species and the number of individuals (abundance) observed for each species within the checklist. We then used the species and abundance data from the checklists to derive interaction probabilities for each species, and compared these predicted values with the observed number of interactions. We first focused on calculating an expected number of interactions based on the abundance data in the checklist. We calculated this checklist-specific interaction probability under the assumption that species interact at a rate proportional to their relative abundance during that observation period. The denominator of this probability was calculated as the sum of the lower triangle of the outer product of the vector of all species' abundances from that FeederWatch count (see Appendix, Fig. A1). The numerator of this probability was calculated as the product of the number of downy and hairy woodpeckers seen during that FeederWatch count. Thus, the overall checklist-specific probability of downy and hairy woodpeckers interacting was the product of the abundances of hairy and downy woodpeckers over the sum of products of abundances of all species present at that feeder. As an alternative approach, we repeated the analysis restricting the species in the denominator to those species known to interact with any eastern North American woodpecker species. Species' standardized interaction rates between approaches were nearly identical ( $r^2 = 0.99$ ), so we present the unrestricted analysis here.

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