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.

competition

game theory

interspecific

Picidae

Explaining the dynamics that influence phenotypic diversity and biodiversity is an ongoing challenge for evolutionary biologists seeking to decipher variation in and evolution of phenotypes (Cook et al., 2012; Darwin, 1859; Darwin & Wallace, 1858; Jiggins et al., 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 et al., 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 et al., 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 et al., 2008; Londono et al., 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 evidence that members of these mimicry complexes avoid predation. 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 Jønsson et al. (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 coloration 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).

<H1>METHODS

<H2>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). 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.

We took the checklist-specific probabilities and performed a set of Bernoulli trials. If a checklist had N submitted interactions, we simulated N Bernoulli trials with the checklist-specific probability. We did this for all checklists from which an interaction had been submitted, then summed the number of 'successes' (simulated instances of a downy–hairy interaction). This generated a value for the total number of downy–hairy interactions we might expect all FeederWatch participants to have observed over the course of the project. We did this for all species observed to interact with downy woodpeckers, and repeated the process 10 000 times to generate a distribution of the expected number of interactions participants might have observed throughout the project. Based on this distribution, we computed the total observed number of interactions between downy woodpeckers and each of the other species, minus the mean number of expected interactions based on the simulations described above. We performed the same analysis for hairy woodpeckers to facilitate comparisons between these two species.

<H2>Interspecific and Intraspecific Interactions of Hairy and Downy Woodpeckers

To isolate inter- and intraspecific aggression from both hairy woodpeckers and downy woodpeckers, we utilized data collected exclusively in time period 2, as this time period included reports of conspecific aggression. To analyse how hairy and downy woodpeckers treat other species, we isolated interactions where hairy woodpeckers or downy woodpeckers were aggressive towards other species and conspecifics. We used phylogenetic generalized least squares (PGLS) to determine whether body mass influenced aggressive behaviours of hairy and

downy woodpeckers. We used the R computing environment (R Development Team, 2017) for all analyses here and below.

Predicting the Dominance Position of Hairy and Downy Woodpeckers

We used the interspecific displacement database to derive species-specific Bradley–Terry model coefficients (Turner & Firth, 2012). Following the same procedure as Miller et al. (2017a), but focusing on the region of highest data density as described above (see Data), we used these as our species-level measures of dominance among North American bird feeder-visiting birds. Based on results from Miller et al. (2017a), we knew that body mass determined dominance to some degree. However, phylogenetic position also played a role, with some lineages more or less dominant than expected based on their constituent members' body masses alone. Woodpeckers were one such clade that tended to be more dominant than expected based on body mass. To test whether downy woodpeckers are more dominant than expected based on their body mass and phylogenetic position, as would be predicted if their mimetic plumage had evolved to fool not only the model hairy woodpeckers but also third parties, we used the package 'Rphylopars' (Goolsby et al., 2016) to fit a multivariate Brownian motion model (Clavel et al., 2015). This model included both log body mass and species-specific Bradley–Terry coefficients. Before fitting the model, we removed the Bradley–Terry model coefficients of the downy woodpecker, then used the fitted model to predict its dominance position.

We performed a similar analysis in an MCMC Bayesian framework using online code from Nunn and Zhu (2014). We ran this for 501 000 generations, discarding the first 1000 as burn-in and sampling every 500 generations for a total of 1000 samples. For these analyses, we

used a maximum clade credibility tree from birdtree.org (Jetz et al., 2012), pruned to the focal species.

Ethical Note

All behavioural data were collected by citizen scientists while watching feeders. The feeder interactions represent behaviour of unmanipulated birds and no tags or experimental treatments were applied to individuals.

RESULTS

Interactions Data Set

In the final data set, subset to eastern North America and to species with at least 10 interactions, participants observed 3982 total observations (1935 observations in the first season and 2047 observations in second season) from 1274 checklists. This resulted in a final interaction data set including species from 58 genera as either the source ($N = 99$ species) or the target ($N = 92$) species. The mean ($\pm$SE) number of times a species was a source of aggression was 40.2 ± 7.6 while the mean number of times a species was the target of aggression was 43.3 ± 9.6. Of these observations, 56 involved hairy and downy woodpeckers, 54 of which involved a hairy woodpecker successfully displacing a downy woodpecker, and two of hairy woodpeckers unsuccessfully displacing a downy woodpecker (Fig. 1). When we scaled interactions based on a second pair of woodpeckers, we found that hairy woodpeckers and downy woodpeckers

interacted as much as one would expect assuming woodpeckers interact more than expected due to foraging preferences (see Appendix, Fig. A1).

Hairy and Downy Woodpecker Interactions

We isolated all instances where hairy woodpeckers behaved aggressively towards other species. Phylogenetic generalized least-squares (PGLS) regression detected no relationship between the mean mass of bird species and the rate of attack from hairy woodpeckers (β = -0.01, t = -0.6, P = 0.57; Fig. 2a). Contrary to predictions, hairy woodpeckers targeted downy woodpeckers more than any other species (Fig. 2a). We found that downy woodpeckers targeted other downy woodpeckers at the highest rate (Fig. 2b); downy woodpeckers were thus attacked at the highest rate by both hairy woodpeckers and other downy woodpeckers.

Predicted Hairy and Downy Woodpecker Dominance Positions

According to the fitted multivariate Brownian motion evolution models, downy woodpeckers were notably, but not statistically significantly, more dominant than expected (Fig. 3). In a likelihood framework, their predicted Bradley–Terry coefficient of -0.23 (95% CI: -3.11, 2.66) was lower than their observed coefficient of 0.90. Similarly, in the Bayesian framework, the observed coefficient was larger than 76% of the posterior distribution (mean predicted coefficient = -0.51). The predicted coefficient of downy woodpeckers (-0.23) would position downy woodpeckers lower in the dominance hierarchy than eastern bluebirds, *Sialia sialis*, house sparrows, *Passer domesticus*, white-throated sparrows, *Zonotrichia albicollis*, song sparrows,

Melospiza melodia, Carolina wrens, *Thryothorus ludovicianus*, and yellow-rumped warblers, *Setophaga coronata*, while the Bayesian predicted coefficient of -0.51 would further diminish its standing below that of house finch, *Haemorhous mexicanus*, and white-breasted nuthatches, *Sitta carolinensis*, and red-breasted nuthatches, *Sitta canadensis*.

DISCUSSION

We did not find empirical support for mimicry reducing aggression towards the model species, which is a fundamental prediction of interspecific social dominance mimicry (ISDM) as outlined by Prum (2014) and Prum and Samuelson (2016). Specifically, downy woodpeckers did not experience less aggression than predicted and, in contrast, suffered notably more aggression from hairy woodpeckers than expected by their relative abundances (Fig. 1). This finding contradicts the predicted benefit of mimicry of a subordinate deceiving a dominant model species in order to access resources. If the development of mimetic plumage in downy woodpeckers was driven by an ISDM selection process, it assumes either that this species was historically subject to extremely high levels of aggression from hairy woodpeckers (which remain high) prephenotypic convergence, or that hairy woodpeckers have learned to recognize the mimetic plumage without concomitant evolution away from the mimic. Both assumptions are problematic given that ISDM predicts a coevolutionary plumage arms race. While mimetic plumage may not have evolved to deceive the model, it may confer other selective benefits. Another plausible explanation for the hairy–downy mimetic complex is deception of third parties (Fig. 3), as hypothesized by Wallace (1869), later defined specifically as type-D disjunct defensive antergic mimicry (Rainey & Grether, 2007).

Indeed, we found some evidence for this hypothesis; downy woodpeckers held a nonsignificantly higher position in the dominance hierarchy than would be expected based on their body mass and phylogenetic position alone. These results demonstrate that downy woodpeckers win aggressive contests at a higher rate than expected (even after accounting for the tendency towards increased dominance in woodpeckers; see Miller et al., 2017a). Thus, species that are smaller-bodied and/or less aggressive than hairy woodpeckers (but of larger or comparable size to downy woodpeckers) are more likely to cede ground when challenged or chased by a downy woodpecker (Fig. 3). This is similar to other cases of aggressive mimicry, where the mimic gains access to resources due to mimicry (Cheney, 2010; Nelson & Jackson, 2009).

We propose that reduced aggression from third-party species may be a more plausible hypothesis for avian mimicry than reduced aggression from the model. In general, competition is typically most intense between conspecifics (Anderson & Whiteman, 2015a, 2015b; Hu & Tessier, 1995), and individuals typically need to identify conspecifics to breed successfully. Individuals should therefore be less prone to error when identifying conspecifics compared to identifying individuals of other species; it is therefore expected that hairy woodpeckers are adept at identifying whether or not another individual is a conspecific. Furthermore, vocalizations, well known species-recognition signs across birds, are given regularly by downy and hairy woodpeckers and are quite dissimilar (Birds of North America, 2015). It is possible that other species besides hairy woodpeckers would be more readily fooled by hairy-mimicking downy woodpeckers, given the reduction in selective pressure to identify heterospecifics that are neither major predators, prey, nor close resource competitors. For example, downy woodpeckers often form flocks with white-breasted nuthatches, tufted titmice, *Baeolophus bicolor*, and black-

capped chickadees, *Poecile atricapillus*. By occasionally fooling these nonmodel species into relinquishing resources (e.g. high-value invertebrates), the sum of these successful deceptions may provide the selective pressure that drives mimicry in this complex. Indeed, another study found that mimicking dangerous species can influence the feeding behaviour of target species. Specifically, Davies and Welbergen (2008) demonstrate that the *Accipiter* mimicry by *Cuculinae* cuckoos influences the behaviour of other sympatric species by depressing the feeding behaviour of smaller species.

Prum (2014) highlighted a number of possible cases of mimicry in birds (which we suggest may be specific cases of competitive mimicry sensu Rainey & Grether, 2007), and proposed various methods for testing whether this mimicry is driven by ISDM. Jønsson et al. (2016) tested certain predictions of ISDM, but did not test all the predictions. Specifically, Jønsson et al. (2016) demonstrated that *Philemon* friarbirds evolved on islands as models, and subsequently *Oriolus* orioles on those islands evolved mimetic plumage; additionally, the authors found that longer periods of co-occurrence led to higher levels of plumage similarity. These results provide support that *Oriolus* species are evolving to mimic certain *Philemon* friarbirds, but the species being deceived in that system remains unclear. Our paper is, to our knowledge, the first to test the assumption that ISDM serves to reduce aggression from the model. As aggression can be critically important for the evolution of avian species (Diamond, 1982; Freshwater et al., 2014; Martin & Ghalambor, 2014), we recommend that behavioural ecologists probe the causes of avian mimicry via direct observational measures and/or indirect quantitative methods. For instance, direct foraging observations (Bull et al., 1986; Miller et al., 2017b) are useful for defining overlap in diets, and stable isotope analysis of feathers (Hobson & Bairlein, 2003) or blood (Leighton & Echeverri, 2015) are indirect methods that can detect consumption

of shared resources (Hobson & Clark, 1992; Inger & Bearhop, 2008). Studies should include behavioural observations of interactions between proposed models and mimics and heterospecifics, as it is unlikely that mimicry functions perfectly in ISDM or in any other example of mimicry. If two species do not interact, then it is unlikely that the original ISDM hypothesis is functioning to maintain mimetic plumage. For instance, one of the most dramatic, putative mimicry complexes involves a socially dominant species (robust woodpecker, *Campephilus robustus*, 270 g) that is over twice the size of a subordinate species (helmeted woodpecker, *Celeus galeatus*, 128 g; Benz et al., 2015), and it seems possible these species exhibit very little overlap in resource use. With respect to hairy and downy woodpeckers, the most complete assessment of these two species' diets to date shows moderate dietary overlap (Beal, 1911), while more recent studies show dietary divergence in the winter (Conner, 1981). Quantifying a sufficient level of dietary overlap is important, if difficult, in testing for ISDM.

There are several caveats to this study that may be relevant for inference about ISDM. The first is that we studied behavioural interactions at feeders, and while aggressive interactions at foraging resources may be important for fitness, deception may occur elsewhere. For instance, downy woodpeckers may deceive hairy woodpeckers while entering and leaving nest or roost cavities, which could reduce hairy woodpecker eviction of downy woodpeckers. A second concern is that feeders are highly concentrated food resources and may facilitate aggression that would rarely take place in natural settings. In this case, hairy woodpeckers would show elevated aggression because they are drawn to an extremely valuable resource that is not present in nature. If this were the case, however, then it seems unlikely that hairy woodpecker aggression would so consistently be directed at downy woodpeckers. Aggressive interactions likely also take place beyond the feeders themselves, and careful behavioural observation of species will be necessary

to confirm or refute the findings presented here. Finally, the distance at which a receiver must discriminate between a model and a mimic is relevant to ISDM. Prum (2014) showed that a downy woodpecker at 5 m and a hairy woodpecker at 7.5 m may not be readily distinguished by size by other bird species as both species appear similarly sized at these distances. For the results presented in this study to be relevant for ISDM, or third-party deception, individuals would need to make decisions about aggression from some distance away. For instance, we consider it plausible that individuals perched on branches several metres away from a feeder may mistake a downy woodpecker for a hairy woodpecker. However, if decisions about aggression are made within a certain distance (i.e. in the immediate vicinity of the feeder), then hairy woodpeckers and downy woodpeckers can be distinguished based on size alone. Although difficult to test, future work should consider at what distance individuals make behavioural commitments to aggressive interactions.

In this study we tested a critical mechanism of ISDM: that downy woodpeckers avoid considerable levels of aggression from the socially dominant competitor, the hairy woodpecker. We found no evidence that downy woodpeckers experience reduced aggression from hairy woodpeckers, and instead we found that hairy woodpeckers target downy woodpeckers at a remarkably high rate. It remains possible that this high rate of aggression from hairy woodpeckers represents a reduction from what downy woodpeckers would otherwise receive. However, given the current high level of aggression that they are already subjected to, this seems unlikely. The prevalence of aggression towards downy woodpeckers cannot be explained by the species being a poor social competitor, as we found downy woodpeckers to be slightly, but not significantly, more dominant than expected based on body size. We therefore argue that the current evidence more closely supports the theories of Wallace (1863, 1869) for the evolution of

avian mimicry complexes; specifically, subordinate species appear to evolve plumage similar to dominant species due to benefits arising from the responses of third parties.

Acknowledgments

Competing Interests

We, the authors, have no competing interests or conflicts of interest.

Data, Code and Materials

Data and supporting materials are available from .

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Figure A1. Frequency distributions of the predicted number of interactions between four woodpecker species (northern flicker, hairy woodpecker, red-bellied woodpecker, downy woodpecker) based on the presence of each species in the species checklists. Yellow values represent the predicted number of interactions between the two woodpecker species after scaling the probability of interaction using interactions between red-bellied woodpeckers and northern flickers. Vertical dashed lines represent the observed number of interactions between the two species in the data set. Vertical red line is the median number of expected interactions between hairy woodpeckers and downy woodpeckers after scaling the probability. Note that vertical axes are not on the same scale.

Figure A2. Quasi-workflow for estimating the expected number of interactions from a species checklist. From each checklist we created a matrix to estimate the total number of expected interactions and the target number of interactions. We then placed these numbers in a binomial trial and simulated the number of expected interactions according to these probabilities. For example, for hairy–downy woodpecker interactions, there were 9 possible target interactions and 29 total possible interactions. The chance of seeing an interaction between these two species, assuming random interaction, is 9/29. If three interactions were observed in a checklist, we performed three binomial trials with 9/29 as the probability of success. We calculated this probability for every checklist, then simulated these trials for every checklist, and repeated the simulation 10 000 times.

Figure 1. Interaction rates between hairy and downy woodpeckers and all other species they have interactions with. The horizontal axis is the difference between the observed and the

estimated number of interactions based on the abundance of these species in FeederWatch checklists. The colour scale represents the proportion of interactions the focal species won, where yellow represents high proportions of winning and purple represents low proportions of winning. The species on the vertical axis are ordered by these proportions of success against the two focal species.

Figure 2. Phylogenetic generalized least squares (PGLS) analysis of the rate of aggression on log-transformed mass (g) for (a) hairy and (b) downy woodpeckers. Rate of aggression is the number of aggressive interactions directed toward species X over the total number of checklists that observed both the focal woodpecker species and species X. Neither PGLS relationship was significant (Ps > 0.05). Solid arrows in (a) and (b) point towards downy woodpecker values; the dashed arrow in (a) points towards the hairy woodpecker value. Plotted points were computed from the data and the plotted line is the predicted relationship according to the PGLS relationship.

Figure 3. Summary of interactions between downy woodpeckers and the nine species that interact with downy woodpeckers the most. Arrows pointing towards downy woodpeckers represent aggressive displacements of downy woodpeckers whereas arrows originating from downy woodpeckers represent aggressive displacements from downy woodpeckers. Wider arrows represent more interactions. The colours are scaled between black and red and represent differences in dominance rank between the species in question and downy woodpeckers. Redder arrows represent interactions with species that are dominant to downy woodpeckers whereas blacker arrows represent interactions with species that are subordinate to downy woodpeckers.

Figure 1.

Downy Woodpecker Interaction Rates

Yellow–rumped Warbler
White–throated Sparrow
White–breasted Nuthatch
Purple Finch
Pine Warbler
Pine Siskin
Mourning Dove
House Finch
Common Redpoll
Carolina/Black–capped Chickadee
Carolina Wren
Black–capped Chickadee
American Goldfinch
Tufted Titmouse
Red–breasted Nuthatch
Carolina Chickadee
House Sparrow
Northern Cardinal
Eastern Bluebird
Red–winged Blackbird
Red–bellied Woodpecker
Northern Mockingbird
Northern Flicker
Hairy Woodpecker
European Starling
Common Grackle
Blue Jay

−20   0   20   40   60

Hairy Woodpecker Interaction Rates

Yellow–rumped Warbler
White–breasted Nuthatch
Tufted Titmouse
Pine Siskin
Northern Cardinal
House Sparrow
House Finch
Downy Woodpecker
Chipping Sparrow
Carolina/Black–capped Chickadee
Brown–headed Cowbird
Black–capped Chickadee
American Goldfinch
Red–breasted Nuthatch
Blue Jay
Common Grackle
European Starling
Red–bellied Woodpecker
Northern Flicker

0   20   40

Proportion of
Interactions Won

1.00
0.75
0.50
0.25
0.00

Observed − Expected Number of Interactions

Figure 2.

Figure 3.