



Original Article

Fighting over food unites the birds of North America in a continental dominance hierarchy

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Members of different species often engage in aggressive contests over resources. This series of aggressive contests between species may result in an interspecific dominance hierarchy. Such hierarchies are of interest because they could be used to address a variety of research questions, for example, do similarly ranked species tend to avoid each other in time or space, and what will happen when such species come into contact as climates change? Here, we propose a method for creating a continental-scale hierarchy, and we make initial analyses based on this hierarchy. Leveraging the existing network of citizen scientists from Project FeederWatch, we collected the data with which to create a continent-spanning interspecific dominance hierarchy that included species that do not currently have overlapping geographic distributions. We quantified the extent of intransitivities (rock-paper-scissors relationships) in the hierarchy, as intransitivities can promote local species' coexistence. Overall, the hierarchy was nearly linear, and largely predicted by body mass, although there were clade-specific deviations from the average mass–dominance relationship. Warblers and orioles, for instance, were more dominant than expected based on their body mass, while buntings, grosbeaks, and doves were less dominant than expected. Intransitive relationships were rare. Few interactions were reported between close relatives and ecological competitors like Mountain and Black-capped Chickadees, as such species often have only marginally overlapping geographic distributions, restricting opportunity for observation. Yet, these species' ranks—emergent properties of the network—were often in agreement with targeted studies of dominance relationships between them.

Key words: aggression, citizen science, displacement, interspecific dominance hierarchy.

INTRODUCTION

Many animals congregate at food resources that can be patchily abundant. Examples include carcasses on the Serengeti Plain and bird feeders in suburban St. Louis, USA. Frequently, individual animals maintain access to the resource by physically dominating others. Such interactions are overt examples of interference competition (Alcock 2013). When the direction of aggression between individuals of different species is consistent, an interspecific dominance hierarchy is created (Drews 1993), with important

consequences for access to resources (LeBrun 2005). Dominance hierarchies are more often studied at the intraspecific level, where previous work has focused on social interactions between individual animals (Farine and Whitehead 2015). Of the studies on interspecific social dominance, those hierarchies studied to date typically have included only small numbers of closely related and/or ecologically similar species (Morse 1974; Wallace and Temple 1987).

Studies at the interspecific level have tended to focus on competitive rather than social dominance. Competitive dominance exists when, under some set of particular environmental conditions, individuals of one species have higher fitness than individuals of another species (Tilman 1982; Zamudio and Sinervo 2000). Social interactions, the purview of this paper, are not necessarily

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relevant to competitive dominance. As an example of where social dominance has clearly not equated to competitive dominance, consider the case of Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Red-bellied Woodpecker (*M. carolinus*). Although Red-headed is socially dominant to Red-bellied Woodpecker (Reller 1972; Nichols and Jackson 1987; Ingold 1989), Red-headed Woodpecker numbers have declined dramatically, particularly in the North and West of its range (King et al. 2007), while Red-bellied Woodpecker numbers have increased in those same areas (Kirchman and Schneider 2014). As an example of when social dominance does appear to equate to competitive dominance, in Australia the socially-dominant Yellow-throated Miner (*Manorina flavigula*) aggressively ousts most other co-occurring passerine birds to such a degree that the miner's presence demonstrably reduces other species' abundances (Kutt et al. 2016). Similar interspecific aggression by Bell Miners (*M. melanophrys*), another aggressive Australian bird, initiates a trophic cascade wherein exclusion of insectivorous passerines by Bell Miners leads to local infestations by tree sap-feeding psyllids (Hemiptera), and these high-density psyllids ultimately cause the local decline of multiple *Eucalyptus* species (Loynt et al. 1983). Aggressive interactions may even influence continental-scale patterns of occupancy; for example, dominant long-distance migrant bird species arrive to their breeding grounds earlier, and subordinate species are forced to migrate longer distances (Freshwater et al. 2014). In spite of the potential importance of interspecific social dominance hierarchies, even basic information on their structure and correlates is typically lacking.

Dominance hierarchies can take many structural forms (Figure 1), from perfectly linear pecking orders (Perrin 1955), to despotic systems where one species (or individual in the traditional intraspecific context) is dominant and all others are subordinate, to corporative systems where a ranking order exists but some species hold equivalent ranks (Fushing et al. 2011). With respect to interspecific competitive dominance, a current research focus is quantifying the structures of these dominance hierarchies, particularly the presence of mathematical intransitivities (Gilpin 1975; Laird et al. 2006; Allesina and Levine 2011). An example of an intransitivity is when species A is dominant to species B, B is dominant to C, but C is dominant to A. Known as a rock-paper-scissors relationship in behavioral ecology (Zamudio and Sinervo 2000), such a relationship indicates that despite pairwise competitive advantages, no species is able to gain preferential access to resources over all species, and therefore no single species can exclude all others. Network theory provides methods with which to quantify the prevalence of intransitive relationships within those hierarchies, as well as the structure of dominance hierarchies and species' positions therein (Shizuka and McDonald 2012; Farine and Whitehead 2015; Shizuka and McDonald 2015), although tests of the prevalence of intransitive interspecific relationships in empirical systems are sorely lacking (Levine et al. 2017).

Studies of relatively small taxonomic scope have suggested that species' traits, particularly body mass, are important predictors of a species' social dominance. Martin and Ghalambor (2014) showed that in pairwise interactions, socially-dominant species were typically larger. There also appears to be variation at broader taxonomic scales (i.e., between genera or families), although the traits in question, be they behavioral or morphological, have rarely been identified. In one such rare study, among the 4 bird families studied by Martin and Ghalambor (2014), some groups, for example, those that foraged on trunks, were less dominant than expected based on their body mass. It is still unknown whether clade-level determinants of interspecific social dominance overwhelm the signal of body mass in structuring dominance hierarchies at broader taxonomic scales.

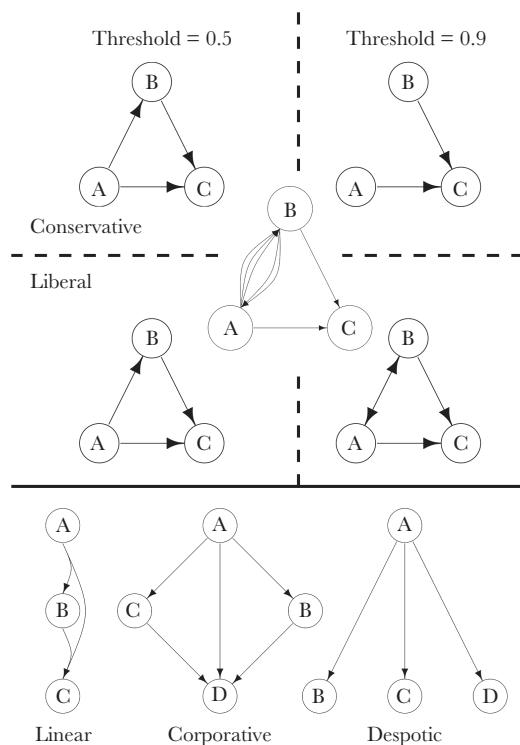


Figure 1

The upper panel uses a series of schematics to explain the network simplification step of the directed acyclic graph (DAG) method for identifying intransitivities in the continental interspecific dominance hierarchy. Given an input of 7 unique observations like those represented by the middle subnetwork, we converted the raw observations into networks where interactions between species were either absent, unidirectional, or bidirectional. For each pairwise interaction (e.g., A vs. B), if one of the species won more than the threshold proportion of wins (0.5 in the left-hand subnetworks, 0.9 in the right-hand side), then we collapsed all A versus B interactions down to a unidirectional interaction running from the dominant to the subordinate species. If neither species won more than the threshold, then we either removed all A versus B interactions (conservative DAG, top row of subnetworks), or set A versus B to a bidirectional interaction (liberal DAG, bottom row of subnetworks). We then detected intransitivities in the subnetworks by determining whether the graph was directed acyclic or not, with the caveat that not all cyclic graphs are necessarily intransitive with the liberal DAG method; for instance, the bottom right subnetwork in the upper panel contains a cycle, but $A = B > C$ is not an intransitive relationship. The lower panel shows a series of example dominance hierarchies of different forms.

Defining the structure of a large interspecific dominance hierarchy requires the observation of an even larger number of individual aggressive interactions. Acquiring such data is difficult because aggressive interactions occur only sporadically between species in the field, and are seldom observed by researchers. Thus, the structure of interspecific dominance hierarchies remains understudied, though some work has been done with hummingbirds (Feinsinger 1976; Wolf et al. 1976), and research into the ramifications of intraspecific dominance hierarchies is also relevant (Hobson and DeDeo 2015). One approach to address this difficulty of gathering behavioral data at a large scale is to partner with citizen science initiatives that engage the public in protocol-driven research. Because supplemental feeding concentrates birds at high density and in a context that facilitates the logging of standardized behavioral observations, bird feeders provide an excellent venue at which to observe

interspecific interactions. We collaborated with citizen scientists to catalog interspecific aggressive interactions (displacements) between birds at feeders, and used these behavioral observations, collected across the breadth of the North American continent, to rank numerous, distantly related species within a common hierarchy. We used this dominance hierarchy to address 2 hypotheses: 1) feeder-attending birds follow a predictable and roughly transitive “pecking-order” dominance hierarchy across a broad spatial extent; and 2) body size mediates species’ positions within this dominance hierarchy, with heavier species more dominant than lighter species. We quantify network intransitivities and identify the species involved in these relationships.

METHODS

Data collection

Aggressive interactions between birds can take several forms. In this study, we focused on the most overt of these: displacements in which one bird displaces or chases another from a perch at or near a bird feeder. We did not include subtle interactions such as one bird waiting until another finished feeding, or accidental displacements such as one bird arriving suddenly and temporarily frightening off birds that had been present.

To collect these behavioral data, we partnered with Project FeederWatch (PFW). PFW engages more than 20 000 people annually to monitor the abundance and distribution of feeder birds in the United States and Canada (Bonter and Cooper 2012) during the nonbreeding season (early November until early April). Participants follow a standard observation protocol and submit counts of the maximum number of individuals of each species that are simultaneously using their feeder over a 2-day period. Beginning in February 2016, we augmented the data input protocol to allow participants to report displacements observed during their counts. Data from PFW, including the new behavioral interactions, are freely available online (most recent data at: <http://feederwatch.org/explore/raw-dataset-requests/>, accessed 5 August 2017). The interactions database grew by over 100 observations per day through the 2016–2017 feeder season. Roughly 11% of FeederWatch participants supplemented their checklists with behavioral data. The data used in the analysis of this paper were those observations submitted prior to 5 April 2017.

Many participants in PFW already exhibit a high level of natural history knowledge. Nevertheless, to better standardize observations among participants, we used the online PFW blog to communicate to participants the behaviors of interest and provide accompanying example videos (<http://feederwatch.org/uncategorized/different-bird-behaviors-explained/>, accessed 5 August 2017). To further quality-check our database, we both manually monitored incoming observations, and wrote R scripts to automatically flag unusual interactions. Examples of such observations were those involving rarely seen species, or between species where previous evidence would suggest the reported direction of aggression would be rare. Approximately 15% of observations were flagged during this initial stage, but many of these observations were manually approved by FeederWatch staff (i.e., with no further contact with the participant) after reading through comments provided by participants. Participants responsible for observations still flagged after this point were contacted directly (approximately 2% of all observations). If the participant responded with details confirming the observation, we removed the flag and the observation was included in the data used in this paper. Prior to November 2016, participants were

unable to delete their submitted interactions. Flagged, unconfirmed observations from before this date were removed from the database by the authors (approximately 2% of total data at that time). Participants are now able to delete and correctly re-enter observations, so flagged, unconfirmed observations are simply excluded from analysis, rather than removed from the database (less than 1% of total observations). We also excluded from analyses observations involving potential predators and vultures, as interactions with potential predators and vultures can be difficult to categorize, and between Broad-billed and Costa’s Hummingbirds, as these hummingbird species were only observed to interact with one another. The final dataset consisted of 7,685 interspecific observations of 136 species (Miller et al. 2017).

Network creation and calculation of rank

We used the displacement observations to create a directed, weighted network. Each unique interspecific interaction was represented by a directed edge (an arrow) between nodes (species). We developed and used a modified form of Bradley-Terry model to rank species in a hierarchy. The original Bradley-Terry model fits a function wherein all species are ranked against a single focal species (Turner and Firth 2012). In preliminary analyses we found that Bradley-Terry models (Bradley and Terry 1952) returned a ranking in general agreement with published pairwise interactions (Rodewald 2015). However, the focal species is not ranked with this traditional Bradley-Terry model. Thus, our modification was to consider each species in turn as the focal species, and then take species’ median coefficients across all fitted models as their overall dominance scores. We sorted these and assigned ranks accordingly. We have made available an R (R Development Core Team 2016) package, *networkTricks* (<https://github.com/eliotmiller/networkTricks>, accessed 5 August 2017), that includes this modified Bradley-Terry method.

To confirm that our results were not sensitive to inclusion of species with limited information, we repeated all analyses after excluding species for which fewer than ten interactions were observed, and we also repeated all analyses restricting observations to the eastern United States, our area of highest data density. Results were qualitatively identical, and Farine and Whitehead (2015) caution against simplifying networks in this manner, so we present results from the complete dataset here. We visualized the dominance hierarchy with an attribute-ordered network layout (Hobson et al. 2015). In this graphical representation of the dominance hierarchy, species’ positions along the vertical axis represent their rank in the hierarchy, blue lines represent observed interactions where a species of higher rank displaced one of lower rank, and red lines represent observations where a species of lower rank displaced one of higher rank. Based on code from Hobson et al. (2015), we have included in *networkTricks* a function for creating such plots.

We evaluated and eliminated from consideration other approaches to creating a dominance hierarchy. We did not use eigenvector centrality (Hobson et al. 2015), David’s scores (Gammell et al. 2003), or Elo scores (including a recent modified method, Sánchez-Tójar et al. 2017). With our dataset these approaches artificially inflated the ranks of species that had interacted a limited number of times, but that when observed had interacted with highly-ranked species. For example, based solely on the fact that it had lost to the fairly high-ranked House Finch (*Haemorhous mexicanus*) and White-crowned Sparrow (*Zonotrichia leucophrys*), these approaches consistently ranked Mountain Chickadee (*Poecile gambeli*) as dominant to Black-capped Chickadee (*P. atricapillus*), a species to which Mountain Chickadee is known to be subordinate to (Minock 1972;

Grava et al. 2012). We also experimented with the recently developed ADAGIO method (Douglas et al. 2017). We found that results using ADAGIO were in better agreement with biological reality than the other approaches listed above that we considered but did not use (i.e., fewer observed interactions were oriented counter to the inferred rank—seen as red lines in an attribute-ordered network like that in Figure 2). However, the ordinal ranks returned by ADAGIO were less suitable for our downstream analyses, and ADAGIO did not perform as well as our modified Bradley-Terry method with infrequently observed species, for example, Red-headed Woodpecker and Mountain Chickadee were tied and both ranked at the bottom of the hierarchy. We therefore present results in this paper from analyses using only our modified Bradley-Terry approach. To facilitate comparison, we include a table with species scores/ranks according to these additional methods in the supplementary material.

Phylogenetic signal of dominance and relation to body size

As a test of whether social dominance is a trait that exhibits phylogenetic signal, we calculated Pagel's lambda (Pagel 1999) for species' median Bradley-Terry model coefficients and for species' body masses. Pagel's lambda varies from zero to one, where one indicates that variance in dominance is well predicted by a Brownian motion model of evolution, that is, phylogenetic covariance predicts dominance. That said, signal in dominance rank detected here might be a byproduct of body mass, which is well known to exhibit strong phylogenetic signal (Blomberg et al. 2003). Moreover, clade-level deviations from the overall dominance-mass relationship are potentially interesting. To address these issues, we tested the degree to which body mass can explain the variance in species' Bradley-Terry model coefficients with a phylogenetic generalized least squares (PGLS) regression (Grafen 1989; Martins and Hansen 1997), implemented in the R package *caper*. We used the maximum-likelihood optimized lambda in the model (a measure of the phylogenetic covariance of the residuals in dominance rank) and log-transformed species' average body masses as published in Dunning (2007). We used a pruned version of the maximum clade credibility global bird tree (Jetz et al. 2012), with the recently taxonomically separated Woodhouse's Scrub-Jay (*Aphelocoma woodhousei*) manually inserted using the R package *addTaxa* (Mast et al. 2015), since this species was absent from the global bird tree. To identify clades with notably positive or negative dominance scores given their body mass, we examined species' residuals from the fitted PGLS.

Calculation of network transitivity

If we have a dominance hierarchy where pairwise relationships are represented by a single direction of aggression, and it is still possible to trace a route from one species back to itself in that network, then it contains at least one intransitivities of the sort thought to promote species coexistence (Allesina and Levine 2011). Put differently, such a situation arises when all pairwise species interactions are consistent in direction, and there are no contested relationships where sometimes species A wins and other times B wins, but it is still possible to follow directed aggression through the network and return to the same player. In network theory terminology, if a network has no parallel and/or bidirectional edges, and if it is not a directed acyclic graph, then somewhere in that dominance hierarchy an intransitive relationship exists.

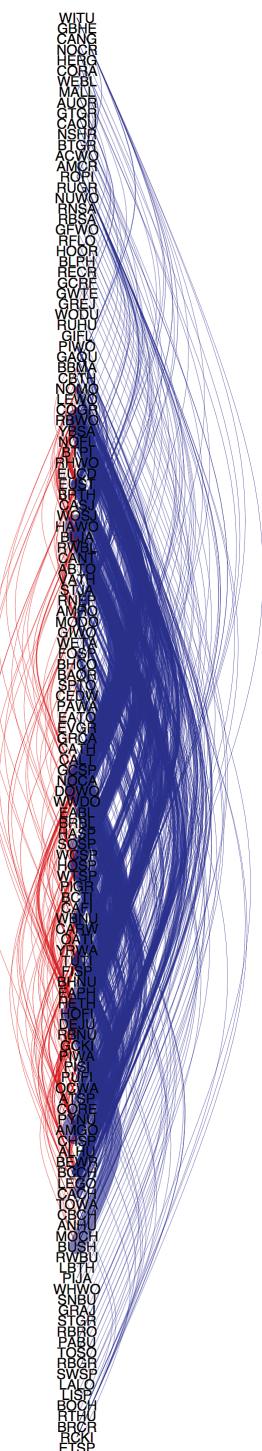


Figure 2

Attribute-ordered network (Hobson et al. 2015) showing the species ranked from most dominant (top) to most subordinate (bottom) according to their median Bradley-Terry model coefficients. Species are identified by their 4-letter codes, explained in Supplementary Table S1. Blue lines represent observed displacements from an inferred dominant to an inferred subordinate species, while red lines represent observations where a species with an inferred lower dominance rank displaced one with an inferred higher rank. The preponderance of blue lines emphasizes that most observed interactions were in the direction that would be expected given a linear dominance hierarchy.

Among the members of a triad, we can visualize this as a biological version of rock-paper-scissors, but intransitivity can manifest itself across larger numbers of species. Quantifying the degree of intransitivity in a network with more than a few nodes (species) is computationally challenging. Most algorithms work by assessing all possible subnetworks of a given size within the actual dominance hierarchy. For instance, with 136 species (the number included in our study), there are 9180 possible dyads to consider, 410040 possible triads to consider, and 5.9^{39} possible 68-species subnetworks to consider. Because it has an elegant empirical solution, we employed the triangle transitivity method (Shizuka and McDonald 2012), which works by calculating the proportion of transitive triangles (3-species subnetworks) relative to all triangles. This measure, P_t , can be thought of as a measure of how many rock-paper-scissors relationships there are within the larger network. The triangle transitivity method has limitations, however: P_t is assessed at the triad level, with no tests for intransitivity within groups of 4 or more species, and by default it simplifies pairwise interactions according to a majority rule. For example, if 2 participants observed a Downy Woodpecker (*Picoides pubescens*) displace a Red-breasted Nuthatch (*Sitta canadensis*), but one observed the opposite direction of aggression, the triad approach by default simplifies this to Downy Woodpecker as dominant to Red-breasted Nuthatch. Additionally, this approach does not consider the transitivity of triads where one relationship is unknown. The triad census method (Davis and Leinhardt 1972) does quantify the prevalence of these sorts of relationships: double-dominant ($A > B, A > C$), double-subordinate ($B > A, C > A$), and pass-along ($A > B, B > C$) (Shizuka and McDonald 2015). To compare our results to the intraspecific network motif survey of Shizuka and McDonald (2015), we also implemented the triad census method (after network simplification with the 50% conservative DAG method, see below).

To examine some of the complexity lost to the aforementioned methods, we additionally developed a directed acyclic graph (DAG) method. Here, the degree of intransitivity in the entire dominance hierarchy is calculated as the number of cyclic subnetworks divided by the total number of subnetworks for which data is available to assess transitivity. Subnetworks where at least one pair of interacting species was never observed to interact are excluded from the analysis entirely, but all other subnetworks are considered. We used the DAG method to determine how our calculations of intransitivity varied over 2-, 3-, and 4-species subnetworks, and over variable thresholds (proportions of wins) a species needed to have over a competitor before it was considered dominant. Subnetworks involving more than 4 species proved computationally infeasible to examine using available computers, but were it to be implemented in a distributed file system like Hadoop (Shvachko et al. 2010), the DAG method could be scaled to assess transitivity over larger subnetworks. After initial exploration of how the degree of intransitivity varied across different values, we chose to examine the following thresholds of percentages of wins by the dominant competitor: 50%, 55%, 60%, 70%, 80%, 90%, and 100%. Altering these thresholds allowed us to quantify variation in dominance between species, and also enabled us to understand how dominance definitions can influence network transitivity calculations (e.g., majority rule versus requiring a species win all its interactions to be considered dominant). We also explored the sensitivity of the intransitivity results to how ties were handled. When neither species in a pairwise interaction won more than the threshold proportion of interactions, we either removed the interaction entirely or set it to a tie (i.e., created a bidirectional edge where $A = B$). Note that in

either case, if the subnetwork originally had observations between the species in question, it is included in the denominator of the DAG calculation. We refer to the first of these approaches (i.e., in which we remove edges in which neither species wins the threshold proportion of interactions) as the “conservative DAG” method, as it identifies intransitivities only when there is high confidence in the pairwise relations. In contrast, we refer to the second approach (i.e., in which edges where neither species wins the threshold proportions of interactions are assigned as bidirectional edges) as the “liberal DAG” method (Figure 1). Note that the conservative, 3-species DAG approach with a 50% threshold is similar to the triangle transitivity method, except that our method also considers double-dominant, double-subordinate, and pass-along relationships, so the exact results of proportion of intransitive versus transitive subnetworks differs slightly. Also, our method allows us to identify which species are involved in such relationships, which currently is not part of the triangle transitivity method.

We identified the species that tended to be involved in these intransitive relationships by deriving species-specific standardized effect sizes (SES) that reflected the proportion of intransitive relationships in which species were involved, compared with expectations. To do this, we focused on the 3-species, 50% threshold, conservative DAG method’s results. We compared the observed number of intransitive relationships in which each species was involved to the expected number based on 999 runs for which we randomized the winner and loser of every observation in the input data, and summarized the resulting network with the conservative DAG method. Thus, per species, we derive a SES that describes the number of intransitive relationships it is actually involved in as compared with what would be expected given an identically wired network with varying directionality between interacting species (similar to the trait field method (Miller, Wagner et al. 2017)). Large negative values of this SES measure reflect species that, after accounting for prevalence in the dataset, were involved in few intransitive relationships relative to expectations, while large positive values reflect species that were involved in more transitive relationships than expected by chance.

RESULTS

Network creation, calculation of rank, and relationships to body mass

We sorted and ranked species’ median Bradley-Terry model coefficients to produce a hierarchy for 136 species of North American feeder birds (Figure 2). This hierarchy included large species like Wild Turkey (*Meleagris gallopavo*) and Great Blue Heron (*Ardea herodias*) at the top of the hierarchy, and small species like Eurasian Tree Sparrow (*Passer montanus*), Ruby-crowned Kinglet (*Regulus calendula*), and Brown Creeper (*Certhia americana*) at the bottom. The network density was 0.06, meaning that 6% of possible species pairs were observed to interact by participants. On average, each species interacted with 7.8 other species, and displaced species that weighed 131.9 g less ($SD = 94.4$) or ranked 23.9 ranks below them ($SD = 16.0$). Displaced species were, on average, supplanted by species that weighed 122.0 g more ($SD = 96.4$) or ranked 22.7 ($SD = 17.6$) ranks above them.

Pagel’s lambda, a measure of the phylogenetic signal in dominance, was 0.76, while that for the log of body mass was 1.0; both were significantly different from zero ($P < 0.001$). Body mass explained a considerable fraction of the variance in species’ coefficients from the fitted models (PGLS pseudo- $R^2 = 0.40$, $P < 0.001$). The optimized PGLS

lambda value of 10^{-6} , however, denotes very limited phylogenetic covariance in the residuals (distinct from the explanatory power it has with respect to species' dominance scores per se). Taken together, these results show that, on average, larger bird species are more dominant, but that dominance is affected by other factors that render entire clades (e.g., families, as illustrated with continuous character maps [Revell 2012], Figure 3) more or less dominant than the average; additionally, there is substantial variance in dominance that remains unexplained. As examples of these clade-specific effects, we found that parulid warblers tended to be more dominant than expected based on their body mass, while other lineages such as doves tended to be less dominant than expected based on body mass (Figure 3).

Calculation of network transitivity

According to the triangle transitivity method (Shizuka and McDonald 2012), the continental interspecific dominance hierarchy was more transitive than expected based on chance ($P_t = 0.99$, $t_{tri} = 0.94$, $P < 0.001$). Put differently, 99% of all known 3-species

subnetworks were transitive. Some of the pairwise interactions that generated intransitivities can be seen as red lines in Figure 2, though note that these red lines also depict the occasional observation where a lower-ranked species was able to displace a typically higher-ranked species. The triad census method corroborated the rarity of intransitive relationships in the data; of triads where at least 2 of the 3 relationships was observed, 20% were double-dominant, 27% were double-subordinate, 33% were pass-along, 20% were transitive tournaments (i.e., all 3 pairwise relationships were observed), and 0.4% were intransitive cycles.

We developed the directed acyclic graph (DAG) method to further examine subtleties in species' interactions. Here, we considered 2-, 3-, and 4-species subnetworks, exploring 1) various thresholds (proportions of wins) a species needed to attain to be named the dominant member of a 2-species interaction, and 2) 2 alternative methods of handling tied 2-species interactions. A tie was defined as neither member of a species-species interaction winning more than the threshold proportion of observed interactions. Across all thresholds and both tie methods, the proportion of subnetworks

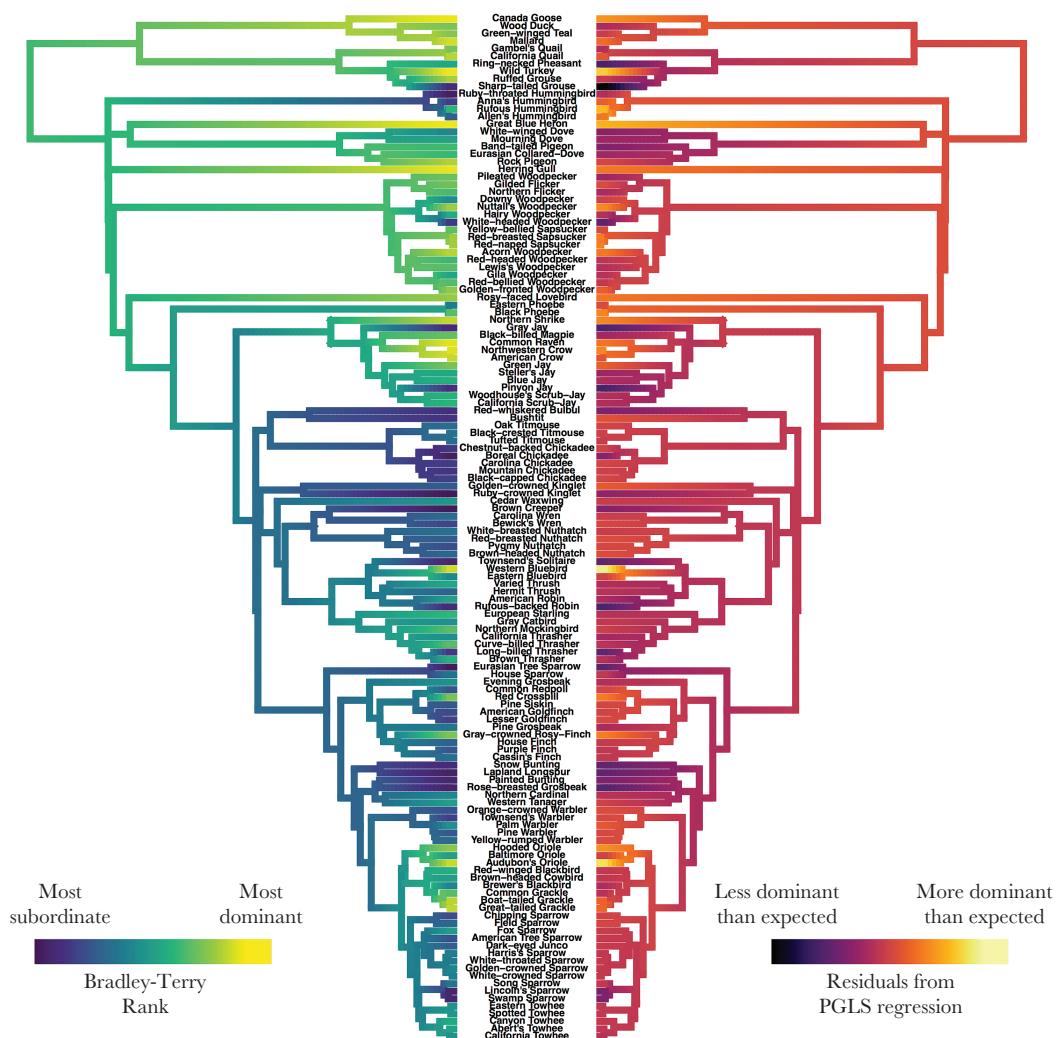


Figure 3

Continuous character maps (Revell 2012) illustrating dominance ranks and deviations from expected dominance. In the phylogeny on the left, more dominant species are colored in yellow, while more subordinate species are colored in blue. The phylogeny on the right depicts residuals from the PGLS regression of species' Bradley-Terry coefficients as a function of their body mass. Here, species that are more dominant than expected based on their body mass are colored in pale yellow, while those that are less dominant than expected are colored in purple.

that were intransitive increased with the size of the subnetwork. For instance, with a 50% threshold and the conservative DAG approach, 0%, 0.1%, and 0.2% of the 2-, 3-, and 4-species subnetworks, respectively, were not DAGs, while with the same threshold and the liberal DAG approach, these percentages were 4.3%, 5.3%, and 6.5%, respectively. When we increased the threshold with the liberal DAG approach, a larger proportion of subnetworks were no longer DAGs, while the opposite was true of the conservative DAG approach (Figure 4). This is expected, given that tied interactions are converted to bidirectional edges with the liberal approach, which by definition imposes cycles in the subnetwork. Generally, these results show that the threshold at which dominance is defined has a large influence on the resulting transitivity calculations.

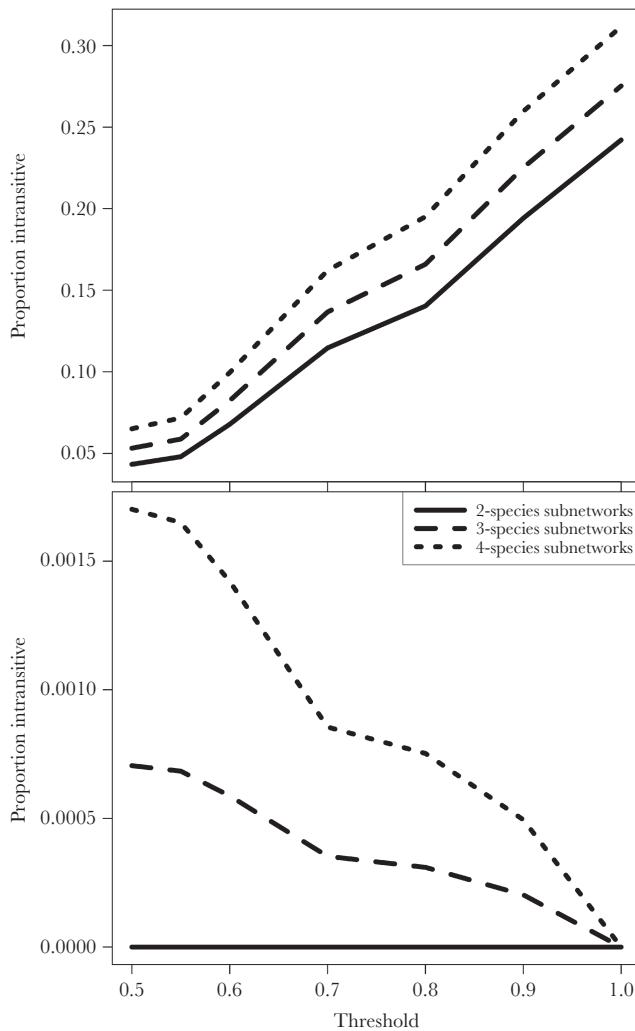


Figure 4

Illustration of how the proportion of subnetworks that are intransitive varies as a function of threshold and method of handling ties. With the conservative DAG approach (bottom panel), pairwise interactions where neither species won more than the threshold are removed, and intransitivity therefore decreases as the threshold increases. With the liberal DAG approach (top panel), pairwise interactions below the threshold are set to bidirectional arrows. The proportion of subnetworks that are intransitive therefore increases when the threshold is increased with this method, with the caveat (Figure 1) that not all networks identified as cyclic are truly intransitive here.

These tests of intransitivity also show that while the network approximated a linear dominance hierarchy, it was not perfectly so: even at the pairwise level, 24.2% of species pairs were embroiled in interactions in which a single species was not universally the winner (as assessed with the 100% threshold, liberal DAG method). Results from our null model simulations with the 50% threshold, conservative DAG approach showed that American Goldfinch (*Spinus tristis*), Downy Woodpecker, and Dark-eyed Junco (*Junco hyemalis*) had the smallest SES values, meaning that they were involved in the fewest cyclic relationships given expectations based on their occurrence in the dataset. Overall, almost all species had negative SES values (Supplementary Table S1), indicating that most triads were transitive. Only the poorly sampled Cassin's Finch (*Haemorhous cassinii*), Harris's Sparrow (*Zonotrichia querula*) and Townsend's Warbler (*Setophaga townsendi*) had positive SES values. In general, species infrequently observed at feeders (kinglets, orioles, buntings, creepers, etc.) tended to most frequently be involved in intransitive relationships (Supplementary Table S1). In summary, the dominance hierarchy approximated a linear pecking order when assessed at the triad level, although our ability to explore the extent of intransitivity within large subnetworks was hampered by computational limitations.

DISCUSSION

In this paper, we used a large database of citizen-scientist-observed behavioral interactions to derive an interspecific social dominance hierarchy of North American feeder birds (Figure 2). Despite observations encompassing an ecologically wide range of bird species across the breadth of the North American continent, the resulting hierarchy was nearly linear. Whether assessed with the triangle transitivity method (Shizuka and McDonald 2012), the triad census (Davis and Leinhardt 1972; Shizuka and McDonald 2015), or the directed acyclic graph (DAG) method introduced here, most interactions were transitive. Thus, the continental dominance hierarchy of feeder birds, as determined by citizen scientists, appeared to deviate only slightly from a linear pecking order; near linear hierarchies are frequently observed in biology (Landau 1951; Chase 1982). Our results set up a number of interesting questions. For example, can the presence of a similarly ranked species preclude another's occurrence, and is there geographic or temporal variation in a species' ranking?

Species' positions in the dominance hierarchy were related to body mass, although certain lineages were more or less dominant than expected for their mass (e.g., warblers, Figure 3, right panel). Martin and Ghalambor (2014) suggested that morphological adaptations for foraging on trunks might reduce performance in aggressive encounters. This suggestion was based on the inclusion of woodcreepers (Furnariidae) in their analysis, which did not consider woodpeckers. Our results, which do not include woodcreepers, show many woodpeckers were more dominant than expected based on their body mass (although there was variation within the group, and some species like Pileated Woodpecker [*Dryocopus pileatus*] were actually less dominant than expected given their body mass). Thus, trunk foraging per se does not appear to explain these clade-level differences. Alternatively, a woodpecker can sustain impressive forces on its skull without suffering brain injury (Wang et al. 2011), a morphological character that seems relevant for an animal that fights in large part with its head. In general, woodpeckers held high absolute ranks in the dominance hierarchy; for many participants, because higher ranked species are infrequent

feeder visitors, woodpeckers are among the most dominant species at their feeders. Identifying additional morphological or behavioral characteristics that explain clade-level shifts in dominance, beyond body mass, awaits future study. In addition to these large shifts in dominance towards the root of the phylogeny, leading certain clades (e.g., families and genera) to deviate from the overall mass-to-dominance relationship, there were also a number of large contrasts in dominance toward the tips of the phylogeny (hence, the low lambda from the PGLS regression). For instance, Canyon Towhee (*Melozone fusca*) was inferred to be notably more dominant than California Towhee (*M. crissalis*), even though these 2 species are phenotypically similar enough to have once been classified as the same species. Both species were infrequently observed by participants (Supplementary Table S1), so this apparently large shift in dominance between closely related species may simply be a function of limited information. Confirming these patterns, and identifying which factors explain changing dominance relationships, both between higher taxonomic units and between closely related species, requires further data collection and analyses.

A large body of theoretical literature supports the notion that intransitivity in dominance relationships promotes species coexistence (Laird et al. 2006; Laird and Schamp 2008; Allesina and Levine 2011). This has been empirically demonstrated in the lab (Kerr et al. 2002), and it has received some attention in plant competition literature (Keddy and Shipley 1989; Soliveres et al. 2015); however, empirical tests of this idea are infrequent, particularly in animal systems (Levine et al. 2017). Overall, we found few well-supported intransitive relationships between plausible ecological competitors at the 3- and 4-species scale. Of those, we found the House Finch, Purple Finch (*Haemorhous purpureus*), and Dark-eyed Junco (*Junco hyemalis*) subnetwork to be intransitive, with the House Finch dominant to the Purple Finch (House Finch won 16 of 18 pairwise interactions), the Purple Finch dominant to the junco (Purple Finch won 6 of 8 interactions), and the junco dominant to the House Finch (junco won 59 of 90 interactions). Competitive coexistence theory would predict increased negative consequences of competition by Dark-eyed Junco on House Finch in areas such as the southwestern USA, where Purple Finches do not regularly occur.

We do not speculate further on the biological implications of intransitive relationships, because we believe that further work is needed to clarify the extent to which intransitivity in this system is a biological phenomenon or the result of currently inadequate sampling. Most of the intransitive relationships we detected were based on small sample sizes. Indeed, when we removed all single interactions (i.e., those where species A had only interacted once with B), and summarized the network with the conservative DAG method and an 80% threshold, the entire dominance hierarchy was transitive (this filtered hierarchy contained 99 species). Moreover, multiple intransitive relationships might be driven by a single odd observation, that is, knock-on effects. For instance, a number of intransitive relationships were rooted in a single observation of a White-throated Sparrow (*Zonotrichia albicollis*) interacting with a European Starling (*Sturnus vulgaris*), an interaction where the former displaced the latter. It seems likely this relationship, and perhaps others, will be reversed given more data. We did find well-supported instances of contested dominance relationships, but these were not truly intransitive relationships. For instance, both White-breasted Nuthatch and Tufted Titmouse (*Baeolophus bicolor*) tended to displace Black-capped Chickadee (*Poecile atricapillus*), but the nuthatch and titmouse displaced one another at approximately equal rates, a fact that has been noted before (Waite and Grubb 1988), and may be

related to sexually associated intraspecific differences in dominance (i.e., male titmice may be dominant to female nuthatches).

Numerical measures of intransitivity are complicated by the rules used to identify and deal with ties. In general, transitivity decreases when ties are converted to bidirectional edges, while it increases when these ties are removed from the network; transitivity also decreases as larger numbers of species are considered in subnetworks of the broader dominance hierarchy. Our DAG method differs slightly from the triangle transitivity method in that the former considers all possible subnetworks of a given size, while the latter only considers triads where all 3 relationships are known (Shizuka and McDonald 2012). The triad census method considers all forms of triads, but only cyclic, rock-paper-scissors relationships are truly intransitive, and we found these to be rare with all analytical approaches. We note that unlike Shizuka and McDonald (2015), who reviewed triad motifs across a breadth of intraspecific studies, we found pass-along relationships to be quite common in interspecific feeder bird interactions (33% of triads with at least 2 known relationships). This is likely driven by the broad geographic scope of our study, where given the triad A > B > C, A and C may be allopatric. Additionally, the median network size analyzed by Shizuka and McDonald (2015) was 10 nodes, as compared to our 136-species network. Regardless of the method used, the result is qualitatively the same: the hierarchy was mostly transitive as assessed at the computationally accessible scale of 3- and 4-species subnetworks. Certainly, diversity-promoting intransivities may be present in the dominance hierarchy of North America's feeder birds, but we are currently limited in our ability to identify them.

As we know of no other research describing dominance hierarchies with comparable geographic scope, we use this opportunity to ask whether the definition of a continent-wide dominance hierarchy (Figure 2) is biologically meaningful. For example, given that a Black-billed Magpie (*Pica hudsonia*) in Alberta and a Brown-headed Nuthatch (*Sitta pusilla*) in South Carolina stand very little chance of directly interacting, is it reasonable to rank them on the same scale? One way of testing this is to consider closely related species with minimal geographic overlap for which previous studies have identified that one species is behaviorally dominant to the other, and for which we have scant data. For example, Mountain Chickadee and Black-capped Chickadee are ecologically similar, closely related taxa that tend to segregate locally along elevational and habitat gradients throughout western North America where they co-occur regionally (Rodewald 2015). Few FeederWatchers are located within these narrow overlap zones, and we therefore have no interactions between Mountain and Black-capped Chickadees in our database. Despite this lack of direct observation, our hierarchy places Black-capped as dominant to Mountain, in agreement with previous focused studies (Minock 1972; Grava et al. 2012). Similarly, we found Red-naped Sapsucker (*Sphyrapicus nuchalis*) to be ranked higher than Red-breasted Sapsucker (*S. ruber*), in agreement with published work (Billerman and Carling 2016), and again despite a lack of direct observation between the species in our study. Conversely, an emergent property of our hierarchy was to rank Black-capped above Carolina Chickadee (*P. carolinensis*), in contrast to careful experimental study of interactions between these species (Bronson et al. 2003). While we do not suggest that the small difference in rank we detected between the species is strong evidence that Black-capped is in fact dominant to Carolina Chickadee, given that previous work included genetically introgressed birds and an overall small sample size (Bronson et al. 2003), like Curry et al. (2007), we suggest that dominance relationships between these species warrant

further study. That our methods can correctly assess dominance between closely related taxa even when lacking direct observation of interactions improves confidence in the biological validity of drawing inferences from our continent-wide dominance hierarchy. We note that such situations—when closely related species inhabit largely parapatric distributions—are perhaps the most likely cases where behavioral interactions may contribute to the delimitation of species' range limits (Martin and Martin 2001; Freeman and Montgomery 2015). Moreover, the structure of the dominance hierarchy is interesting in its own right, and it can be brought to bear on a wide variety of research questions. For example, as no-analog communities (Jackson and Overpeck 2000; Graham et al. 2017) are generated as a product of climate change, species introductions, and other anthropogenic activities, interspecific dominance hierarchies linking currently geographically separated taxa may actually provide a predictive framework for understanding which species will and will not be able to coexist.

Social dominance interactions like those studied here have well-documented consequences for species' acquisition of resources (e.g., Samuels et al. 1984). In our study, this interference competition from dominant species provided these species with preferential access to food at feeders. Whether a link exists between social dominance interactions and competitive dominance (measurable fitness impacts of a dominant species on a subordinate species) over longer evolutionary timescales is unknown. Certainly, these interactions shape species' behaviors indirectly. For instance, species may shift their foraging times and locations to avoid close competitors that they are unable to exclude. As an example, less dominant hummingbirds may feed on lower-quality nectar patches (Wolf et al. 1976), or less nectarivorous honeyeaters may avoid aggressive interactions by gleaned methodically in vegetation (Miller, Wagner et al. 2017). Behavioral interactions at a local scale may therefore scale up to larger phenomena on continental scales, including migration timing and distance (Freshwater et al. 2014), and such interactions may even play a role in shaping species' distributions on a continental scale (Robinson and Terborgh 1995; Pasch et al. 2013). These biological hypotheses can be examined only by describing dominance relationships across communities of birds over very large regions. By partnering with an existing citizen science project, we provided the first continental-scale view of these local, infrequently observed interactions at communal food resources. We see our work, where a targeted behavioral study was linked with an existing citizen science project, as a model for gathering robust natural history data at broad spatiotemporal scales.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Miller, Bonter, et al. 2017), and R code available from <https://github.com/eliotmiller/networkTricks>.

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