

# Repeated patterns of trait divergence between closely related dominant and subordinate bird species

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**Abstract.** Ecologically similar species often compete aggressively for shared resources. These interactions are frequently asymmetric, with one species behaviorally dominant to another and excluding it from preferred resources. Despite the potential importance of this type of interference competition as a source of selection, we know little about patterns of trait divergence between dominant and subordinate species. We compiled published data on phylogenetically independent, closely related species of North American birds where one species was consistently dominant in aggressive interactions with a congeneric species. We then compared the body size, breeding phenology, life history, ecological breadth, and biogeography of these species. After accounting for body size and phylogeny, we found repeated patterns of trait divergence between subordinate and dominant species within genera. Subordinate species that migrated seasonally arrived 4–7 days later than dominants on their sympatric breeding grounds, and both resident and migratory subordinates initiated breeding 7–8 days later than their dominant, sympatric congeners. Subordinate species had a 5.2% higher annual adult mortality rate and laid eggs that were 0.02 g heavier for their body mass. Dominant and subordinate species used a similar number of different foods, foraging behaviors, nest sites, and habitats, but subordinates were more specialized in their foraging behaviors compared with closely related dominant species. The breeding and wintering ranges of subordinate species were 571 km farther apart than the ranges of dominant species, suggesting that subordinate species migrate greater distances. Range sizes and latitudinal distributions did not consistently differ, although subordinate species tended to breed farther north or winter farther south. These results are consistent with dominant species directly influencing the ecological strategies of subordinate species (via plastic or genetically based changes), either by restricting their access to resources or simply through aggression. Alternatively, these ecological traits may covary with patterns of behavioral dominance, with no direct consequences of interactions. Regardless of the mechanism, recognizing that the relative position of a species within a dominance hierarchy is correlated with a suite of other ecological and fitness related traits has far-reaching implications for the mechanisms underlying species distributions and the structure of biological assemblages.

**Key words:** aggressive interactions; behavioral dominance; birds; body mass; ecological breadth; ecological traits; interference competition; life history; migration; phenology; social dominance; species interactions.

## INTRODUCTION

Ecologically similar species often interfere with each other's access to shared resources. This interference competition has played a central role in shaping our views on the ecology and evolution of niche breadth, patterns of resource use, and species coexistence (Case and Gilpin 1974, Morse 1974, Dhondt 2012, Grether et al. 2013). In animals, interference may include physically aggressive behaviors, with one species biting, chasing, displacing, or even killing another to monopolize preferred resources (Morse 1974, Donadio and Buskirk

2006), and signals (e.g., call or smell) that cause avoidance or abandonment of a preferred resource (Robinson and Terborgh 1995, Grether et al. 2009). The outcomes of interference among animal species are rarely symmetric: one species typically wins the majority of aggressive encounters with another species (Morse 1974, Persson 1985, Young 2003, Donadio and Buskirk 2006), leading to priority access to resources. Douglas Morse (1974) referred to this priority access to resources as social or behavioral dominance, and predicted that if interspecific aggression could result in the formation of long-lasting dominance hierarchies, then it may also act as a force of directional selection. In support of this prediction, Morse (1974) found that subordinate species often had larger fundamental niches than dominants, a

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potential evolved response to reduce the costs of competitive exclusion.

Evidence suggests that dominant species commonly exclude subordinate species from mutually preferred or high-quality resources and impose selection for divergence in traits that reduce the fitness cost of sympatry (Morse 1974, Chappell 1978). Past studies have documented consistent differences between dominant and subordinate species with respect to body size (Morse 1974, Donadio and Buskirk 2006), foraging and related behaviors (Feinsinger 1976, Daily and Ehrlich 1994), nest site defense (Pearce et al. 2011), tendency to form conspecific and heterospecific groups (Daily and Ehrlich 1994, Palomares and Caro 1999), development of weapons and fighting behavior (Young 2003, Donadio and Buskirk 2006), bill size (Daily and Ehrlich 1994), wing morphology (Feinsinger and Chaplin 1975; although this pattern was not found by Altshuler et al. 2004), breadth of diet (Blowes et al. 2013), daily activity patterns (Shields and Bildstein 1979, Daily and Ehrlich 1994), local abundance (Pierpont 1986), geographic range size (Glazier and Eckert 2002), and ability to persist in degraded habitats (Daily and Ehrlich 1994). Collectively this research suggests that dominant species often possess traits useful in aggression, and subordinate species are often forced to use a greater diversity of lower quality resources, or a reduced range of resources (Morse 1974, Ziv et al. 1993, Kimura and Chiba 2010).

To date, previous research on the patterns of trait divergence between dominant and subordinate species has largely been limited to a small group of species and traits, and we know of no attempts to test whether closely related species that exhibit asymmetric aggressive interactions consistently differ with respect to a broad array of ecological traits and strategies. Here, we address this issue using a comparative approach in which we ask if subordinate species have diverged from closely related dominant species in a predictable manner across a suite of ecological traits. We first compiled a data set on aggressive interactions among closely related North American bird species, coupled with data on their migratory and breeding phenologies, life histories, ecological breadths, and geographic distributions. We used phylogenetically independent comparisons of closely related species of birds (congeners) that share many ecological traits through recent shared ancestry, but also show a consistent asymmetric relationship in aggressive contests, where one species is behaviorally dominant to the other (see Supplement 1 for results of aggressive contests). Because larger species are typically dominant to smaller species in aggressive contests (Morse 1974, Schoener 1983, Persson 1985, Donadio and Buskirk 2006), we included body mass in all of our tests of our predictions. We recognize that we cannot distinguish between the direct effects of interactions among species vs. the secondary effects of traits that may be associated with behavioral dominance, but are as yet poorly known (e.g., testosterone; Owen-Ashley

and Butler 2004). We also recognize that differences between dominant and subordinate species may reflect either plastic responses to current ecological interactions, or evolved differences. Nevertheless, any repeated patterns would reveal a novel connection between ecological traits and behavioral dominance and provide an opportunity for future work to identify causal mechanisms.

### *Predictions*

If behaviorally dominant species restrict access to resources for subordinate species (Morse 1974, Pimm et al. 1985, Ziv et al. 1993, Kimura and Chiba 2010), then we hypothesized that subordinates would exhibit consistent and divergent patterns in ecological characteristics that would reflect these interactions. Specifically we made the following predictions:

- 1) *Phenology*: Subordinate species may arrive on breeding grounds and initiate clutches later than dominant species. Without access to preferred resources, subordinate species may be unable to depart wintering grounds early (Studds and Marra 2005), have to migrate greater distances, or be delayed during migration (Moore and Yong 1991, Salewski et al. 2007). Subordinate species may also delay their arrival or breeding if they are restricted to suboptimal conditions by dominant species early in the breeding season (Møller 1994).
- 2) *Life history*: Subordinate species may suffer higher adult mortality if they are restricted in their access to preferred resources (Studds and Marra 2005), leading to an increase in their investment in annual reproduction (e.g., clutch size, egg mass; Stearns 1992) compared to behaviorally dominant species.
- 3) *Ecological breadth*: Behaviorally subordinate species may show greater ecological breadth compared with dominant species if the dominant species forces subordinates to use alternative resources, in addition to using preferred resources when the dominant species is absent (Morse 1974, Minot and Perrins 1986). Ecological specialization may also increase the value and importance of a resource, leading to stronger selection for traits that enhance behavioral dominance with competitor species, and thus causing greater specialization in dominant species (Blowes et al. 2013).
- 4) *Biogeography*: If competitively dominant species are widespread and force subordinates to use regions on the periphery of their geographic ranges, then subordinate range sizes may be smaller (Glazier and Eckert 2002, Duckworth and Badyaev 2007). Alternatively, subordinate species may have larger geographic ranges if they occupy widespread and diverse, marginal habitats less preferred by dominant species (Glazier and Eckert 2002). Dominant species may force subordinates to breed farther north or winter farther south, as well drive subordinates to

migrate greater distances to find suitable resources (Cox 1968, Feinsinger et al. 1985, Greenberg 1986, Holmgren and Lundberg 1993).

We tested all of these predictions across 65 phylogenetically independent comparisons of closely related North American birds.

#### METHODS

We examined closely related species (congeners) that are expected to share many traits through recent common ancestry, thus improving our chances of isolating ecological traits that covary specifically with behavioral dominance. We compiled data on aggressive interactions among congeneric species for which behavioral dominance data were available. We preferentially selected the most closely related (youngest) congeneric species that were phylogenetically independent from other groups in our study (i.e., members of each focal pair were part of a monophyletic group that did not include any other species in our study). Once we had identified focal species pairs that showed a significant asymmetry in wins vs. losses in aggressive contests, we compiled data on body mass, phenology, life history, ecological breadth, and biogeography to test the predictions of our hypotheses. We assessed the significance of asymmetries in wins vs. losses using binomial tests. Phylogenetic information and details of the methods that we used in our study are available in Supplement 2.

##### *Aggressive interactions*

We compiled published data on aggressive interactions between focal bird species, resulting in 4589 total interactions. These interactions were typically observed during the course of resource acquisition or defense, and thus provide insight into the outcome of interference competition and behavioral dominance. The following aggressive interactions were included in our data set: chases, supplants and displacements, kleptoparasitism, and physical attacks (see the Appendix for definitions and details).

In addition to species pairs with quantitative data on aggressive interactions, we included species pairs with published descriptions of behavioral dominance among species in peer-reviewed sources where we could not access the original data ( $N = 19$  comparisons). In total, we included 65 phylogenetically independent comparisons (see Supplement 1 for details). Our data come from many sources and cannot account for all confounding variables that could influence the outcome of aggressive contests. Nonetheless, we can think of no way that the diversity of data sources could bias our results with respect to the specific predictions that we tested.

##### *Body mass*

We compiled raw mass data from areas of sympatry between interacting species (see Appendix for detailed

methodology). Mass data were used as a covariate in statistical analyses that tested our predictions.

##### *Phenology*

We recorded earliest arrival dates on the breeding grounds (migratory species) and breeding initiation dates (all species) for focal species pairs in areas of sympatry (see Supplement 1 for details). We recorded breeding initiation dates (e.g., first egg dates) instead of mean or median breeding dates because we were interested in when breeding commenced during the annual cycle, and mean or median dates are influenced by reneesting later in the breeding season. In total, we compiled 1119 phenological records representing 63 species comparisons.

##### *Life history*

*Clutch size.*—We compiled average clutch sizes (number of eggs laid per nest) for all of our focal species for which data were available. We only included data from areas where our focal species pairs were sympatric, and we compiled data from the same site or region (e.g., state and province summaries) for each species pair (see Appendix for details). In total, we compiled 265 clutch size records representing all 65 species comparisons.

*Egg mass.*—We compiled fresh egg mass data for our focal species from Schönwetter (1960–1992), who used the length, width, and shape of eggs, plus the mass of the egg shell and standard mass of yolk and albumin to estimate fresh egg masses for most of the world's birds (for rationale see Appendix A). We preferentially used estimates for subspecies of our focal species pairs that occur in areas of sympatry. In total, we compiled 165 estimates of fresh egg mass, representing all 65 species comparisons.

*Number of broods.*—The number of broods per year is the number of successful nesting attempts (i.e., young fledged from the nest) that an adult or pair will attempt in one year and is an important contribution to annual fecundity. We compiled the most common number of broods per year for each of our species, based on data from across North America (Poole 2013).

*Adult survival.*—We compiled estimates of apparent annual adult survival for our focal species from the literature. Estimates of apparent adult survival can vary substantially depending on the methods and models used to estimate survivorship (Cilimburg et al. 2002, Sandercock 2006), and require large sample sizes to produce accurate estimates (Krementz et al. 1997, Franklin et al. 2002). To address these issues, in addition to geographic and temporal variation in survival rates, we compiled estimates of apparent adult survivorship where estimates for both species within a comparison were (1) based on data from the same location or region of study, (2) estimated using the exact same methods, (3) analyzed in the same study (or series of studies), and (4) estimated with a minimum sample size of 100 adults for

each species (see Appendix A for details). In total, we compiled 74 estimates of annual adult survival that met our criteria, representing 20 species comparisons.

#### *Ecological breadth*

We examined four characteristics of ecological breadth: diet, foraging behavior, nest site, and habitat use. We compiled data on focal ecological traits from locations or regions of sympatry for our focal species pairs, including only published studies or theses with sample sizes of at least six individuals per species. We used the categories of diet, foraging behavior, nest sites, and habitats that were specified by the source, and also included data from different spatial scales (e.g., habitat use from breeding bird atlases, habitat use in foraging within a study site). For each variable, we compiled the number of different categories of diet, foraging behaviors, nest sites, or habitats that were used by each species within a focal species pair, and the frequency with which each category was used. These data allowed us to calculate two metrics of ecological breadth for each study and resource: (1) richness is the number of different resource categories used by each species, and (2) diversity is the Shannon-Weaver diversity index,  $H$ , for each resource used by each species:

$$H = -\sum_{i=1}^R p_i \ln(p_i)$$

where  $R$  is the number of different categories of a resource, and  $p_i$  is the proportion of observations in each resource category (Weaver and Shannon 1963). Richness provided us with a simple measure of the number of different resource categories used by each species, while the Shannon-Weaver diversity index provided us with additional information on how the frequency of resource use differed across the categories.

In total, we compiled 136 estimates of diet breadth, representing 33 independent species comparisons, 64 estimates of foraging behavior breadth (17 species comparisons), 116 estimates of nest site breadth (31 species comparisons), and 410 estimates of habitat use breadth (49 species comparisons). Details of each ecological breadth category may be found in Appendix A.

#### *Biogeography*

We measured biogeographical traits using range maps from BirdLife International and NatureServe (2011) in ArcGIS 10.1 (ESRI, Redlands, California, USA). For species with additional populations outside of the Americas, we measured only the ranges of the populations breeding and wintering within the Americas, where the majority of our interaction data originated. For each focal species, we measured the size of the breeding and wintering ranges in km<sup>2</sup> using a Lambert Azimuthal Equal Area projection, and calculated the latitude and longitude of the centroid (the area-weighted mean of the range) of each breeding and wintering range in decimal

degrees. We used the latitude and longitude of the breeding and wintering ranges to calculate the distance (in km) between the centroid of the breeding range and the centroid of the wintering range, using an *online calculator*.<sup>5</sup>

#### *Statistical methods*

We tested the hypothesis that ecological traits differed between dominant and subordinate species using linear mixed-effects models (Pinheiro et al. 2012) for Gaussian distributions and generalized linear mixed models (Bates et al. 2011) for Poisson or binomial distributions, using the statistical program R (R Development Core Team 2012) and following Zuur et al. (2009). We used Akaike's information criteria, adjusted for small sample sizes (AIC<sub>c</sub>), to assess model performance with different predictor variables (Zuur et al. 2009). Because we performed statistical tests on 19 different variables, we controlled for false discovery rates using the methods of Benjamini et al. (2006), following Pike (2010). We present  $P$  values controlling for false discovery ( $q$  values; see Pike 2010). For generalized linear mixed models, we ran all of our analyses with two different packages, lme4 (Bates et al. 2011) and MASS (Ripley et al. 2012), to ensure that our results were consistent across packages (Zuur et al. 2009). Please see the Appendix for detailed statistical methods.

After discovering significant differences between dominant and subordinate species, we conducted two additional analyses to test for relationships among ecological traits. Specifically, we tested the hypothesis that a greater distance between breeding and wintering ranges for subordinate species ("migration distance") could explain the delayed arrival of subordinates on their shared breeding grounds. We also tested the hypothesis that a greater migration distance for subordinate species could explain their lower rates of annual adult survival. These two analyses were performed using the same methodology as for the previous tests, except that both dominance and migration distance were the predictor variables in the analyses.

#### RESULTS

North American birds showed consistent ecological differences in phenology, life history, breadth of foraging behaviors, and biogeography that covaried with the outcome of aggressive interactions with another closely related species (Tables 1 and 2). Of the most closely related species pairs with quantitative data on behavioral interactions, 98% (64 of 65 pairs) showed statistically significant ( $P < 0.05$ ) asymmetries in wins vs. losses in aggressive contests, illustrating that dominance asymmetries predominate among interacting congeners of North American birds. In 59 of the 65 focal species comparisons, the heavier congener was behav-

<sup>5</sup> <http://www.csgnetwork.com/gpsdistcalc.html>



TABLE 1. Parameters and models used in testing for differences in ecological traits as a function of behavioral dominance, body mass, and the interaction between behavioral dominance and body mass, among congeners of North American birds.

Parameter	Model	Sample size	
		Comparisons	Observations
Phenology			
Arrival date	glmm	49	525
Breeding date	glmm	62	594
Life history			
Clutch size	lme	65	265
Egg size	lme	65	165
Broods/year	glmm	65	135
Annual adult survival	glmm	20	74
Ecological breadth: richness			
Diet	lme	32	130
Foraging behavior	lme	17	64
Nest site	lme	31	116
Habitat	lme	49	410
Ecological breadth: diversity			
Diet	lme	31	132
Foraging behavior	lme	17	64
Nest site	lme	29	108
Habitat	lme	46	392
Biogeography			
Breeding range size	lme	65	135
Wintering range size	lme	65	135
Breeding range latitude	lme	65	135
Wintering range latitude	lme	65	135
Migration distance	lme	57	118

Notes: Model types are generalized linear mixed model (glmm) and linear mixed effects model (lme). Comparisons are the number of congeneric species pairs analyzed. Observations represent the summed number of records (e.g., unique studies and sites) across all species.

iorally dominant to the lighter congener (Supplement 1). However, the significant effects of dominance status remained even after statistically controlling for any significant effects of body mass (Table 2). We present  $AIC_c$  values for all models for each response variable (Appendix: Table A1), and the results of statistical tests that include dominance without body mass (Table A2), and body mass without dominance (Table A3) in the Appendix.

### Phenology

Migratory subordinate species arrived on their shared (sympatric) breeding grounds 4.2 days later (95% confidence interval: 1.30–7.01 days) than their closely related, dominant congeners, 6.4 days later (95% CI: 2.40–10.13 days) after controlling for body mass; see Fig. 1, Table 2). This pattern was robust across species comparisons, where 33 of 49 (67%) showed delayed arrival of subordinate species, representing 15 of 21 (71%) taxonomic families. Subordinate species (migratory and resident together) also initiated breeding 7.4 days later (95% CI: 4.20–10.54 days) than their closely related dominant congeners (Fig. 1, Table 2). Across

species comparisons, 48 of 62 (77%) showed delayed breeding initiation of subordinate congeners, representing 25 of 28 (89%) taxonomic families. Delayed breeding by subordinates was also observed in all eight resident species comparisons (defined as nonmigratory by Ridgely et al. 2011), initiating breeding 7.7 days later (95% CI: 2.16–13.26 days; likelihood  $L = 7.23$ ,  $df = 1$ ,  $P = 0.0072$ ,  $P_{adj} = 0.021$ ; Fig. 1). Body mass did not significantly predict differences in phenology between congeners, either alone, or in an interaction with dominance status (Table 2); however, body mass was included in the best-performing model (lowest  $AIC_c$ ) for arrival date.

### Life history

Behaviorally subordinate species laid significantly smaller eggs (Appendix), but significantly larger eggs for their body mass, and had significantly lower estimated annual adult survival rates, compared with their dominant congeners (Fig. 2, Table 2; see Appendix). Controlling for the effects of body mass, subordinate species laid eggs that were 0.02 g heavier (95% CI: 0.011–0.027 g), and were 5.2% (95% CI: 1.39–9.14%) less likely to survive over one year as adults, compared with their dominant congeners. Subordinate species laid larger eggs for their body mass compared with their dominant congeners in 45 of 65 (70%) comparisons, representing 26 of 30 (87%) taxonomic families. Subordinate species showed lower survival rates for their body mass compared with their dominant congeners in 13 of 20 (65%) comparisons, representing 13 of 15 (87%) taxonomic families. Estimates of survival based on studies with local recapture efforts may confound permanent emigration (dispersal) with mortality (Cilimburg et al. 2002). However, the difference in survival estimates between dominant and subordinate congeners did not vary significantly between studies that recovered banded birds locally ( $N = 62$  estimates) vs. studies that recovered banded birds across North America ( $N = 12$  estimates;  $P > 0.50$ ), suggesting that our results reflect differences in mortality rather than dispersal. Clutch size and the number of broods per year did not differ between dominant and subordinate congeners (Table 2). Larger species laid larger eggs, had fewer broods per year, and had higher annual adult survival rates compared to their smaller, closely related congeners (Table 2).

### Ecological breadth

Dominant and subordinate species did not differ in the number of different foods, foraging behaviors, nest sites, or habitats that they used in sympatry (Table 2). Subordinate species, however, used their foraging behaviors differently than dominant congeners (Fig. 3, Table 2). Subordinate species concentrated their foraging on fewer behaviors, leading to a significantly lower diversity index for foraging behavior compared with their dominant congeners in sympatry, a difference of

TABLE 2. Results of our best-performing statistical models (lowest AIC<sub>c</sub> scores) testing for differences in ecological traits as a function of behavioral dominance, body mass, and the interaction between behavioral dominance and body mass, among congeners of North American birds.

Parameter	Behavioral dominance					Body mass				
	Estimate	SE	$\chi^2$	<i>P</i>	<i>P</i> <sub>adj.</sub>	Estimate	SE	$\chi^2$	<i>P</i>	<i>P</i> <sub>adj.</sub>
Phenology†										
Arrival date	−0.075	0.024	8.91	<b>0.003</b>	<b>0.014</b>	−0.037	0.024	2.34	0.13	0.23
Breeding date	−0.063	0.014	16.01	<b>&lt;0.0001</b>	<b>0.0005</b>					
Life history										
Egg size	0.007	0.038	27.54	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.794	0.019	307.93	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Broods/year						−0.941	0.529	5.42	<b>0.020</b>	<b>0.049</b>
Annual adult survival	−0.212	0.080	5.89	<b>0.015</b>	<b>0.033</b>	0.349	0.042	30.20	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Ecological breadth: diversity‡										
Foraging behavior	−0.153	0.062	5.83	<b>0.016</b>	<b>0.033</b>					
Nest site						0.034	0.019	3.27	0.071	0.15
Biogeography										
Wintering range size						25.394	9.647	6.40	<b>0.011</b>	<b>0.034</b>
Breeding range latitude§						−0.055	0.018	8.73	<b>0.003</b>	<b>0.012</b>
Wintering range latitude§						−0.061	0.021	8.60	<b>0.003</b>	<b>0.012</b>
Migration distance¶	0.911	0.330	7.28	<b>0.007</b>	<b>0.021</b>					

Notes: Estimates are given for the behaviorally subordinate species (those species losing significantly more than half of aggressive contests) relative to their dominant congener. For all variables, *df* = 1. Adjusted *P* values (*P*<sub>adj.</sub>) have been adjusted for false discovery rates following Benjamini, Krieger, and Yekutieli (2006); boldface denotes statistically significant results (*P* < 0.05) after controlling for false discovery. Results of the dominance × body mass interaction model are not shown because none were significant except egg size (0.015 ± 0.007, estimate ± SE;  $\chi^2$  = 4.31; *P* = 0.038; *P*<sub>adj.</sub> = 0.38). See Appendix for AIC<sub>c</sub> scores for all models.

† Phenological dates were inverted prior to analysis to improve model fit; thus, a negative effect of dominance reflects a delayed phenology of subordinate species relative to their dominant congeners.

‡ Sample size was included as a covariate in all models, but was removed if it did not improve model performance (assessed by AIC<sub>c</sub>).

§ Latitude was inverted prior to analysis; thus, a negative effect of body mass reflects an increase in body mass with latitude.

¶ Distance between the centroids (area-weighted means) of the breeding and wintering ranges.

0.15 (95% CI: 0.030–0.277; Fig. 3, Table 2). Across species comparisons, 22 of 32 (69%) showed lower foraging behavior diversity for subordinate congeners, representing 10 of 11 (91%) taxonomic families. The diversity of diets, nest sites, and habitats did not differ between dominants and subordinates, and body size did not covary significantly with any index of ecological breadth (Table 2).

### Biogeography

The centers of the breeding and wintering ranges of subordinate species were 571 km farther apart (95% CI: 154–1108 km) compared with their dominant congeners, suggesting that subordinate species migrate farther (Fig. 4, Table 2). In 36 of 57 (63%) species comparisons, subordinates showed a greater distance between breeding and wintering ranges compared with dominants,

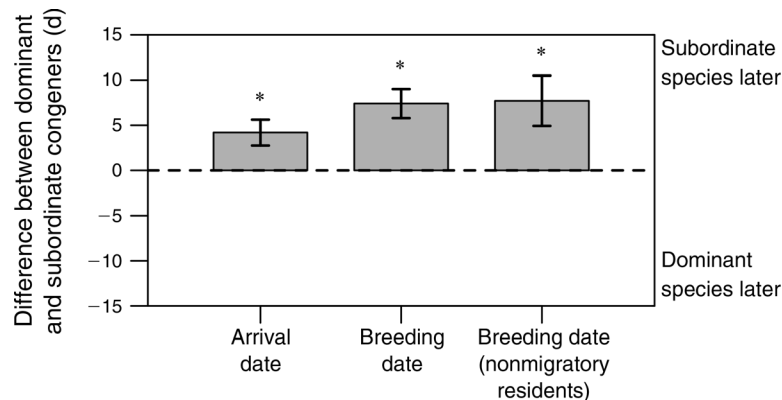


FIG. 1. Differences (mean ± SE) in phenology between subordinate and dominant congeners of North American birds, controlling for variation among different species pairs. Positive values indicate later dates for subordinate species relative to their dominant congeners. Asterisks indicate significant differences in phenologies (*P* < 0.05, adjusted for false discovery rates; see Table 2).

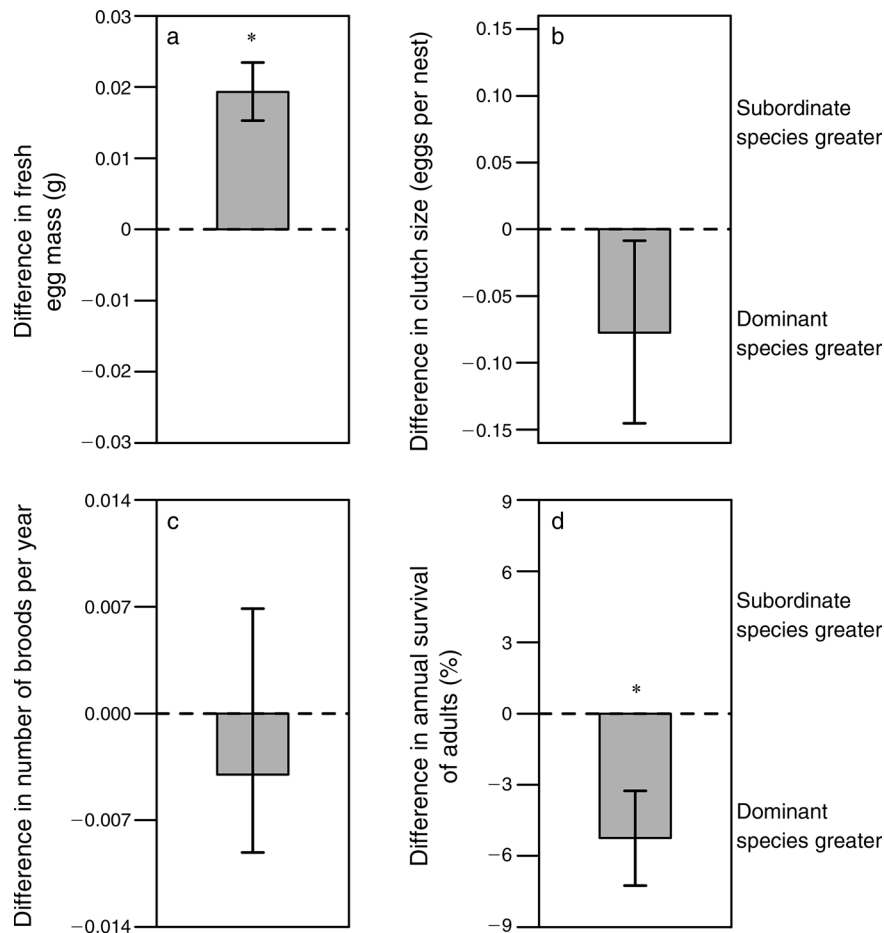


FIG. 2. Differences (mean  $\pm$  SE) in life history traits between subordinate and dominant congeners, controlling for variation among different species pairs: (a) fresh eggs mass, (b) clutch size, (c) broods per year, and (d) annual adult survival. Positive values indicate larger subordinate values relative to their dominant congeners. Asterisks indicate significant differences in life history traits ( $P < 0.05$ , adjusted for false discovery rates; Table 2). Estimates for egg mass, number of broods, and adult survival control for the significant effects of body size (see Table 2).

representing 18 of 26 (69%) taxonomic families. The greater distances between the breeding and wintering ranges of subordinate species did not reflect any significant differences in the latitudes of their ranges, although subordinate species tended to breed farther north or winter farther south (Table 2; Fig. 4c). Similarly, geographic range sizes did not differ between dominant and subordinate congeners (Table 2). Consistent with Bergmann's rule, body size was significantly larger in congeners that bred and wintered at higher latitudes (Table 2). Body mass also increased with wintering, but not breeding, range size (Table 2).

#### *Interactions among traits*

Species with greater distances between their breeding and wintering ranges (migration distance) arrived later on their breeding grounds ( $\chi^2 = 25.6$ ,  $df = 1$ ,  $P < 0.0001$ ). However, subordinate species still arrived 3.0 days later ( $\chi^2 = 3.0$ ,  $df = 1$ ,  $P = 0.08$ ) after accounting for differences in migration distance. Species with greater

distances between their breeding and wintering ranges did not suffer higher annual rates of mortality ( $\chi^2 = 0.02$ ,  $df = 1$ ,  $P = 0.90$ ).

#### DISCUSSION

Interference competition plays an important role in the structuring of ecological communities (Case and Gilpin 1974, Morse 1974, Grether et al. 2013). In animals, this interference is often asymmetric, with one species able to exclude another from a shared resource (Chappell 1978, Ziv et al. 1993), resulting in potentially strong selection on a diversity of ecological traits (Morse 1974). Here we compared closely related dominant and subordinate congeneric bird species, and found a repeated, general pattern of divergence: subordinate species showed delayed arrival and breeding phenologies, distinct life history strategies, and longer distances between wintering and breeding ranges compared to their closely related dominant congeners (Table 2, Figs. 1, 2, and 4). Subordinate species did not use a broader

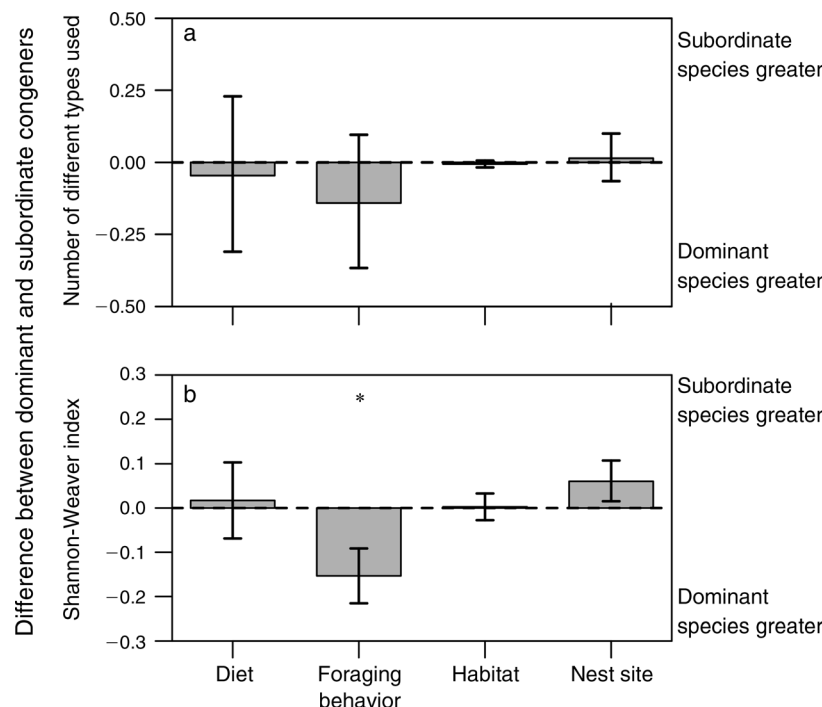


FIG. 3. Differences (mean  $\pm$  SE) in ecological breadth between subordinate and dominant congeners, controlling for variation among different species pairs: (a) richness (number of different food items, foraging behaviors, habitats, or nest sites used) and (b) diversity (Shannon-Weaver index of different food items, foraging behaviors, habitats, or nest sites used). Positive values indicate larger subordinate values relative to their dominant congeners. Asterisks indicate significant differences in ecological breadth ( $P < 0.05$ , adjusted for false discovery rates; Table 2).

or narrower array of resources, but did show evidence of greater specialization in foraging behaviors compared with their dominant congeners (Table 2, Fig. 3). Although body size was strongly associated with success in aggressive bouts, variation in body mass could not explain differences in foraging strategy (Table 2), and did not covary significantly with differences in phenology, ecological breadth, or migration distance between dominant and subordinate species. Body mass, however, was a significant covariate for most life history traits (Table 2), consistent with life history theory (Stearns 1992). Our results suggest that asymmetric interference in competitive interactions may have important direct or indirect consequences for diverse ecological and fitness related traits among ecologically similar species.

#### *Causes of differing ecological strategies with dominance*

Our results are consistent with the hypothesis that behaviorally dominant species restrict access to resources for subordinate species, causing plastic or evolved changes in the subordinates' phenologies, life histories, diversity of foraging behaviors, and distributions. Our results, however, are also consistent with other alternative explanations. Rather than direct competition over resources, dominants could be exhibiting misdirected conspecific aggression toward subordinate species, leading to shifts in ecological traits of subordinates independent of resources. Another alternative hypothe-

sis is that the association between ecological traits and behavioral dominance is independent of direct interactions between species. For example, the suite of traits associated with behavioral dominance may be related to differences in metabolism and physiology that influence resource use, migration speed, ability to tolerate cold environments, or aging. Such relationships could secondarily influence the phenologies or life histories of species, potentially in complicated or even opposing ways. Although we accounted for differences in body mass between dominant and subordinate species (Table 2), other traits associated with behavioral dominance could play an important role in explaining the ecological differences that we found.

Nonetheless, previous experimental and observational work provides support for direct interactions among species determining how resources are used in nature. Experimental removals have revealed that behaviorally dominant species commonly exclude subordinates from preferred habitat, food, and nest sites, and directly reduce their overall fitness (Dhondt 2012). Although both behaviorally dominant and subordinate species interact aggressively and suffer costs of co-occurrence (Grether et al. 2013), subordinate species probably experience greater fitness costs through reduced access to resources. As a result, ecological traits that allow subordinates to avoid dominant species should be favored, unless other aspects of habitat quality outweigh



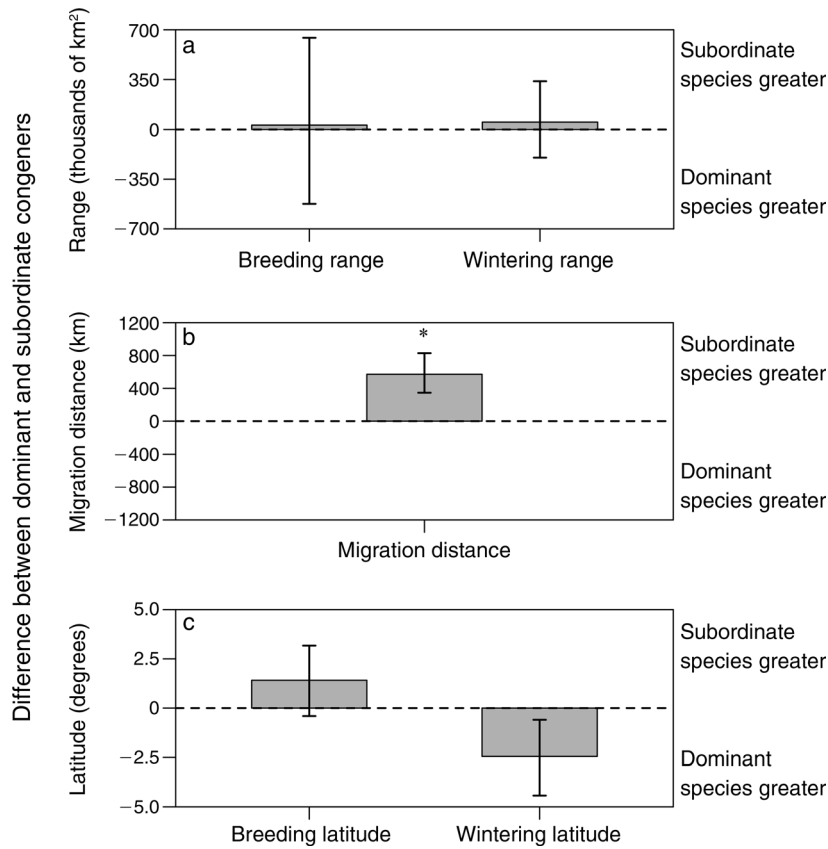


FIG. 4. Differences (mean  $\pm$  SE) in biogeographic traits between subordinate and dominant congeners, controlling for variation among different species pairs: (a) geographic range (thousands of km<sup>2</sup>), (b) migration distance, and (c) area-weighted latitude (centroid; degrees). Positive values indicate larger values for subordinate species relative to their dominant congeners. Asterisks indicate significant differences in phenotypes ( $P < 0.05$ , adjusted for false discovery rates; Table 2). Estimates of winter range size and latitude control for the significant effects of body size (Table 2).

the costs of occurring with the dominant (Martin and Martin 2001a, b). These cost–benefit dynamics can shift with the density of dominant and subordinate species, and with other biotic and abiotic conditions such as predation pressure and climate, to ultimately determine the distributions of species at different spatial scales (Case and Taper 2000, Case et al. 2005).

*Patterns of trait divergence across species mirrors patterns within species*

Some of the ecological differences between dominant and subordinate species parallel differences between dominant and subordinate individuals within species. For example, behaviorally dominant individuals (older birds in better condition) typically arrive on the breeding grounds first (Møller 1994, Newton 2006), breed earlier (Perrins and Moss 1974), and migrate shorter distances relative to subordinate individuals (Cox 1968), similar to the patterns between dominant and subordinate congeners. Although the direct causes of these within-species patterns are poorly known, experiments on the wintering grounds suggest that dominant American Redstarts (*Setophaga ruticilla*) behaviorally exclude subordinate

individuals from preferred winter habitat, thereby delaying their departure for the breeding grounds (Studds and Marra 2005). Similar interference mechanisms have been proposed to explain delayed breeding and greater migration distance of subordinate individuals (Cox 1968, Feinsinger et al. 1985, Greenberg 1986, Holmgren and Lundberg 1993); however, the relationships may also be caused by other traits that covary with dominance, independent of direct interactions.

*Life history traits*

Subordinate species had 5.2% lower estimated annual adult survival compared with their dominant congeners (Fig. 2). Mortality during migration is significant in many species of birds (Sillett and Holmes 2002, Newton 2006); however, migration distance did not explain the differences in estimated survival between dominants and subordinates in our study, suggesting that the costs of migrating farther are insufficient to explain high subordinate mortality rates by themselves. A higher adult mortality rate for subordinates, however, is predicted if dominant species exclude subordinates from resources important for survival, such as safe foraging,

nesting, or roosting sites, or areas of high food abundance. This prediction is upheld within an intra-specific dominance hierarchy (Studds and Marra 2005), as well as among distantly related, but aggressively competitive species (tits, *Parus* spp., and Collared Flycatchers, *Ficedula albicollis*; Merilä and Wiggins 1995).

Subordinate species laid heavier eggs for their mass compared to their dominant congeners (Fig. 2), suggesting greater investment in their eggs. Although egg production is costly for birds (Williams 2005), the difference in egg mass between dominant and subordinate species was very small—0.02 g or 0.5% of the average egg mass. The numbers of broods produced per year and clutch size were not correlated with position in a dominance hierarchy; however, previous studies have detected reduced hatching and fledging success within subordinate species despite stable clutch sizes (Brazill-Boast et al. 2011). Unfortunately, we do not have data on other aspects of reproductive investment (e.g., hatching success, parental care), but the differences in estimated adult survival, coupled with the differences in egg mass, are consistent with a shift in annual investment from survival to reproduction in subordinate species (Stearns 1992). If true, this shift in investment should be evident in other important life history traits, such as defense against the threat of predation (Ghalambor and Martin 2001).

#### *Ecological breadth of dominant and subordinate species*

We found that dominant and subordinate congeners used similar numbers of resources, providing no evidence that subordinate species were more likely to represent ecological specialists or generalists relative to their dominant congeners (Fig. 3). The lack of a difference in ecological breadth between dominant and subordinate congeners in our study may reflect the broad ecological strategies of the majority of our focal species; our study included few ecological specialists, in contrast to studies where specialization of dominant species has been observed (Blowes et al. 2013). Our results appear to contrast with those of Morse (1974), who presented evidence that ecological breadth was greater in behaviorally subordinate species when considering areas where they co-occur with behavioral dominants, and areas where they do not. Our comparisons of ecological breadth, however, involved data from regions of sympatry only; thus, we would be unable to detect instances where behaviorally dominant species cause subordinates to narrow or shift their resource use in sympatry relative to allopatry.

Our estimates of ecological breadth also hinge on the definition of categories of resources that we used to define breadth. These definitions of resource categories were taken directly from the original studies. If birds view resource categories differently than researchers' definitions, then we may misrepresent ecological breadth from the perspective of the organisms. Nonetheless, if

differences in ecological breadth between dominant and subordinate species were strong, we might expect consistent trends across resources. The lack of consistent trends across resources (Fig. 3) suggests that dominant and subordinate species may not show consistent differences in ecological breadth when they occur in sympatry.

Behavioral subordinates did use their foraging behaviors differently, focusing on fewer foraging behaviors (Fig. 3). We do not know why the use of foraging behaviors differed between dominant and subordinate species, while diet, nest sites, and habitat use did not. One possible explanation is that foraging behaviors can change or evolve more quickly than other traits, providing a rapid means of avoiding the costs of living with a dominant congener, particularly if the interactions are over food. Habitat differences, however, are often the first traits to diverge when closely related species of birds expand into sympatry (Schluter 2000), suggesting that any difference in ecological breadth between dominant and subordinate congeners should be first evident in habitat use.

#### *Consequences of differing ecological strategies with dominance*

Dominant and subordinate congeners differed in their phenologies, life histories, use of foraging behaviors, and distributions (Table 2), suggesting that the relative position of a species within a dominance hierarchy has important consequences for a suite of integrated traits (Daily and Ehrlich 1994, Donadio and Buskirk 2006, Blowes et al. 2013). These integrated traits link behavioral interactions between species with ecological strategies that ultimately influence where and when dominant and subordinate species occur. The patterns uncovered here occur across a taxonomically diverse group (15 orders, 30 families) representing various ecological strategies (vertebrate and invertebrate predators and herbivores that eat nectar, leaves, seeds, and fruit) and environments (freshwater, terrestrial, marine) across North America, suggesting that agonistic interactions and competitive interference among species may be more important as a selective pressure than previously recognized (Persson 1985, Grether et al. 2009, 2013, Peiman and Robinson 2010, Pfennig and Pfennig 2012). Identifying the mechanistic links between interference and broader ecological strategies will help to clarify when and how aggressive interactions among species influence the ecology and evolution of species in nature.

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## SUPPLEMENTAL MATERIAL

### Appendix

Detailed methods and supplementary results (*Ecological Archives* E095-207-A1).

### Supplement 1

Focal species pairs and results of interspecific aggressive interactions (*Ecological Archives* E095-207-S1).

### Supplement 2

Raw phenological, life history, and ecological breadth data (*Ecological Archives* E095-207-S2).