Why do crows attack ravens? The roles of predation threat, resource competition, and social behavior

Authors: Freeman, Benjamin G., and Miller, Eliot T.

Source: The Auk, 135(4) : 857-867

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-18-36.1

RESEARCH ARTICLE

Why do crows attack ravens? The roles of predation threat, resource competition, and social behavior

Benjamin G. Freeman[1]* and Eliot T. Miller[2]

[1] Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada
[2] Cornell Lab of Ornithology, Ithaca, New York, USA
* Corresponding author: freeman@zoology.ubc.ca

ABSTRACT

Interspecific aggression is common in birds—Individuals regularly chase and attack members of other species. We analyzed cases of interspecific aggression between crows (American Crow [*Corvus brachyrhynchos*] and Northwestern Crow [*C. caurinus*]) and ravens (Common Raven [*C. corax*]) using ∼2,000 citizen scientist observations of interspecific aggression between crows and ravens from across North America. Crows and ravens may attack one another for nonadaptive reasons, because they compete with each other for food and space, or because they are nest predators of each other. We report 3 main results. First, although ravens are much larger than crows, crows chased and attacked ravens in ∼97% of observations. We observed this strong asymmetry in the direction of interspecific aggression throughout North America. Second, crow aggression toward ravens was most frequent during the crows' nesting season (∼March–May), but also occurred in other seasons. Third, crows typically attacked ravens in small groups, with relatively few observations of aggression in one-on-one contests. The pattern of seasonality in crow attacks on ravens suggests that nest predation by ravens is an important factor driving interspecific aggression from crows. Aggression also occurred outside the breeding season, particularly in the winter, indicating either that crows compete with ravens for resources at this time of year or that crows preemptively harass potential nest predators in advance of the breeding season. This study is an example of how citizen scientists can contribute to the study of behavioral interactions of birds at a continental scale.

Keywords: behavioral interactions, citizen science, interspecific aggression, interspecific competition, mobbing, sociality

¿Por qué *Corvus brachyrhynchos* y *C. caurinus* atacan a *C. corax*? Los roles de la amenaza de depredación, la competencia por recursos y el comportamiento social

RESUMEN

La agresión interespecífica es común en las aves—los individuos regularmente persiguen y atacan a miembros de otras especies. Analizamos casos de agresión interespecífica de *Corvus brachyrhynchos* y *C. caurinus* a *C. corax* usando observaciones de 2,000 científicos ciudadanos de agresión interespecífica entre estas especies a lo largo de América del Norte. *C. brachyrhynchos* y *C. caurinus* pueden atacar a *C. corax* por razones no adaptativas, porque compiten entre ellos por alimento y espacio, o porque son mutuos depredadores del nido. Encontramos tres resultados principales. Primero, aunque *C. corax* es mucho más grande que *Corvus brachyrhynchos* y *C. caurinus*, estos últimos persiguieron y atacaron a *C. corax* en ∼97% de las observaciones. Observamos esta fuerte asimetría en la dirección de la agresión interespecífica a través de América del Norte. Segundo, la agresión de *C. brachyrhynchos* y *C. caurinus* hacia *C. corax* fue más frecuente durante la estación de anidación de *C. brachyrhynchos* y *C. caurinus* (∼marzo-mayo), pero también ocurrió en otras estaciones. Tercero, *C. brachyrhynchos* y *C. caurinus* atacaron típicamente en pequeños grupos a *C. corax*, con relativamente pocas observaciones de agresión en disputas de uno a uno. Los patrones de estacionalidad en los ataques de *C. brachyrhynchos* y *C. caurinus* sobre *C. corax* sugieren que la depredación del nido por parte de *C. corax* es un factor importante en determinar la agresión interespecífica por parte de *C. brachyrhynchos* y *C. caurinus*. La agresión también ocurrió fuera de la estación reproductiva, particularmente en el invierno, indicando ya sea que *C. brachyrhynchos* y *C. caurinus* compiten con *C. corax* por recursos en este momento del año o que *C. brachyrhynchos* y *C. caurinus* acosan de modo preventivo a los potenciales depredadores de nidos antes de la estación reproductiva. Este estudio es un ejemplo de cómo los científicos ciudadanos pueden contribuir al estudio de las interacciones comportamentales en las aves a una escala continental.

Palabras clave: agresión interespecífica, asediar, ciencia ciudadana, competencia interespecífica, interacciones comportamentales, socialidad

INTRODUCTION

Interspecific aggression is common in animals (Peiman and Robinson 2010), and is especially well-documented in birds (Dhondt 2011). But why do individuals chase and attack members of different species? Aggressive interactions incur costs: There is an energetic cost to confronting another individual, and encounters that escalate to physical tussles could lead to bodily harm. There are at least 5 general explanations for why individuals aggressively confront heterospecifics (reviewed by Peiman and Robinson 2010). First, this behavior may be nonadaptive. That is, there may be a cost but no benefit to the individual, for example, if interspecific aggression occurs when heterospecifics are mistakenly treated as if they are conspecifics ("mistaken identity"; Murray 1971). The remaining 4 explanations all assume that the behavior is adaptive, with benefits that outweigh costs, but differ in whether the benefit received is a food resource, space (i.e. interspecific territoriality; Orians and Willson 1964), a mate (e.g., when 2 species hybridize and hybrids suffer a fitness cost), or predator-free space (often termed "mobbing").

Interspecific aggression in birds is typically viewed through the lens of competition for food resources or space. Two general observations support this perspective. First, interspecific aggression is most common between closely related species that are ecologically similar (Dhondt 2011). This pattern is consistent with the idea that interspecific aggression is a mechanism of interference competition between species, though measurements of the fitness consequences of interspecific aggression are rare (but see, e.g., Martin and Martin 2001). Second, when interspecific aggression is measured experimentally (e.g., by using playback experiments), it often occurs in the presence of the putative competitor but not in its absence ("sympatry vs. allopatry" comparisons; e.g., Jankowski et al. 2010, Freeman et al. 2016). Again, this pattern is consistent with the idea that interspecific aggression is a mechanism of interference competition (but, when taxa are not reproductively isolated, it is also consistent with the possibility that reproductive interactions are important). In addition, patterns of interspecific aggression between close relatives are nonrandom, with larger species tending to be dominant over smaller species (Martin and Ghalambor 2014, Miller et al. 2017a), and with a strong tendency for interspecific aggression in pairwise interactions to be asymmetrical, with one species (typically the larger species) consistently the aggressor in contests (Martin et al. 2017). Lastly, interspecific aggression (which presumably underpins interspecific competition) can have evolutionary consequences: Species' positions within interspecific dominance hierarchies affect both the evolution of their life history traits (Grether et al. 2013,

Freshwater et al. 2014) and ecological traits such as their realized niches (Morse 1974, Robinson and Terborgh 1995).

However, as previously described, competition for food resources and space is not the only factor that could explain interspecific aggression. In addition to nonadaptive explanations, interspecific aggression could provide benefits related to reproductive interactions and predation. Here we focus particularly on the possibility that interspecific aggression may provide the benefit of reducing the risk of predation by providing a predator-free space. Nearby predators are threatening and, rather than flee, many species actively confront their predators and attempt to drive them away (Altmann 1956, Shedd 1982). Interspecific aggression toward a predator is termed "mobbing," and typically occurs when multiple individuals cooperate to attack or harass a predator (Altmann 1956). Mobbing often causes potential predators to move away and thus decreases short-term predation risk (Pavey and Smyth 1998, Pettifor 1990). In the context of recent work on interspecific aggressive interactions, mobbing is also intriguing in that, by attacking in groups, small species may be able to break the pervasive pattern of big species behaviorally dominating small species in contests for food (Miller et al. 2017a).

In this paper, we explore patterns of interspecific aggression between a pair of North American congeneric corvids, crows (American Crow [*Corvus brachyrhynchos*] and Northwestern Crow [*C. caurinus*])—we consider these 2 taxa to be a single unit of analysis, simply "crows," because they are phenotypically indistinguishable and appear to lack barriers to reproduction (Verbeek and Butler 1999)—and ravens (Common Raven [*Corvus corax*]). Crows and ravens last shared a common ancestor ~7 million years ago and are essentially completely reproductively isolated (Boarman and Heinrich 1999; but see Jefferson (1994) for a rare observation of a hybrid pair), so interspecific aggression between these taxa cannot be due to reproductive interactions (e.g., hybridization). Crows and ravens differ in their social behavior in ways that may be relevant to their agonistic interactions. Crows tend to be extremely social; cooperative breeding occurs in some populations, they often forage in family groups or large flocks, and they sometimes roost in aggregations of thousands of individuals during the nonbreeding season (Verbeek and Caffrey 2002). Ravens also sometimes forage and roost in large flocks (especially juveniles), but are more typically found as pairs or single birds (Boarman and Heinrich 1999).

We first consider evidence for crows and ravens competing with each other for food and space. Crows and ravens are generalists with broadly overlapping diets (Boarman and Heinrich 1999, Verbeek and Butler 1999, Verbeek and Caffrey 2002). Ravens and crows sometimes

directly compete for a limited, defendable food item. When this happens, ravens are behaviorally dominant over crows at food resources, including carcasses (Heinrich 1988) and bird feeders (Miller et al. 2017a, E. Miller personal observation). In addition, both ravens and crows in the contiguous United States typically defend year-round territories, such that space within territories is potentially a defensible resource (American Crow populations north of ~50° are mostly migratory and defend breeding season territories only; Boarman and Heinrich 1999, Verbeek and Butler 1999, Verbeek and Caffrey 2002). We are not aware of reports of interspecific territoriality between crows and ravens, and, to our knowledge, only one study has experimentally measured interspecific competition between crows and ravens. Bodey et al. (2009) removed Hooded Crows (*Corvus cornix*), a close relative of the American Crow, from an island in Northern Ireland, and found that ravens responded to the absence of crows by significantly increasing their territory size. This indicates that competition from crows (likely interference competition) previously limited raven territories on this island.

In addition to competition for food or space, crows and ravens may be predators of one another. Both taxa are nest predators of other birds (Boarman and Heinrich 1999, Verbeek and Butler 1999, Verbeek and Caffrey 2002), and ravens have been observed depredating crow nests (Swift 2017). There are few studies that have identified predators at crow and raven nests (reviewed by Boarman and Heinrich 1999, Verbeek and Caffrey 2002), but, because ravens are 2–3 times heavier than crows (Dunning 2007), it is likely that raven predation of crow nests is much more common than vice versa (K. McGowan personal communication). Thus, crows and ravens are both potential competitors with and predators of each other (e.g., intraguild predators; Polis et al. 1989).

Different hypotheses to explain interspecific aggression between crows and ravens make different predictions about the direction and seasonality of this interaction. We first note that interspecific aggression could be nonadaptive. For example, interspecific aggression may simply be correlated with intraspecific aggression, particularly if crows and ravens are unable to recognize each other as distinct taxa. Because crows and ravens are highly intelligent species that exhibit different behaviors in response to different taxa (e.g., both consistently mob taxa that are nest predators but do not mob taxa that are not threats; Boarman and Heinrich 1999, Verbeek and Caffrey 2002), it is doubtful that they mistakenly identify congeners as conspecifics. If, on the other hand, interspecific aggression between crows and ravens is driven primarily by competition for resources, we would predict that ravens would be asymmetrically aggressive toward crows, as they are larger and behaviorally dominate crows in aggressive contests at food resources (Harlow et al.

1975, Heinrich 1988). Complicating this naïve prediction is the fact that there is some evidence that crows may constrain raven territory size (Bodey et al. 2009), potentially through interference competition. Also, as described above, crows tend to be more social than ravens. Thus, crows may potentially be able to band together to be the aggressors against ravens; we note that socially driven reversals in dominance such as this have been poorly studied. Conversely, if interspecific aggression between crows and ravens is driven largely by predation of crow nests by ravens, we would predict that crows would asymmetrically be aggressive toward (mob) ravens, and that aggression from crows would disproportionately occur during the breeding season (March–May) when crows have eggs and nestlings that are vulnerable to raven predation. We tested these predictions by compiling a large number of observations of aggressive interactions between crows and ravens across North America from user comments in eBird, a citizen science database. We used these observations to address 3 questions: (1) Is interspecific aggression between crows and ravens in North America asymmetrical? (2) Does the direction of interspecific aggression depend on the number of individuals involved in the interaction? (3) Does interspecific aggression between crows and ravens vary seasonally?

METHODS

Data Compilation

We have occasionally noticed aggressive interactions between crows and ravens while birding, gardening, or driving. Yet, while our small number of personal observations was sufficient to spark an interest in this behavioral interaction, it was insufficient to meaningfully study interspecific aggression between crows and ravens. To counteract this small sample size problem, we turned to citizen science. Specifically, we compiled a data table of aggressive interactions between crows and ravens from eBird. eBird is a citizen science program to which participants contribute bird abundance and distribution data by uploading checklists of species that they have observed at a specific location at a particular date and time (Sullivan et al. 2009). The eBird database does not include specific fields to document behaviors such as predation or interspecific aggression, but a subset of eBird participants describe behavioral interactions that they have observed in the "species comments" field in eBird checklists. We manually scanned this species comments field to build the data table that we analyze in this manuscript.

We first downloaded all eBird records for the Common Raven and American and Northwestern crows from the publically available November 2016 version of the global eBird Basic Dataset. Within these data there were 307,845 records of crows or ravens with species comments, from
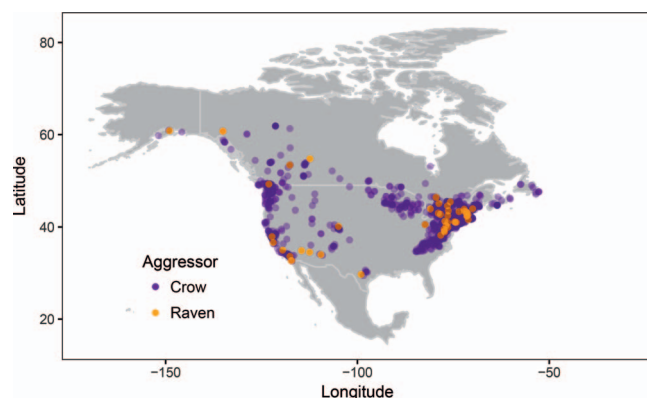
FIGURE 1. Map of observations of interspecific aggression between crows (American Crow [*Corvus brachyrhynchos*] and Northwestern Crow [*C. caurinus*]) and Common Ravens (*Corvus corax*) in North America.

which we selected records in which the heterospecific was mentioned by name (i.e. "raven" in records of crows, and "crow" in records of ravens). We then read the entry in the species comments field for each of these records to build a data table of citizen science observations that met 2 criteria: (1) they unequivocally described an aggressive interaction between crows and ravens (e.g., included descriptions such as "chase," "aggress," "harass," "pursue," or "dive-bomb"), and (2) they clearly stated which species was the aggressor and which species was the target of aggression. We found 2,014 such observations. For each unique record of an interaction between crows and ravens that met these 2 criteria, we recorded: (1) the aggressor species, (2) the species that was the target of the aggression, (3) the date, (4) the geographic location (latitude and longitude), and, if possible, (5) the number of individuals of the aggressor species, and (6) the number of individuals of the species that was the target of the aggression (see Supplemental Material Table S1). The latter 2 variables could be recorded only for checklists in which eBird users specified the number of individuals of crows and ravens involved in the aggressive interaction.

Asymmetry in Aggression

To examine whether aggressive interactions between crows and ravens deviated from symmetry (i.e. with crows the aggressors in 50% of interactions and ravens the aggressors in 50% of interactions), we conducted a binomial test. To conduct a coarse analysis of whether patterns from the larger analysis were recapitulated in smaller regional analyses, we examined patterns by mapping our data (Figure 1), and then used distinct binomial tests to examine the symmetry of interspecific aggression between crows and ravens in western (west of the 100th meridian) vs. eastern (east of the 100th meridian) North America (data were very sparse down the 100th

meridian, making eastern and western regions natural groups within the data). All statistics were performed in R (R Core Team 2017).

The Effect of Number of Birds on Aggression

To test how the number of interacting individuals of crows and ravens influenced the direction of interspecific aggression, we calculated the ratio of the number of aggressors involved in a contest to the number of individuals that were the target of aggression. While all observations in our data table described the direction of interspecific aggression, many observations did not include specific numbers of individuals involved in the aggressive interaction. This was particularly true for crows, which were often defined as a group of uncertain number (e.g., a "flock"). In such cases, we knew that ≥ 2 crows were involved, but not the precise number of crows. We used information gleaned from the species comments field to define 3 ecologically relevant ratios: (1) the aggressors outnumbered the target of aggression ("strength in numbers"), (2) equal numbers of aggressors and targets of aggression ("fair fight"), and (3) the targets of aggression outnumbered the aggressor ("outnumbered"). We were able to assign observations to 1 of these 3 categories in 1,704 of the 2,014 instances (852 observations that noted the precise numbers of crows and ravens involved in the interaction, and 852 additional observations that described a flock of crows and a solitary raven involved in the interaction). In total, we were able to assign observations to 1 of the 3 ratio categories for 85% of records of crows attacking ravens, and for 66% of records of ravens attacking crows. We then used a chi-square test to examine how crow–raven attack rates varied across these 3 categories.

Seasonality of Interspecific Aggression

If interspecific aggression is primarily driven by the threat of nest predation, it should be more prevalent during the breeding season. In contrast, if interspecific aggression is a result of resource competition, then interspecific aggression is predicted to be most prevalent during lean times of food scarcity (which could potentially be in winter, or perhaps in late spring when parents are feeding nestlings). To address how crow attack rates varied as a function of seasonality, we focused on observations of American Crow attacks on Common Ravens, because the bulk of our dataset (~90%) consisted of such interactions. We first summed the number of aggressive attacks by American Crows on ravens for each month, and divided the number of crow attacks on ravens by the total number of American Crow observations with species comments per month. This calculated the proportion of species comments for American Crow observations that described crow attacks on ravens for each month. While a set of 12 proportions (1
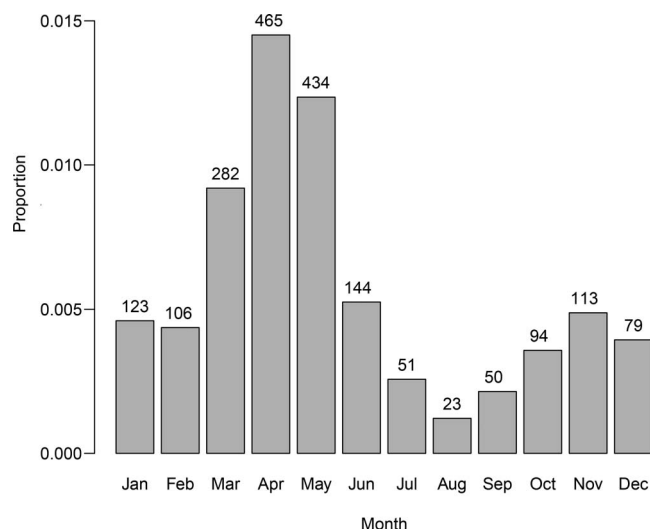
FIGURE 2. Seasonality of crow (American Crow and Northwestern Crow) aggression toward Common Ravens in North America based on per-month counts. Crows most commonly attacked ravens during the crow breeding season (March–May), but also attacked ravens during all months, particularly in the winter (November–February). The *y*-axis shows the proportion of eBird checklists per month with species comments for crows in which the comment described crows attacking ravens; the raw numbers of crow attacks on ravens are given above bars.

for each month) is sufficient to illustrate seasonal trends in crow attacks (Figure 2), it is not suitable for statistically analyzing these seasonal trends.

To statistically assess seasonal trends in crow attacks on ravens, we used generalized additive models (GAMs). We first constructed data tables suitable for use in logistic regressions. Reported attacks by American Crows were considered positive detections (i.e. values of "1" in our models). Absences (i.e. values of "0" in our models) were defined as all records of crows with comments that did not pertain to interactions with ravens. We further restricted these records to those that came from the region of sympatry, where the 2 species had the opportunity to interact with one another. We operationally defined the region of sympatry as all counties and townships within the United States and Canada where both species occurred, and also 2 Mexican provinces (Baja California North and Chihuahua) where both species occur. This left us with 1,842 presences (attacks), and 238,454 absences (records of crows with user comments not pertaining to attacks on ravens). We repeated this process for the subset of interactions for which it was known that crows had mobbed ravens (see "strength in numbers" above; $n = 1,276$ presences), and for those in which crows had attacked ravens in an even match or when they were outnumbered (union of "fair fight" and "outnumbered"; $n = 305$).

Our initial datasets contained fewer than 1% positive detections of interactions. Because logistic regression is known to be sensitive to imbalanced datasets (King and Zeng 2001), we used a combined upsampling–downsampling approach to create balanced datasets for analysis. Downsampling here refers to removing absences from the dataset in a spatially even manner. Thus, we laid a geographic grid over mapped instances in which crows did not attack ravens (values of "0" in our models), where vertical (longitudinal) divisions were drawn every 0.588 decimal degrees, and horizontal (latitudinal) divisions were drawn every 0.385 decimal degrees. We chose these divisions because they qualitatively satisfied our goal of significant majority class downsampling in a fashion that did not jeopardize geographic coverage. We then used this grid to randomly sample up to 2 observations from each cell, which provided a reduced but geographically stratified sample of absences.

Upsampling here refers to adding synthetic pseudopresences to the dataset. To do this, we used the "synthetic minority oversampling technique" (SMOTE; Chawla et al. 2002) to upsample presences (crow attacks on ravens), implemented in the R package DMwR (Torgo 2010). This technique creates synthetic positive observations by adding new records along any of the lines joining small sets of nearest neighbor records (e.g., Robinson et al. 2018). We upsampled at 200% and with 5 nearest neighbors per set, meaning that 2 of the lines joining the nearest neighbors were randomly selected and a point was added along each of these chosen lines. This approach produced a final, balanced dataset of 5,853 crow–raven attacks and 5,853 observations where no such attack was observed. We used the same approach to create balanced datasets of mobbing and evenly matched (or outnumbered) attacks on ravens by crows. We also repeated this process of splitting the data and spatially downsampling absences, but without upsampling with SMOTE, to confirm that the upsampling procedure did not bias our results. Because results were qualitatively identical, we do not further discuss the unbalanced datasets.

After constructing the balanced datasets, we used GAMs (Wood 2006) implemented in the R package mgcv (Wood 2000) to model seasonal trends. Because crows are absent from high latitudes in the winter, and may breed slightly later in these areas as well (Verbeek and Caffrey 2002), we expected a complex relationship, and perhaps an interaction, between seasonality and latitude and their influence on attack rates. Therefore, we fit GAMs in which the interaction between the ordinal date and latitude was modeled with a tensor spline. We used this spline to model whether an attack was documented during a given American Crow or Common Raven observation as a binomial logistic regression. Ordinal date is a circular variable (e.g., day 1 and day 365 are only 1 day apart), and we therefore used a cyclic cubic spline to force the start and end of the fitted spline to match.

TABLE 1. Number of instances of interspecific aggression between crows (American Crow and Northwestern Crow) and ravens (Common Raven) in North America in 3 categories: (1) "Strength in numbers," in which aggressors outnumbered the target of aggression; (2) "Fair fight," in which there were the same number of aggressor(s) and target(s) of aggression; and (3) "Outnumbered," in which the aggressor(s) were outnumbered by the targets of aggression. The top row gives the number of observations for which crows were aggressive toward ravens; the bottom row gives the number of observations for which ravens were aggressive toward crows.

Aggressor	Strength in numbers	Fair fight	Outnumbered
Crow	1,357	294	20
Raven	5	19	9

RESULTS

Aggressive interactions between crows and ravens in North America were highly asymmetrical; crows were the aggressor in nearly all (~98%; 1,964 of 2,014) contests between these congeners. Our dataset included aggressive interactions throughout North America (Figure 1), with a higher density of interactions in regions where both ravens and eBird users were common (e.g., New England, the Appalachian Mountains, the Great Lakes area, and the Pacific coast). We found no indication that the direction of aggression between crows and ravens varied geographically within North America (Figure 1); crows were the aggressor ~97% of the time in both eastern and western North America (divided by the 100th meridian; P-values of binomial tests both $<<$ 0.001).

When we quantified how the number of interacting individuals influenced the direction of interspecific aggression, we found a marked difference between the categories that described crow attacks on ravens and those that described raven attacks on crows (Table 1). When crows were the aggressor, they typically had numerical superiority over the raven(s) that were the target of aggression (81% of observations), less frequently had the same number of individuals as the raven(s) they were attacking (18% of observations), and seldom were outnumbered by ravens (1% of observations). There were few observations in which ravens were the aggressor. However, in most of these instances, the number of ravens was the same as the number of crows (58% of observations) or crows outnumbered ravens (27%); seldom did ravens have numerical superiority over crows (15% of observations). This difference between the ratios of "strength in numbers," "fair fight," and "outnumbered" scenarios between crows as aggressors and ravens as aggressors was highly significant ($\chi^2_2 = 175.12$, $P << 0.001$). Moreover, the seasonality of crow attacks varied between different categories. In particular, "fair fight" attacks were especially
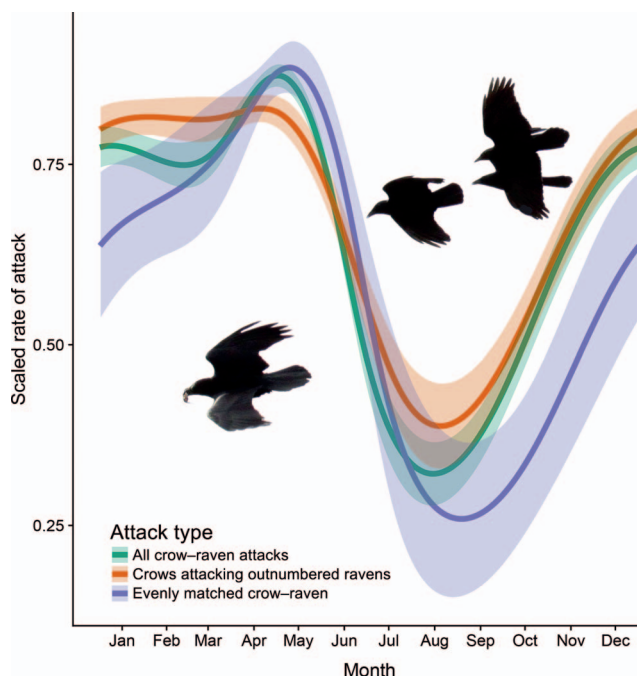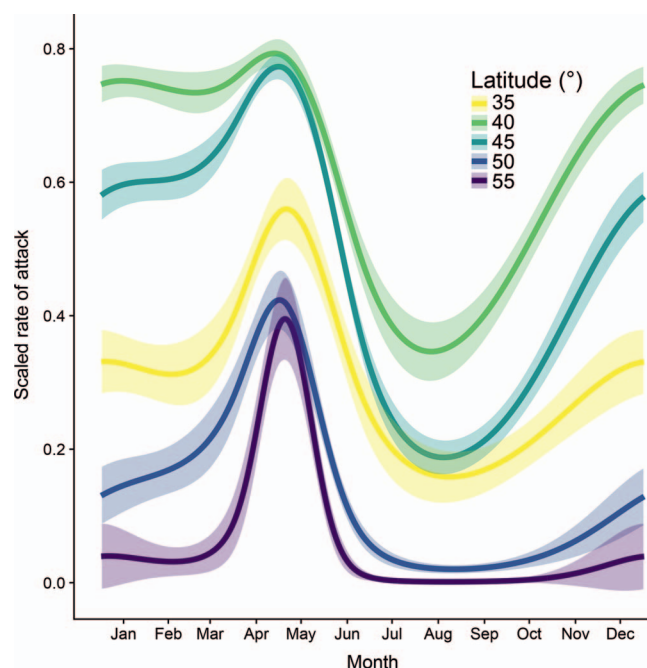

FIGURE 3. Seasonality of American Crow aggression toward Common Ravens in North America based on generalized additive models. Crow aggression toward Common Ravens was rare during the summer and fall, regular during winter, and peaked in spring during the crow breeding season (March–May). Instances of "fair fight" scenarios (e.g., 1 crow attacking 1 raven) were most common during the crow breeding season and rare at other times of the year. In contrast, "strength in numbers" attacks (e.g., a flock of crows attacking a single raven) were more common outside the crow breeding season. Trendlines with shaded 95% confidence intervals show predictions from generalized additive models. This figure illustrates predictions of a generalized additive model with latitude constant at the median of the dataset (42.99°N). Because we balanced the datasets, we were able to plot these predictions on the same scale; 0.5 along the y-axis corresponds to the dataset average crow attack rate. Photo of crow–raven interaction by Robin Robinson.

common during the breeding season and scarce in other seasons (Figure 3). These results were qualitatively identical without upsampling (Appendix Figure 5).

We found strong seasonality overall in crow attacks on ravens. The majority of instances of American Crows attacking ravens took place between March and May (Figures 2–4), which corresponds to the breeding season of crows in most places in North America (i.e. when crow eggs and nestlings are present; Verbeek and Butler 1999, Verbeek and Caffrey 2002). We quantified this seasonal trend using a generalized additive model (GAM). Model predictions from this GAM echoed the raw data and showed that, across North America, crow aggression toward ravens was most common in spring (Figures 3 and 4). This spring peak in aggression occurred at all

FIGURE 4. Seasonal patterns in American Crow aggression toward Common Ravens across a latitudinal gradient within North America. Crow attacks on ravens were much more common in all seasons at middle latitudes (40–45°) than at lower (35°) or higher (50–55°) latitudes. However, seasonal patterns varied by latitude: Crow attacks on ravens were rare outside the breeding season at higher (50–55°) latitudes, and this seasonal pattern was diminished at middle latitudes (40–45°). Trendlines with shaded 95% confidence intervals show predictions from generalized additive models. Because we balanced the datasets, we were able to plot these predictions on the same scale; 0.5 along the y-axis corresponds to the dataset average crow attack rate.

latitudes (35–55°) but began slightly later in the year at higher latitudes (50–55°), corresponding to a later breeding season there (Figure 4). More apparent was the elevated attack rate in general and particularly in winter months at lower latitudes (35–45°; Figure 4). These results were qualitatively identical without upsampling (Appendix Figure 6).

DISCUSSION

We compiled citizen science data which showed that crows attacked ravens in 97% of aggressive interactions between these 2 taxa, despite the fact that ravens outweigh crows by a factor of 2 to 3. This asymmetrical pattern wherein crows nearly always attacked ravens—and ravens rarely attacked crows—occurred in the Pacific Northwest, California, the intermontane West, the Great Lakes region, New England, and the Appalachians (Figure 1); that is, across most, if not all, of North America. While this interaction appeared to be geographically consistent, there were strong temporal

shifts in this behavioral interaction. Although crows attacked ravens in all months, they did so particularly during the breeding season (Figures 2–4); nearly half of all observations of crow attacks on ravens were in April or May. In addition, although crows typically attacked ravens when crows were in flocks, in the breeding season crows sometimes attacked ravens when they did not outnumber them; such "fair fight" crow attacks were rare outside the breeding season.

We found an overwhelming tendency for crows to attack ravens rather than vice versa. In general, larger species dominate smaller species in contests for defendable resources (Miller et al. 2017a), yet crows are ~2–3 times smaller in mass than ravens (Dunning 2007). We suggest that the social behavior of crows largely explains this reversal of the typical "Goliath beats David" scenario. By aggressively confronting heterospecifics as a group, individuals within groups may be able to gain access to food resources (or, as may be more likely in this case, repel potential predators) that would not be available to solitary birds. This benefit of sociality is seldom considered but potentially powerful. However, this strategy of "ganging up to beat Goliath" comes at a cost, in that intraspecific competition increases with every additional conspecific in the group. Further studies investigating the tradeoffs between increased intraspecific competition in a smaller, social species vs. an improved ability to contest for resources with a larger heterospecific would be illuminating. For example, larger groups of wolves have reduced foraging success compared with smaller groups of wolves. But large groups of wolves are better able to defend their kills from scavenging ravens, and hence selection pressure from raven scavengers may explain why wolf pack sizes are larger than what would be expected for optimal foraging (Vucetich et al. 2004). An ornithological example is that, although the predominantly insectivorous Brown-headed Honeyeater (*Melithreptus brevirostris*) loses one-on-one contests to the primarily nectarivorous (and larger-bodied) New Holland Honeyeater (*Phylidonyris novaehollandiae*), en masse the Brown-headed Honeyeater is able to swarm and gain access to floral resources defended by the New Holland Honeyeater (Paton 1980, McFarland 1986, Miller et al. 2017b). We speculate that the crow–raven example is a possible case of a socially mediated reversal in dominance. Data that shows that crows use their larger numbers to gain access to food resources defended by ravens would be necessary to support this contention.

Our results showed that aggression by crows peaked during the breeding season. There are various potential reasons for this seasonal pattern in aggression. The simplest interpretation is that nest predation by ravens is a particularly important factor driving interspecific aggression by crows. Alternative explanations include that the breeding season is when demand for food resources is

greatest and thus when resource competition with ravens is strongest, or that conspecific aggression peaks during the breeding season and increased aggression toward heterospecifics is simply a nonadaptive carryover effect. Our data is potentially consistent with all of these hypotheses, and further studies are needed to decisively favor one explanation over the others. However, we consider the nest predation interpretation to be the most likely for 3 reasons. First, crows vigorously mob avian and mammalian nest predators during the breeding season (Verbeek and Caffrey 2002). If ravens are a nest predator of crows, as we suggest, then nest predation alone could explain why crows tend to attack ravens in the spring, including elevated crow attack rates when crows do not have a numerical advantage over ravens ("fair fight" scenarios). Second, the resource competition hypothesis would most plausibly apply to the period when crows are feeding nestlings, but crow attacks on ravens begin to increase in frequency in March, which is typically before crows have nestlings. Lastly, crows likely do exhibit increased conspecific aggression during the breeding season when territorial defense is strongest, but, in the absence of additional evidence, we consider it unlikely that elevated aggression would cause crows to mistake ravens for conspecifics at this time of year, given that crows are able to correctly identify potential nest predators (they mob nest predators but do not mob taxa that are not nest predators; Verbeek and Caffrey 2002).

Finally, we found that crows still attacked ravens during the nonbreeding season when they (crows) were not vulnerable to nest predation from ravens. This result is also consistent with multiple interpretations. First, crow attacks on ravens could be nonadaptive. Second, when crows defend year-round territories, they may harass ravens (and other nest predators) at all times of year in order to reduce the chances of nest predation that occurs only in spring. Third, crows may attack ravens at any time of the year because the 2 taxa compete for limiting resources (food or space). It is likely that winter is the leanest time of the year for crows. If so, competition for food (or space, where space is a proxy for food resources) may explain why crow attacks on ravens are common during the winter months at middle latitudes where crows and ravens overlap broadly in their wintering distributions. Most crow attacks on ravens during the nonbreeding season occurred at middle latitudes (40–45°), with fewer attacks at higher (50–55°) and lower (35°) latitudes. The drivers of this pattern are unclear. Crows are present in winter across North America up to ~50°; populations that breed farther north migrate south in winter. One possible explanation of the pattern that most winter aggression occurs at middle latitudes is that crows at these latitudes may be year-round residents that defend winter territories, with crows at higher latitudes less likely to defend year-round territories

and those at lower latitudes less likely to encounter ravens. If so, we speculate that territoriality may be important to explaining why crows attack ravens in winter, either due to resource competition or because crows take a proactive approach to deterring nest predators for the upcoming breeding season. Quantifying the space use and food consumption of crows and ravens in winter would be helpful for distinguishing between these alternative explanations.

We have shown that crows attack ravens in nearly all contests between these 2 corvids. While asymmetrical interspecific aggression can constrain species' geographic distributions at large and small spatial scales (MacNally et al. 2012, Grether et al. 2013), it is unknown whether persistent attacks by crows affect raven populations in North America. In regions where crows and ravens co-occur, crows tend to occupy urban and agricultural land, whereas ravens tend to occupy less developed terrain (Marzluff and Neatherlin 2006). This tendency for crows and ravens to segregate in space could simply reflect divergent habitat preferences or availability of resources, but it could also partially be due to interactions between ravens and crows. Future studies should investigate whether frequent crow attacks affect the spatial use or abundance of ravens; that is, whether crows may actually constrain raven populations as suggested by Bodey et al. (2009).

Another profitable avenue of inquiry would be to analyze crow and raven habitat use in places where only 1 of the 2 taxa occurs (allopatry vs. sympatry comparisons). However, because crows and ravens co-occur across the vast majority of North America, rigorous comparisons of habitat use may be challenging to undertake. Both crows and ravens have increased in population size and distributional extent within the last century as a result of land use changes and diminishing persecution from humans (Boarman and Heinrich 1999, Marzluff et al. 2001, McGowan 2001). Thus, one possible approach would be to compare habitat use in different regions with different recent histories of crow and raven population densities.

Our study is one of the first to investigate behavioral interactions between bird species at a continental scale (Miller et al. 2017a). A wide geographic scope is necessary to evaluate how an interaction changes over space. Situations in which the identity of the dominant species changes over space or time (e.g., "rock–paper–scissor" relationships, termed "intransitivities") have been hypothesized to be particularly ecologically important (e.g., they may promote coexistence between similar species; Levine et al. 2017). Yet, interspecific aggression is typically studied at only 1 or 2 sites (Martin et al. 2017) because it is difficult and laborious to observe behavioral interactions in the wild. We used citizen science data to solve this problem, but note that citizen science data carry

some of their own assumptions. For example, we analyzed citizen scientist observations of interactions between 2 species of medium-to-large, all-black corvids. Given their phenotypic similarity (but quite different voices), it is reasonable to assume that there were instances of misidentification in our data, though this would have introduced noise but not bias into our analysis. One promising avenue for analyzing the quality of citizen science data is to use algorithms that quantify the expertise scores of specific users (Kelling et al. 2015, Johnston et al. 2018). In addition, groups of crows harassing ravens may be more detectable than single crows harassing ravens, which could have introduced bias into our data; we cannot evaluate this possibility with our current dataset but note that our main results are robust to this potential bias. Lastly, although citizen science data hold promise for increasing the geographic sampling of a behavioral interaction, they are not a panacea. For example, the data that we analyzed in this study were indeed continental in scope, but certain regions were much more densely sampled than others due to geographic bias in submissions from eBird participants. Despite these caveats, we have shown that citizen scientists have the potential to provide data with which to examine the possibility of spatial variation in rates and directions of behavioral interactions (Miller et al. 2017a). We anticipate that citizen science data will provide increasingly powerful datasets to test behavioral hypotheses at large spatiotemporal scales.

ACKNOWLEDGMENTS

LITERATURE CITED

Altmann, S. A. (1956). Avian mobbing behavior and predator recognition. The Condor 58:241–253.

Boarman, W. I., and B. Heinrich (1999). Common Raven (*Corvus corax*), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.476

Bodey, T. W., R. A. McDonald, and S. Bearhop (2009). Mesopredators constrain a top predator: Competitive release of ravens after culling crows. Biology Letters 5:617–620.

Chawla, N. V., K. W. Bowyer, L. O. Hall, and W. P. Kegelmeyer (2002). SMOTE: Synthetic minority over-sampling technique. Journal of Artificial Intelligence Research 16:321–357.

Dhondt, A. A. (2011). Interspecific Competition in Birds. Oxford University Press, Oxford, UK.

Dunning, J. B., Jr. (Editor) (2007). CRC Handbook of Avian Body Masses, second edition. CRC Press, Boca Raton, FL, USA.

Freeman, B. G., A. M. Class Freeman, and W. M. Hochachka (2016). Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient. Ibis 158:726–737.

Freshwater, C., C. K. Ghalambor, and P. R. Martin (2014). Repeated patterns of trait divergence between closely related dominant and subordinate bird species. Ecology 95:2334–2345.

Grether, G. F., C. N. Anderson, J. P. Drury, A. N. G. Kirschel, N. Losin, K. Okamoto, and K. S. Peiman (2013). The evolutionary consequences of interspecific aggression. Annals of the New York Academy of Sciences 1289:48–68.

Harlow, R. F., R. G. Hooper, D. R. Chamberlain, and H. S. Crawford (1975). Some winter and nesting season foods of the Common Raven in Virginia. The Auk 92:298–306.

Heinrich, B. (1988). Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. Behavioral Ecology and Sociobiology 23:141–156.

Jankowski, J. E., S. K. Robinson, and D. J. Levey (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. Ecology 91:1877–1884.

Jefferson, E. (1994). Successful hybridization of Common Raven and American Crow. Ontario Birds 12:32–35.

Johnston, A., D. Fink, W. M. Hochachka, and S. Kelling (2018). Estimates of observer expertise improve species distributions from citizen science data. Methods in Ecology and Evolution 9:88–97.

Kelling, S., A. Johnston, W. M. Hochachka, M. Iliff, D. Fink, J. Gerbracht, C. Lagoze, F. A. La Sorte, T. Moore, A. Wiggins, W.-K. Wong, et al. (2015). Can observation skills of citizen scientists be estimated using species accumulation curves? PLOS One 10:e0139600.

King, G., and L. Zeng (2001). Logistic regression in rare events data. Political Analysis 9:137–163.

Levine, J. M., J. Bascompte, P. B. Adler, and S. Allesina (2017). Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546:56–64.

MacNally, R., M. E. Bowen, A. L. Howes, C. A. McAlpine, and M. Maron (2012). Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. Ecology 93:668–678.

Martin, P. R., and C. K. Ghalambor (2014). When David beats Goliath: The advantage of large size in interspecific aggressive contests declines over evolutionary time. PLOS One 9:e108741.

Martin, P. R., and T. E. Martin (2001). Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. Ecology 82:189–206.

Martin, P. R., C. Freshwater, and C. K. Ghalambor (2017). The outcomes of most aggressive interactions among closely related bird species are asymmetric. PeerJ 5:e2847.

Marzluff, J. M., and E. Neatherlin (2006). Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. Biological Conservation 130:301–314.

Marzluff, J. M., K. J. McGowan, R. Donnelly, and R. L. Knight (2001). Causes and consequences of expanding American Crow populations. In Avian Ecology and Conservation in an Urbanizing World (J. M. Marzluff, R. Bowman, and R. Donnelly, Editors). Kluwer Academic Publishers, Norwell, MA, USA. pp. 331–363.

McFarland, D. C. (1986). The organization of a honeyeater community in an unpredictable environment. Australian Journal of Ecology 11:107–120.

McGowan, K. J. (2001). Demographic and behavioral comparisons of suburban and rural American Crows. In Avian Ecology and Conservation in an Urbanizing World (J. M. Marzluff, R. Bowman, and R. Donnelly, Editors). Kluwer Academic Publishers, Norwell, MA, USA. pp. 365–381.

Miller, E. T., D. N. Bonter, C. Eldermire, B. G. Freeman, E. I. Greig, L. J. Harmon, C. Lisle, and W. M. Hochachka (2017a). Fighting over food unites the birds of North America in a continental dominance hierarchy. Behavioral Ecology 28:1454–1463.

Miller, E. T., S. K. Wagner, L. J. Harmon, and R. E. Ricklefs (2017b). Radiating despite a lack of character: Ecological divergence among closely related, morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in arid Australian environments. The American Naturalist 189:E14–E30.

Morse, D. H. (1974). Niche breadth as a function of social dominance. The American Naturalist 108:818–830.

Murray, B. G. (1971). The ecological consequences of interspecific territorial behavior in birds. Ecology:414–423.

Orians, G. H., and M. F. Willson (1964). Interspecific territories of birds. Ecology 45:736–745.

Paton, D. C. (1980). The importance of manna, honeydew and lerp in the diets of honeyeaters. Emu 80:213–226.

Pavey, C. R., and A. K. Smyth (1998). Effects of avian mobbing on roost use and diet of powerful owls, Ninox strenua. Animal Behaviour 55:313–318.

Peiman, K. S., and B. W. Robinson (2010). Ecology and evolution of resource-related heterospecific aggression. The Quarterly Review of Biology 85:133–158.

Pettifor, R. A. (1990). The effects of avian mobbing on a potential predator, the European Kestrel, Falco tinnunculus. Animal Behaviour 39:821–827.

Polis, G. A., C. A. Myers, and R. D. Holt (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

R Core Team (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Robinson, O. J., V. Ruiz-Gutierrez, and D. Fink (2018). Correcting for bias in distribution modelling for rare species using citizen science data. Diversity and Distributions 24:460–472.

Robinson, S. K., and J. Terborgh (1995). Interspecific aggression and habitat selection by Amazonian birds. Journal of Animal Ecology 64:1–11.

Shedd, D. H. (1982). Seasonal variation and function of mobbing and related antipredator behaviors of the American Robin (Turdus migratorius). The Auk 99:342–346.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling (2009). eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Swift, K. (2017). RAVENous for crow eggs. https://corvidresearch.blog/2017/06/04/ravenous-for-crow-eggs/

Torgo, L. (2010). Data Mining with R: Learning with Case Studies. Chapman and Hall/CRC Press. http://www.dcc.fc.up.pt/~ltorgo/DataMiningWithR

Verbeek, N. A., and R. W. Butler (1999). Northwestern Crow (Corvus caurinus), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.407

Verbeek, N. A. and C. Caffrey (2002). American Crow (Corvus brachyrhynchos), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.647

Vucetich, J. A., R. O. Peterson, and T. A. Waite (2004). Raven scavenging favours group foraging in wolves. Animal Behaviour 67:1117–1126.

Wood, S. N. (2000). Modelling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society, Series B 62:413–428.

Wood, S. N. (2006). Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC, Boca Raton, FL, USA.
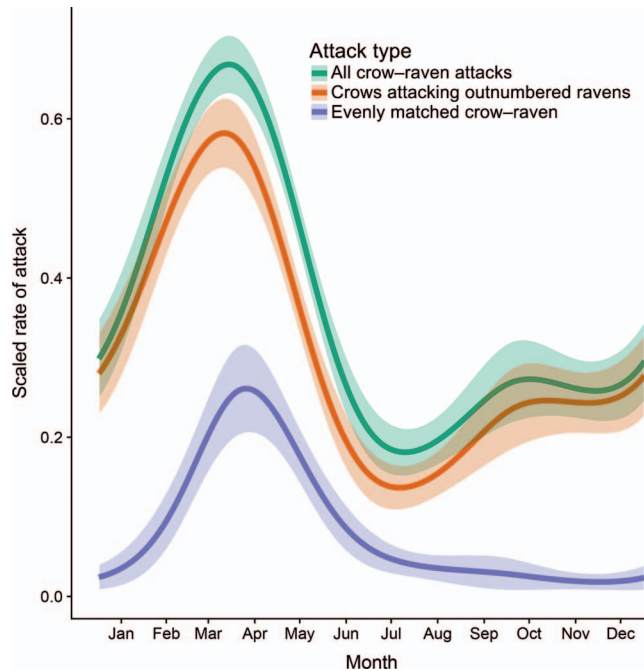
APPENDIX FIGURE 5. Seasonality of American Crow aggression toward Common Ravens in North America based on generalized additive models. This figure is analogous to Figure 3 in the main text, and incorporates spatial downsampling, but does not incorporate the SMOTE upsampling procedure. Results are qualitatively identical to those in Figure 3, namely that crow aggression toward Common Ravens was rare during the summer and fall, regular during winter, and peaked in spring during the crow breeding season (March–May; ordinal date ~60–150).
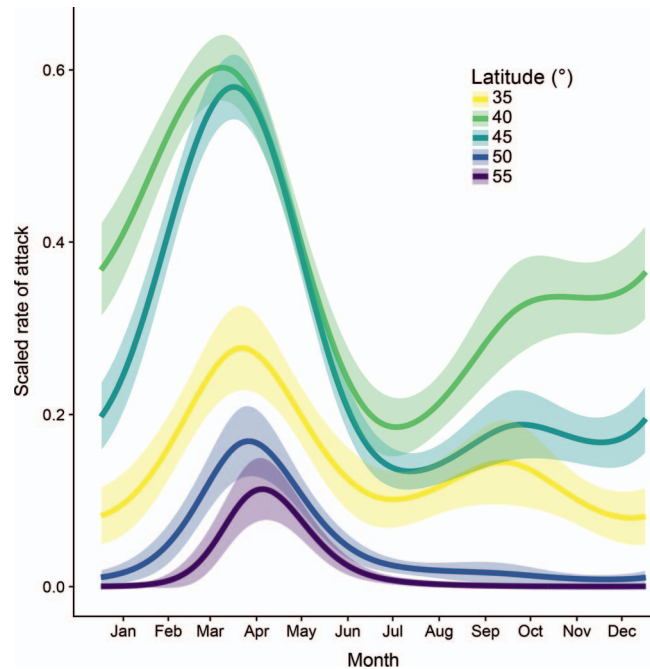
APPENDIX FIGURE 6. Seasonal patterns in American Crow aggression toward Common Ravens across a latitudinal gradient within North America. This figure is analogous to Figure 4 in the main text, and incorporates spatial downsampling, but does not incorporate the SMOTE upsampling procedure. Results are qualitatively identical to those in Figure 4, namely that crow attacks on ravens are much more common in all seasons at middle latitudes (40–45°) than at lower (35°) or higher (50–55°) latitudes.