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Species Identity and Nest Location Predict Agonistic Interactions at a Breeding Colony of Double-crested Cormorants (*Phalacrocorax auritus*) and Great Blue Herons (*Ardea herodias*)

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Abstract.—Recent dramatic growth of the North American Interior population of Double-crested Cormorants (*Phalacrocorax auritus*) has led to concern about potential impacts of this species on co-nesting colonial waterbirds. Previous investigations of these concerns have focused on Double-crested Cormorant interactions with other species within homogeneous breeding environments, making broad patterns difficult to identify. The present study examined how nest location, nest density, and species identity mediate agonistic interactions among Double-crested Cormorants and Great Blue Herons (*Ardea herodias*) nesting at a colony site in central Minnesota, USA. Twenty-six Double-crested Cormorant nests and 27 Great Blue Heron nests were observed for 30 min weekly for 8 weeks during the breeding season to estimate frequency of agonistic behavior and identify species-level patterns of interaction. Most agonistic interactions observed (81%) were intraspecific interactions among Double-crested Cormorants; Great Blue Herons engaged in a higher combined total count of interspecific and intraspecific interactions when they nested near Double-crested Cormorants. Interspecific interactions were more common among ground-nesting birds than among tree-nesting birds. This study suggests that further investigation into impacts of Double-crested Cormorants on co-nesting birds is most warranted for ground-nesting colonies. *Received 9 July 2014, accepted 4 January 2015.*

Key words.—agonistic behavior, *Ardea herodias*, breeding colony, competition, Double-crested Cormorant, Great Blue Heron, *Phalacrocorax auritus*.

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Waterbird colonies provide breeding birds with an important resource: nest sites. Multiple species of colonial waterbirds occupy similar types of nest sites (Burger 1979; Pius and Leberg 1997; Weseloh *et al.* 2002), which can lead to interspecific competition for these sites (Burger 1978; Pius and Leberg 1997), often manifested through agonistic behavior (Brown and Orians 1970). Intense interspecific territoriality may reduce individual reproductive success (Burger 1978; Duckworth 2006). Accordingly, growth of the North American Interior population of Double-crested Cormorants (*Phalacrocorax auritus*; hereafter, "cormorants") since the 1970s (Weseloh *et al.* 1995; Wires and Cuthbert 2006) has led to concern that cormorants will reduce reproductive success of co-nesting colonial waterbird species through nest-site competition (Weseloh *et al.* 2002). Cormorant management is authorized at some locations in the USA specifically to protect other waterbird species believed to be vulnerable to cormorant presence (U.S. Fish and Wildlife Service 2014).

Evidence for negative effects of cormorants on co-nesting waterbirds remains inconclusive. Wading bird abundance has declined at some breeding sites shared with cormorants, but researchers have been unable to identify interspecific competition as the definitive cause of these declines (Skagen *et al.* 2001; Cuthbert *et al.* 2002). Studies of ground-nesting colonies have shown conflicting results on the impacts of cormorants on co-nesters (Somers *et al.* 2007, 2011). For example, Herring Gulls (*Larus argentatus*) engaged in more agonistic (combined inter- and intraspecific) interactions when nesting among cormorants (Somers *et al.* 2007), while American White Pelicans (*Pelecanus erythrorhynchos*) engaged in fewer agonistic interactions when nesting among cormorants (Somers *et al.* 2011), compared to nesting among conspecifics exclusively.

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Somers *et al.* (2011) posited that the observed variability of responses to co-nesting with cormorants could be attributable to habitat structure, nest density, or the identity of the species involved. Because cormorants breed both on the ground and in trees (Hatch and Weseloh 1999) and often nest near other species (Cuthbert and Wires 2013), there is considerable variation among colonies in each of these variables. The behavioral literature supports all three hypotheses: habitat structure (Bukacinska and Bukacinski 1993; Jensen *et al.* 2005; Barley and Coleman 2010); nest or territory density (Butler and Trivelpiece 1981; Stokes and Boersma 2000); and/or species identity (Burger 1978; Mott and Maret 2011).

Our study examined the Somers *et al.* (2011) hypotheses that three potential factors (habitat structure, nest density, and species identity) drive the rate of agonistic interactions in a mixed-species breeding colony. At our study site in Meeker County, Minnesota, cormorants and Great Blue Herons (*Ardea herodias*; hereafter, "herons") nested on the ground and in trees across two islands. Thus, individual cormorants and conesters could be observed in a range of nest microenvironments all subject to the same broad environmental conditions.

METHODS

Study Area

Interactions between cormorants and herons were observed at Pigeon Lake, Meeker County, Minnesota (45° 02' 24" N, 94° 20' 53" W). Three islands in this lake have been used for breeding by both species, as well as by American White Pelicans, Great Egrets (*A. alba*) and Black-crowned Night-Herons (*Nycticorax nycticorax*; Wires *et al.* 2006). In 2012, aerial photographs and a ground count of American White Pelican nests provided estimates of nest abundance at the island complex: Great Blue Heron (159 nests), Great Egret (8 nests), Double-crested Cormorant (3,309 nests), and American White Pelican (191 nests; L. Wires, pers. commun.).

Observations

We observed focal nests of herons and cormorants from 16 April to 11 June 2012. Of the species breeding at the study site, these species were the only two whose nests were both easily visible and abundant. In mid-April, cormorants were completing the nest-building phase of the breeding period and most herons were incubating eggs. Therefore, the colony site was settled before observations began. Focal nests were selected by assigning numbers to all visible nests in each combination of nesting location (tree or ground) and species (heron or cormorant), then randomly selecting 13 nests out of the total available in each category. Selected nests were observed weekly for one 30-min period between 06:55 hr and 18:15 hr with a 20-60x spotting telescope from a roadside overlook. One focal nest of ground-nesting herons failed mid-season and the selection procedure was repeated to choose a replacement from among the ground-nesting heron nests not currently under study. Two focal nests of tree-nesting cormorants failed in the last 2 weeks of observations and were not replaced, resulting in a total sample size of 53 nests. For each focal nest, nest density was defined on a scale from one to five, corresponding to the number of contiguous territories situated around the nest and/or above it (Butler and Trivelpiece 1981). Values were estimated from aerial and ground photographs of the colony because quarantine of the site following a Newcastle disease outbreak prevented us from measuring nest density directly.

Agonistic behaviors (Table 1) were identified according to published ethograms for each species (van Tets 1965; Mock 1976). Both interspecific and intraspecific agonistic interactions were recorded, along with species identities of the birds involved. Potential effects of time of day on interaction rate were minimized by alternating species and nest locations throughout the day (e.g., a ground-nesting heron observation would be followed by a tree-nesting cormorant, then a tree-nesting heron, then a ground-nesting cormorant) and by observing nests in the same order from week to week. Individuals were not marked and could not be reliably distinguished on the basis of plumage or size, so the smallest unit of study was the nest. When both members of a nesting pair were present at the nest, only the incubating or brooding bird's interactions were recorded to promote consistency with nests where only one adult was present.

Statistical Analyses

Generalized linear mixed models were constructed representing the study's alternative hypotheses (i.e., species identity, nest density, and/or nest location influence frequency of agonistic interactions; Table 2). Two response variables were considered: 1) total number of agonistic interactions (both interspecific and intraspecific) involving the focal nest within a 30-min observation period; and 2) number of interspecific agonistic interactions involving the focal nest within a 30-min observation period. Each model contained covariates controlling for date of observation, time of day of observation, and proportion of the four nearest neighboring nests occupied by heterospecific individuals. All these factors may influence rates of aggression (Burger 1984; Bukacinska and Bukacinski 1994; Pius and Leberg 1997; Somers *et al.* 2011). Models of total counts of interspecific and intraspecific interactions including species as a covariate also included an interaction term for species

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Table 1. Descriptions of agonistic behaviors observed in Double-crested Cormorants and Great Blue Herons.

Species	Behavior	Description
Double-crested Cormorant	fight over nest material	aggressive; bird takes or attempts to take nest material from another nest and elicits an aggressive response from the owner of that nest, or two birds engage in "tug-of-war" at opposite ends of a piece of nest material
	threat posture[1]	aggressive; bird leans forward with neck outstretched toward its opponent and waggles its head from side to side
	retreat	submissive; bird backs away in response to aggressive behavior by another bird
Great Blue Heron	arched neck[2]	aggressive; bird raises feathers along full length of neck and curves neck into an arched shape with bill angled downward
	fight over nest material	aggressive; bird takes or attempts to take nest material from another nest and elicits an aggressive response from the owner of that nest, or two birds engage in "tug-of-war" at opposite ends of a piece of nest material
	fluffed neck[2]	aggressive; bird raises head with bill held horizontally, raising feathers along full length of neck
	forward[2]	aggressive; bird holds wings slightly out from body, pulls neck in, raises neck plumes, then shoots bill and neck forward at another bird
	retreat	submissive; bird backs away in response to aggressive behavior by another bird

[1]Full description of behavior can be found in van Tets (1965).
[2]Full description of behavior can be found in Mock (1976).

and proportion of heterospecific neighbors. A random intercept term accounted for non-independence of observations made on the same nest (Zuur *et al.* 2009).

Model fitting and selection were performed in program R (R Development Core Team 2012) using the 'glmmADMB' package (Fournier *et al.* 2012; Skaug *et al.* 2014). The first step of model selection determined appropriate error structure for the full model, considering four types of regression models: Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial. Negative binomial models provided the best fit to the full model for both response variables

Table 2. Candidate model set used to predict two response variables: the total number of interspecific plus intraspecific agonistic interactions involving the focal nest in a 30-min observation period, and count of interspecific agonistic interactions involving the focal nest in a 30-min observation period.

Model Name	Hypothesis Represented
Null	Neither species identity, nor nest density, nor habitat structure affect frequency of interactions.
Species	Only species identity affects frequency of interactions.
Density	Only nest density affects frequency of interactions.
Location	Only nest location affects frequency of interactions.
Density+Location	Nest density and location, but not species identity, affect frequency of interactions.
Species+Location	Species identity and nest location, but not nest density, affect frequency of interactions.
Density+Species	Nest density and species, but not nest location, affect frequency of interactions.
Full	Nest density, nest location, and species identity all affect frequency of interactions.

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Table 3. Top models of total number of interspecific plus intraspecific interactions involving a focal nest per 30-min observation period, ranked according to Akaike's Information Criterion (AIC). *K* indicates number of model parameters, ΔAIC indicates difference in AIC compared with highest ranking model, and w_i indicates AIC weight of model.

Model	*K*	ΔAIC	w_i
Species+Location	9	0.00	0.72
Density+Species+Location	10	1.94	0.28

and were used for selection among reduced models representing alternative hypotheses (Table 2). Model selection was accomplished using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In Tables 3 and 4, we only report models with a difference of AIC ≤ 12 compared to the top model.

RESULTS

During 412 30-min observation periods, we observed 436 agonistic interactions between nesting individuals at Pigeon Lake. Interspecific interactions between cormorants and herons occurred in 54 observation periods (13.1% of all periods). Intraspecific interactions occurred in six (2.9%) heron observation periods and in 104 (50.7%) cormorant observation periods. Most interactions of either type occurred between the focal nest and occupants of neighboring nests. No interactions occurred in 60% of observation periods.

Species identity and nest location were more important predictors of total number of agonistic interactions (interspecific and intraspecific combined) than nest density (Table 3). Great Blue Herons engaged in fewer total interactions than Double-crested Cormorants in the same location, while tree-nesting birds engaged in fewer total interactions than ground-nesting birds (Fig. 1). Proportion of heterospecific neighbors also

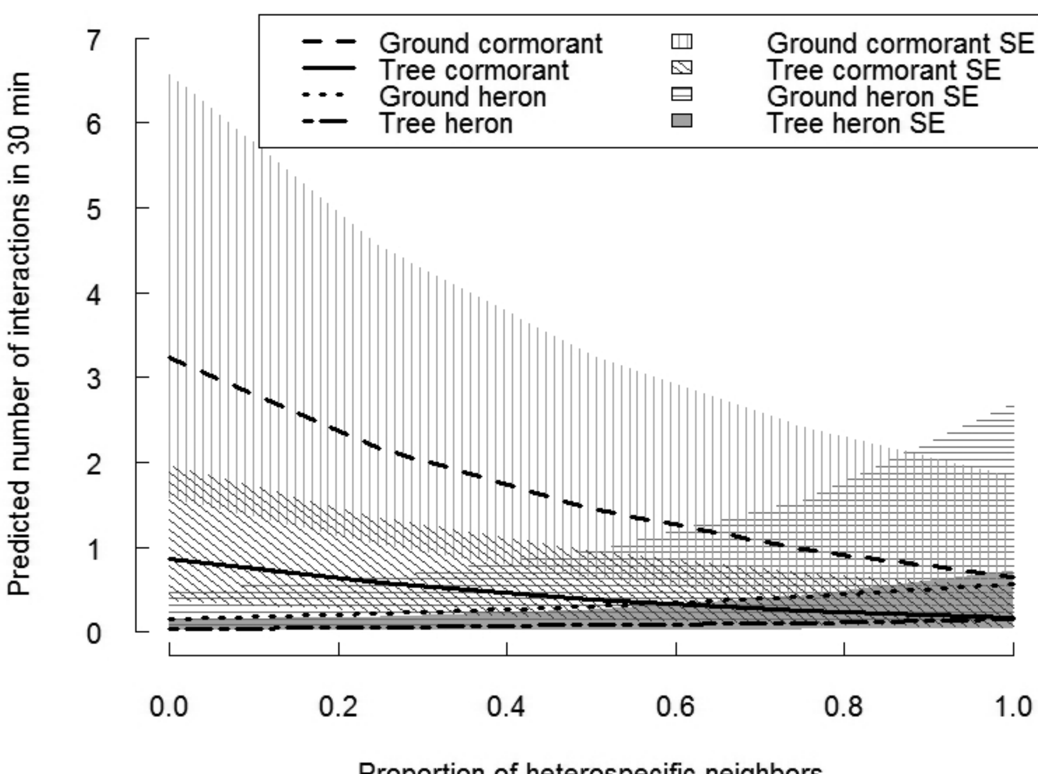

Figure 1. Predicted number of combined interspecific and intraspecific agonistic interactions (± SE) in 30 min for Double-crested Cormorants ("cormorant") and Great Blue Herons ("heron"), by nest location (ground or tree) and proportion of four nearest neighbors that are heterospecifics. Predictions were calculated according to the top model in the candidate set, with date and time fixed at their medians.

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influenced total number of agonistic interactions: herons nesting among conspecifics had fewer total interactions than herons nesting among cormorants, while cormorants nesting among conspecifics had more total interactions than cormorants nesting among herons (Fig. 1).

Nest location was a more important predictor of interspecific interaction rate than species identity or nest density (Table 4). Tree-nesting birds engaged in fewer interspecific interactions than ground-nesters. Heterospecific neighbors also had a strong positive effect on the number of interspecific agonistic interactions (Fig. 2).

DISCUSSION

Our observations at the Pigeon Lake waterbird colony support the hypotheses proposed by Somers *et al.* (2011) that species identity and habitat structure are related to the rate of agonistic interactions among nesting individuals. Species identity of neighbors also had a strong influence on agonistic behavior; arrangement of nests within a colony matters as much as overall species composition.

These results, along with previous research (Skagen *et al.* 2001; Cuthbert *et al.* 2002; Somers *et al.* 2007, 2011), suggest that some co-nesting species may be more affected by nesting among cormorants than others. Spatial structuring of nests within a colony is important; interaction rates can vary with nest location and species identity of neighbors. According to our study, rates of agonistic interaction will likely be highest among ground-nesters. Birds that interact little with conspecific neighbors in single-species colonies will likely engage in more

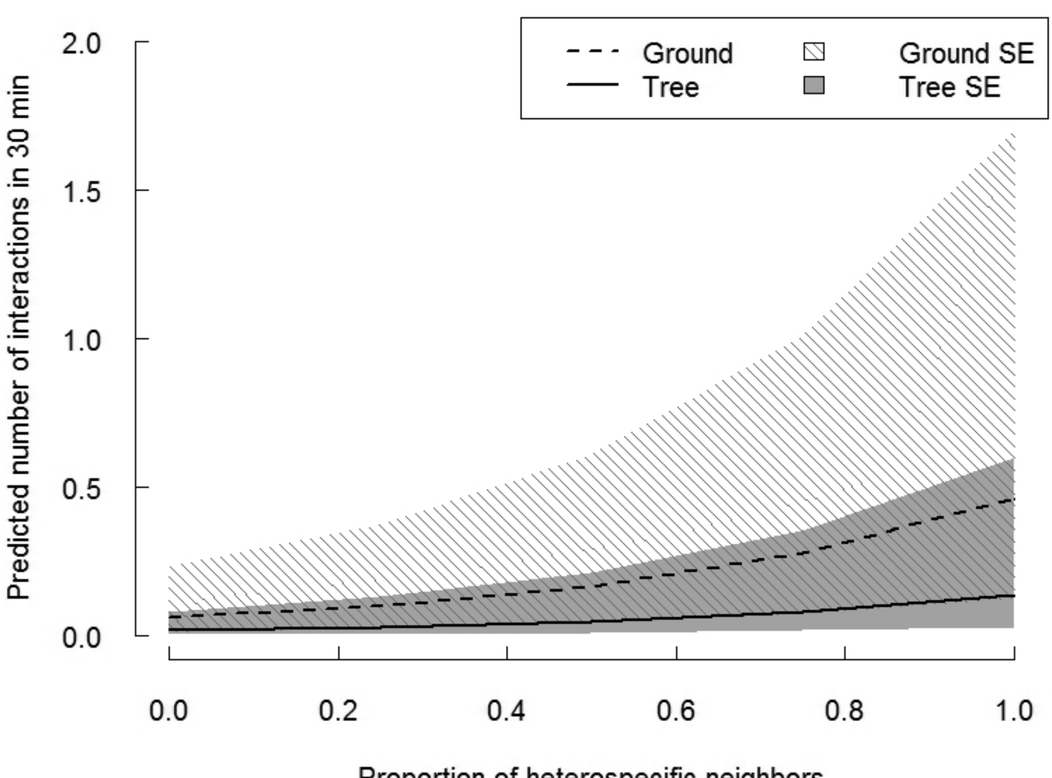

Figure 2. Predicted number of interspecific interactions (± SE) in 30 min involving a nest of either Double-crested Cormorants or Great Blue Herons, by nest location and proportion of four nearest neighbors that are heterospecifics. Predictions were calculated according to the top model in the candidate set, with date and time fixed at their medians.

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Table 4. Models of total number of interspecific agonistic interactions involving a focal nest per 30-min observation period, ranked according to Akaike's Information Criterion (AIC). *K* indicates number of model parameters, ΔAIC indicates difference in AIC compared with highest ranking model, and w_i indicates AIC weight of model.

Model	*K*	ΔAIC	w_i
Location	7	0.00	0.46
Density+Location	8	1.75	0.19
Species+Location	8	2.00	0.17
Density+Species+Location	9	3.75	0.07
Density	7	4.23	0.06
Density+Species	8	6.19	0.02
Null	6	6.45	0.02
Species	7	8.39	0.01

total interactions in mixed-species colonies because of added interspecific interactions. At Pigeon Lake, heron interactions with conspecific neighbors were limited, so presence of cormorant neighbors increased the total number of interactions involving herons. Future research on interactions between cormorants and co-nesters should determine whether, and to what degree, co-nester reproductive success declines when co-nesters engage in agonistic interactions with cormorants.

As cormorant population management has been implemented in the USA over the past 2 decades, cormorant interactions with other members of the ecological community have transitioned from a scientific to a political issue. Although this study suggests that Great Blue Heron behavior changes in the presence of co-nesting Double-crested Cormorants, it does not provide evidence either to support or discourage management activities. Other issues (e.g., reproductive impacts, potential impacts of control activities) must also be considered in decisions of whether and how to apply management to cormorant populations.

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