THE USE OF SOCIAL CUES IN HABITAT SELECTION BY WETLAND BIRDS

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Abstract. Wetlands are dynamic and can be destroyed and created quickly by natural forces. Therefore, birds inhabiting these wetlands must be able to locate new suitable sites rapidly. We investigated the cues wetland birds use when selecting a breeding site. Many species may use both habitat (e.g., vegetation structure) and social cues (presence of conspecifics and/or heterospecifics) when selecting a location for breeding. Using a two-species occupancy-modeling approach, we found certain wetland birds more likely to occur near other species, suggesting the presence of heterospecifics may influence settlement. Species that preferred wetlands with a roughly 50:50 ratio of open water to vegetation (hemimarsh) occurred more frequently than expected with the Pied-billed Grebe (Podilymbus podiceps), suggesting these species may use the presence of grebes when selecting a habitat. Conversely, Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) do not appear to use the presence of other species when selecting a breeding location. Previous research supports this finding, in that the number of young produced at a site the previous year (patch reproductive success) was important in how this species selected its breeding sites. Because settling on the basis of patch reproductive success requires occupancy or visiting a site the previous year, individuals new to a population must use other cues such as habitat. In this population inexperienced Yellow-headed Blackbirds were more prone than experienced individuals to colonize recently created wetlands. Several wetland species we investigated used social cues to select breeding sites, and this behavior may help explain the occurrence and distribution of wetland birds.

Key words: wetland-dependent birds, conspecific attraction, heterospecific attraction, colonization, wetlands.

INTRODUCTION

Every breeding season most birds have a choice of breeding location. In some species, most individuals choose to return to their previous breeding site (i.e., site fidelity is high). Other species decide where to breed on the basis of previous reproductive success, with a positive relationship between prior success and site fidelity (Hoover 2003, Porneluzzi 2003). Both strategies of high site fidelity and site fidelity based on reproductive success assume that there is year-to-year predictability in habitat quality (i.e., reproductive success in that habitat). However, some habitats may not be predictable, and...
decisions of where to breed may be directed via information collected from multiple sources (Orians and Wittenberger 1991). Wetlands are one such dynamic habitat. The potential for high year-to-year variation in hydrologic conditions within wetlands dictates that species residing in these habitats be able to assess and colonize new breeding sites quickly.

Some wetland species assess or prospect for breeding sites on a regular, if not yearly, basis (Pöysä et al. 1999, Ward 2005a, Piper et al. 2006). Although we know these species may be assessing breeding locations regularly, little research has addressed the cues they use when assessing these locations. Clearly, at the coarsest level, obligate wetland species are selecting “wetlands” in which to breed, but what aspects of a potential breeding site leads to a greater probability of settlement? Within wetlands, many species prefer a specific successional stage, hemi-marsh (Weller and Spatcher 1965, Murkin et al. 1997, Rehm and Baldassarre 2007). In addition to the specific successional stage of a wetland, other important factors affecting occupancy may be the wetland’s size or the landscape context of the habitat patch (e.g., Brown and Dinsmore 1986). However, even when the quality of habitat is constant, density and occupancy may not be equal across the landscape (Alonso et al. 2004, Nocera et al. 2009). Studies of ducks have found that their breeding distribution in wetlands may be attributable to the presence of conspecifics (Pöysä et al. 1998), the ducks using social cues (patch reproductive success) when assessing potential breeding locations (Pöysä 2006). A number of studies (as reviewed by Ahlering et al. 2010; this issue) have identified various species that use social cues (most often the presence of conspecifics) when selecting a breeding location.

Nocera et al. (2009) showed that there is not only variation between species but also within a species. They observed that older individuals used previous experience to select high-quality breeding sites, whereas younger individuals used conspecific attraction and settled near older individuals. Research on Texas on the Black-capped Vireo (Vireo atricapilla) illustrated that seemingly high-quality habitat remained unoccupied or occupied at a low density until conspecific cues were provided at these sites (Ward and Schlossberg 2004). Likewise, Betts et al. (2008) demonstrated that conspecific cues can even lure Black-throated Blue Warblers (Dendroica caerulescens) into settling in poor-quality habitats. Social cues, however, are not limited to conspecifics; some species use the presence of heterospecifics when selecting breeding locations (Mönkkönen et al. 1999, Parejo et al. 2005). The Yellow-headed Blackbird (Xanthocephalus xanthocephalus), an obligate wetland species, has been considered an “indicator” species because heterospecifics may use it to locate high-quality habitat (i.e., hemi-marshes; Weller 1969). Because Yellow-headed Blackbirds display frequently and are not as cryptic as many other wetland species, they may not only be a good indicator of hemi-marsh habitat, but their presence can be easily detected by other species. These studies along with others have illustrated how various species use social cues, in particularly the presence of conspecifics and heterospecifics, to select breeding sites.

Although several studies have identified the importance of social cues in the process of habitat selection, few studies have investigated the use of social cues by wetland birds. Ward (2005a) found that Yellow-headed Blackbirds use a social cue, the average number of young produced at a wetland the previous year (i.e., patch-level reproductive success), to guide future decisions of where to breed. Several studies of colonial seabirds have found that they also use social cues when selecting a breeding site (e.g., Danchin et al. 1998). Although little research has addressed heterospecific attraction in wetland birds, the hypothesis of heterospecific habitat copying (Parejo et al. 2005) predicts that a species may assess the quality of a habitat by the information produced by another species. Research on waterfowl suggests that the presence of heterospecifics, even at relatively high densities, does not negatively influence the settlement rates of other waterfowl that are potential competitors (Elmberg et al. 1997). Seppänen et al. (2007) provided a review demonstrating that in various taxa information from other individuals (i.e., social information) is frequently used by both conspecifics and heterospecifics, and this information is conceivably critical in the habitat-selection process. Because the habitat requirements of many wetland species overlap (Weller 1999), the presence of heterospecifics may indicate suitable habitat. Using a large dataset in which interspecific interactions were modeled in a two-species occupancy-modeling framework, we investigated the role of habitat, wetland size, and social cues (conspecific and heterospecific attraction) in the occupancy of wetlands by obligate wetland birds. Second, to determine the role conspecifics play in settlement by this species, we experimentally provided vocalizations and models of the Yellow-headed Blackbird at a subset of wetlands. Last, we took advantage of recently created wetlands, where a potentially important social cue (patch reproductive success) could not be assessed, to investigate whether experienced and inexperienced Yellow-headed Blackbirds use different cues when selecting a breeding location.

METHODS

We used data from 53 wetlands covered by the annual northeastern Illinois Wetland Bird Survey (NEWS) and a concurrent study of the population dynamics of the Yellow-headed Blackbird (Ward 2004). NEWS was conducted from 1980 through 2005 in Cook, Lake, McHenry, Kane, DuPage, and Boone counties in northeastern Illinois. Of these 53 wetlands, 18 were recently created and 35 were established. The recent wetlands had been created by the accidental breaking of drainage tiles in agricultural areas (n = 5), inadvertent changes in hydrology usually associated with suburban development (n = 7), or purposefully as wildlife habitat (n = 6). We located
Because co-occurrence is not necessarily influenced by the co-occurrence is more frequent than expected by chance. Values less frequent than expected by chance, and values >1 indicate that two species occur independently, values <1 indicate co-occurrence is less frequent than expected by chance, and values >1 indicate co-occurrence is more frequent than expected by chance. Because co-occurrence is not necessarily influenced by the presence of the other species and may be due to the two species responding independently to the same environmental conditions, we included covariates on the occupancy parameter ($\psi$) for each species in a pair. In all two-species analyses we included covariates for wetland size and a quadratic effect of wetland interspersion (to account for a potential peak in occupancy at intermediate values; hemi-marsh successional stage). After controlling for the effects of wetland size and interspersion on each species independently, we interpreted negative values of $\psi$ as potential indicators of avoidance or competitive exclusion and positive values of $\psi$ as potential indicators of heterospecific attraction.

Multiple-season models for two-species occupancy have not yet been fully developed and implemented in PRESENCE. However, given the relatively low site fidelity and resulting high turnover of wetland birds at these sites (Ward 2005b, unpubl. data), rather than analyzing each year separately, we combined all years and treated each year–by-site combination as a different site. We incorporated data from ten species in the model: the American Coot (Fulica americana), Black Tern (Chlidonias niger), Blue-winged Teal (Anas discors), Least Bittern, Mute Swan (Cygnus olor), Pied-billed Grebe, Sandhill Crane (Grus canadensis), Sora, Virginia Rail, and Yellow-headed Blackbird. We investigated species-interaction factors among three of the most often encountered species, the Least Bittern, Pied-billed Grebe, and Yellow-headed Blackbird, and between each of these three species and the seven others. We chose these three species because they are relatively common and represent different life histories (the Yellow-headed Blackbird is insectivorous, conspicuous, semi-colonial, and nests in cattails, the Pied-billed Grebe builds floating nests, vocalizes often, and feeds primarily on submerged aquatic prey, and the Least Bittern feeds on a wide variety of items including fish and insects, is very secretive, and nests in cattails). For each pair of species, we built eight models all containing covariates of occupancy of each species of the pair: occupancy of the two species dependent ($\phi = 1$) or independent ($\phi = 0$), each with the four possible combinations of species detected dependently or independently when both are present and the probability of detection of each species being equal or different in the absence and presence of the other species (MacKenzie et al. 2006). We also included covariates of occupancy for wetland size and wetland interspersion.
locations of individual birds on a site map. Playbacks were used as outlined earlier in the methods. At the experimental sites, according to the size of the site, we erected one to three portable CD players (call boxes) on floating platforms (see Ward and Schlossberg 2004 for details on the call-box system). Call boxes were arranged so the researchers could hear the calls throughout the wetland. The call boxes broadcasted vocalizations for a total of 3 hr from 02:00 to 07:00 and then again for an hour between 10:00 and 14:00 and between 17:00 and 19:00. The vocalizations consisted of the calls and songs of not only the Yellow-headed Blackbird but also the Pied-billed Grebe, Least Bittern, Virginia Rail, and Sora. Although the addition of these vocalizations could ultimately result in difficulty analyzing the data, because these four species were present at most but not all of the experimental sites, we want to have a similar heterospecific community at all the experimental sites. The songs and calls were from commercially available CDs of bird vocalizations. The study was conducted in 1999, 2003, 2006, and 2007. In 1999 and 2003 the same sites were used and there were six experimental sites and four control sites. In 2006 and 2007 two new experiment sites and one new control site were added, but the study was discontinued at the sites previously used. At all experimental sites we positioned models of adult male Yellow-headed Blackbirds near the call boxes. We used a multi-season occupancy-modeling approach (MacKenzie et al. 2006) to investigate the differences in occupancy between experimental and control sites.

COLONIZATION OF RECENTLY CREATED WETLANDS

We investigated whether experienced or inexperienced Yellow-headed Blackbirds bred at the 18 recently created sites described previously. Between 1998 and 2004, we captured 423 Yellow-headed Blackbirds and banded each with a unique four-color combination of plastic leg bands (for additional methods see Ward 2004). In any given year of the 6-year study, 67.2% (SD±9.3%) of the males and 51.6% (SD±8.5%) of the females in the population were color-marked. We spot-mapped birds at the recently created wetlands and at all sites known to have breeding Yellow-headed Blackbirds. At both established and recently created sites we inspected Yellow-headed Blackbirds to determine if they were color-marked. Data were collected as part of a larger study of the of the Yellow-headed Blackbird’s population dynamics (Ward 2004, 2005b). G-tests were used to determine if there was a difference in the percentage of color-marked individuals at recently created vs. established sites.

RESULTS

No species had a negative value of $\phi$, suggesting avoidance or competitive exclusion was unimportant for the species we considered. For the American Coot, Blue-winged Teal, Mute Swan, Pied-billed Grebe, Sora, and Yellow-headed Blackbird, $\phi > 1$ with at least one other species, indicating that each of these species occurs with at least one other species more often than expected by chance (Table 1). For the Black Tern, Sandhill Crane, and Virginia Rail $\phi = 1.0$ with all species, indicating that co-occurrence patterns did not deviate from those expected by chance (Table 1). The Least Bittern occurred more than expected with two of the other nine species, while for the Pied-billed Grebe and Yellow-headed Blackbird $\phi > 1$ with five and four other species, respectively. Habitat cues also appear to be important to all of these species in selecting a breeding site (Table 1). Because PRESENCE has difficulty estimating the variance–covariance matrix when parameters are near the limits of the allowable values, we could not calculate 95% confidence intervals for all models. However,

<table>
<thead>
<tr>
<th>Species</th>
<th>Least Bittern</th>
<th>Pied-billed Grebe</th>
<th>Yellow-headed Blackbird</th>
<th>Habitat cue(s)</th>
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<td>American Coot</td>
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<td>1.00</td>
<td>1.00</td>
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</tr>
<tr>
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<td><strong>1.10</strong></td>
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<tr>
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<td>1.00</td>
<td>1.00</td>
<td>Size</td>
</tr>
<tr>
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<td><strong>1.21</strong></td>
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<td>Both</td>
</tr>
<tr>
<td>Sandhill Crane</td>
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<td>1.00</td>
<td>1.00</td>
<td>Size</td>
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<td>1.00</td>
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<td>1.00</td>
<td>Size</td>
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<tr>
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<td>1.00</td>
<td><strong>1.33</strong></td>
<td>—</td>
<td>Interspersion</td>
</tr>
</tbody>
</table>

*The models did not reach convergence so no estimate could be generated.
for those species-interaction factors for which we could calculate the confidence interval, the intervals for the species-interaction factors greater than 1 did not include 1.

Results of the conspecific-attraction experiment suggest that Yellow-headed Blackbirds did not select sites where blackbird vocalizations and models were provided (Fig. 1). Over the course of the study, we observed only six males (three of which were yearlings) and two females at the experimental sites, and none bred at those sites. At the three control sites, over 2 years, we observed three males (two of which were yearlings) and one female. We did not have a sample size large enough to investigate whether the addition of the other four species’ vocalizations resulted in settlement at sites where they were not formerly present.

Recently created wetlands were colonized primarily by unbanded Yellow-headed Blackbirds that were likely new to the population. The percentage of banded and unbanded Yellow-headed Blackbirds at recently created sites differed for both males (difference of 54%; $G_{adj} = 27.67, df = 1, P < 0.01$) and females (difference of 50%; $G_{adj} = 29.64, df = 1, P < 0.01$; Fig. 2). The sample size was the number of color-marked individuals per year over all years, so some color-marked individuals represent multiple data points. Of the 18 recently created sites that Yellow-headed Blackbirds settled, nine were also settled by Pied-billed Grebes, eight by American Coots, eight by Blue-winged Teal, and four by Soras. Five sites were not colonized by any of the other nine species investigated in this study. The remaining five species colonized fewer than three of the recently created sites.

**DISCUSSION**

When selecting a breeding location, wetland birds appear to use not only habitat-based cues but also social cues. There is little support for interspecific exclusion in this system, as no values of $\varphi$ were <1. This finding is supported by experimental research on the Mallard (*Anas platyrhynchos*), an increase of which did not reduce the colonization rate of the Eurasian Green-winged Teal (*Anas crecca*; Elmberg et al. 1997). However, we found several species for which $\varphi > 1$, the largest values being for association with the Pied-billed Grebe. Interestingly, results for all the species that prefer hemi-marsh conditions (interspersion), as well as the Sora, which prefers more open wetlands, suggested attraction to Pied-billed Grebes ($\varphi > 1$). Species that had the greatest affinity for large sites (Black Tern, Sandhill Crane, Virginia Rail) showed no sign of associations with other species ($\varphi = 1$). For all the species with positive species-interaction factors, the factors were positive with more than one species, so more research is needed to determine if these species are cueing on the “community,” a specific species, or an unmeasured habitat variable.

If one species were an indicator for several species, the species that returns earliest in the breeding season may be a good candidate. In our study area not all of the wetland birds arrive at the same time, and the first species to arrive obviously cannot use the presence of other species in the current breeding season. In order of average nest-initiation date (which is highly correlated with arrival date), the species we investigated in
northeastern Illinois are the Sandhill Crane (5 April), Pied-billed Grebe (4 May), Mute Swan (7 May), Yellow-headed Blackbird (8 May), Blue-winged Teal (10 May), American Coot (20 May), Virginia Rail (20 May), Black Tern (21 May), Least Bittern (22 May), and Sora (25 May; Bohlen and Zimmerman 1989, Paine 1997; B. Semel, unpubl. data). Although Sandhill Cranes arrive the earliest, they initiate incubation well before most species even arrive, and, if not incubating, adults spend a large portion of their time foraging in agricultural fields, so their presence may not provide informative cues for other wetland species. The species-interaction factor also suggests other species are not settling in association with the crane. However, the second species to settle is also the species with the most other species positively associated with it, the Pied-billed Grebe. The presence of Pied-billed Grebes may be a good cue to use for several reasons; (1) the species is relatively common compared to most others studied, (2) it arrives several weeks before and breeds earlier than any other species except the Sandhill Crane, and (3) it vocalizes more frequently than many of the other wetland species and its vocalizations carry well and can often be heard throughout a wetland, possibly increasing its detectability by other species.

The Yellow-headed Blackbird had values of $\phi > 1$ with four other species, suggesting heterospecific attraction. However, the failure of the conspecific-attraction experiment and the previous research showing the species colonizes on the basis of the previous year’s patch reproductive success suggest that other species may be cueing in on the Yellow-headed Blackbird rather than the reverse. In addition to Yellow-headed Blackbird vocalizations, we also broadcast the vocalizations of other species, so we were also investigating the role of heterospecifics, although the results suggest that neither conspecific nor heterospecific presence affected the blackbird’s settlement.

Because Yellow-headed Blackbirds use patch reproductive success as a cue, the lack of this information at recently created wetlands may delay their colonization and prompts the question of how new sites are colonized. Although 56% of males and 43% of females that returned to the study area bred at a different wetland (Ward 2004), and 67% of males and 52% of females in the population were color-marked, only 22% of the males and a mere 4% of the females at recently created sites were color-marked. This pattern suggests that individuals at recently created sites may be new to the population, possibly immigrants naïve to the area. These naïve individuals would have no previous experience and therefore could not use the previous year’s patch reproductive success as a cue, but they could use the mere presence of conspecifics. However, the failure of the conspecific-attraction study to attract breeding Yellow-headed Blackbirds further suggests that naïve individuals may be relying simply on habitat cues.

The failure of the study to attract experienced Yellow-headed Blackbirds to sites with vocalizations and models of their species may be explained by the type of social cue provided. If experienced individuals use patch reproductive success, the presence of conspecifics without nests and young suggests a low-quality site. Interestingly, all but one individual observed at the experimental conspecific-attraction sites were unbanded. Although we selected experimental sites that once were suitable for Yellow-headed Blackbirds (breeding population had been present), we may not have selected the highest-quality sites in terms of habitat, and that may explain why only a few birds were observed at these sites and none attempted to breed. These birds may have been simply prospecting for suitable habitat, as has been observed in this population (Ward 2005a).

Many questions associated with the process by which wetland birds select a habitat remain to be addressed. Because there are several habitat and social variables not accounted for in this study, a controlled experimental study is needed to investigate heterospecific attraction, particularly of which species are the most important cues for other species. This study suggests that future research on heterospecific attraction should be directed toward the Pied-billed Grebe. Given the dynamic nature of wetlands, it is not surprising that wetland birds may use both social and habitat-based cues to select a breeding site and that the cues they use may change with their experience.

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LITERATURE CITED


