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A TEST OF CUES AFFECTING HABITAT SELECTION BY WADING BIRDS

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Abstract.—We examined foraging-habitat selection by free-ranging wading birds presented with different social and environmental cues by conducting two experiments in eight replicate ponds adjacent to the northern border of the Florida Everglades. The first experiment examined the relative influence of a social (presence of a flock of decoys) and environmental (water depth) cue on the selection of ponds. The second experiment examined the influence of two environmental cues (water depth and fluctuating water level) on the selection of ponds. In the first experiment, wading birds were most attracted to ponds with both the presence of a flock of decoys and shallow water. The social and environmental cues both had the same attractive potential to wading birds. In the second experiment, birds were again attracted to ponds with shallow water; however, fluctuating water level had no significant influence on foraging-habitat selection. If birds do not perceive fluctuating water levels as a cue to habitat quality, then the well-documented relationship between nesting success and fluctuating water levels likely stems from birds responding to factors that covary with water-level changes. *Received 15 December 2005, accepted 18 October 2006.*

Key words: Everglades, foraging, habitat quality, habitat selection, sociality, wading birds.

Una Prueba de las Señales que Afectan la Selección de Hábitat por Aves Vadeadoras

Resumen.—Examinamos la selección de hábitats de forrajeo por parte de aves vadeadoras de movimientos libres a las que les fueron presentadas diferentes señales sociales y ambientales mediante dos experimentos realizados en el borde norte de los Everglades de Florida, utilizando ocho charcas como réplicas. El primer experimento examinó la influencia relativa de una señal social (presencia de una bandada de señuelos) y una señal ambiental (profundidad del agua) sobre la selección de las charcas. El segundo experimento examinó la influencia de dos señales ambientales (profundidad del agua y fluctuaciones en el nivel del agua) sobre la selección de charcas. En el primer experimento, las aves vadeadoras fueron más atraidas a las charcas que presentaban tanto una bandada de señuelos como aguas pandas. Las señales sociales y ambientales tuvieron el mismo potencial de atraer a las aves vadeadoras. En el segundo experimento, las aves nuevamente fueron atraidas a las charcas con aguas pandas, pero los niveles fluctuantes del agua no tuvieron una influencia significativa sobre la selección de hábitat de forrajeo. Si las aves no perciben las fluctuaciones en los niveles de agua como una señal de la

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calidad del hábitat, es probable que la relación entre el éxito de nidificación y los niveles fluctuantes del agua, que ha sido bien documentada, se desprenda de la respuesta de las aves a factores que covarían con los cambios en el nivel de agua.

IN SEASONALLY FLUCTUATING wetlands, the temporal and spatial movement of foraging patches create a challenge for avian predators. High-quality patches, which contain a high density of prey and shallow water, are interspersed within a landscape mosaic of low- and medium-quality patches. During the dry season, water levels progressively recede across marshes, producing habitat with continually changing hydrologic conditions. Within hours, large rainfall events can disrupt this recession and change the number and location of foraging patches (Kushlan 1981) in an unpredictable way.

Wading birds, a group of the top trophic-level predators, must locate and exploit these ephemeral food patches to nest successfully (Frederick and Spalding 1994). Species are aided by plasticity in foraging behavior (Erwin 1983, Kushlan 1989) to different degrees, which leads to interspecific differences in the response to changing habitat quality. Gawlik (2002) described a continuum of foraging strategies used by wading birds in the Everglades. On one end of the continuum is the "searcher" foraging strategy used by the White Ibis (*Eudocimus albus*), Wood Stork (*Mycteria americana*), and Snowy Egret (*Egretta thula*). These birds select the highest-quality foraging patches but abandon them shortly after they begin to degrade, to search for other high-quality patches. On the other end of the continuum is the "exploiter" foraging strategy, which is used by the Great Egret (*Ardea alba*), Little Blue Heron (*E. caerulea*), and Great Blue Heron (*A. herodias*). These birds continue to forage in a patch after the quality has declined rather than search for a new one.

Selection pressures should be particularly strong for searchers to perceive cues that allow them to reduce search time for finding suitable foraging habitat. Exchanging information with one another via social cues is one way in which wading birds could increase their chances of finding high-quality habitat. When habitat suitability is held constant, wading birds are more likely to select foraging sites with flocks present than those without (Green and Leberg 2005), and they seem to prefer habitat with large flocks over habitat with small flocks (Krebs 1974).

Wading birds also select foraging habitat based on the composition of flocks present, though the patterns are not consistent among studies. Kushlan (1977) found that wading birds as a group were more attracted to flocks composed of white decoy birds compared with dark decoy birds. However, Green and Leberg (2005) found that individual species of wading birds most often selected habitat with flocks that resembled conspecifics. Other authors (Caldwell 1981, Master 1992, Smith 1995) have found that several species of wading birds are most attracted to flocks containing the Snowy Egret, presumably because this searcher species is sensitive to changes in prey availability (Gawlik 2002). Many wading bird species, including all the searcher species, have conspicuous, white plumage, which provides a good social cue, because it allows searching birds to find foraging flocks more rapidly and from greater distances (Kushlan 1981; but see Tickell 2003).

Social cues need not occur only at foraging sites. Because most wading bird species roost and nest in groups, it is possible that information is exchanged among individuals at these communal locations—the "information center" hypothesis (Ward and Zahavi 1973). If birds can determine which individuals have been successful at foraging, they can reduce their search time on subsequent days by simply following successful individuals from a communal location to foraging areas (Krebs 1974, Custer and Osborn 1978).

Environmental cues such as water depth, water recession rate, and pool isolation may also help wading birds assess the quality of foraging habitat (Kushlan 1976a, 1979; Smith 1995; DuBowy 1996; Gawlik 2002). When water levels increase rapidly in the Everglades, birds respond by abandoning their nests (Frederick and Spalding 1994). Conversely, when water levels recede at a rate of >5 mm day^{-1}, birds tend to nest successfully (Kushlan 1976b, Frederick and Collopy 1989). Vegetation type (Kushlan 1979, Hoffman et al. 1994, Safran et al. 2000, Bancroft et al. 2002) and prey activity (D. E. Gawlik pers. obs.) also may be good indicators of prey availability.

A recent review of ecological trap theory (Battin 2004) underscored the importance of understanding the cues that birds use to select habitat. A central premise of ecological trap theory is that attractiveness of habitat to animals can be independent of the actual quality of the habitat, as defined by demographic responses. Traditional studies of habitat selection have not provided information that will allow researchers to evaluate the cues that animals use to assess habitat attractiveness, because the focus has been on simply identifying habitats that are preferred or avoided. Habitat-selection studies must begin to address the conditions under which one set of cues is chosen over another, the relative strength of the various cues, and the link between habitat attractiveness and habitat quality.

We conducted two experiments to determine the relative effects of social and environmental cues on the selection of foraging habitat by free-ranging wading birds. One experiment compared the influence of an environmental cue (water depth) and a social cue (presence of a flock of decoys) on foraging-habitat selection. The other experiment examined the influence of two environmental cues (water depth and fluctuating water level) on foraging-habitat selection. We chose fluctuating water level as a treatment variable, because receding water levels are associated with successful nesting and variation in time of nest initiation (Kahl 1964, Kushlan 1989, Frederick and Spalding 1994, González 1997), and increasing water levels often cause nest failure (Frederick and Collopy 1989). To ensure a treatment effect over the short duration of each daily trial (1 h), we used a much higher recession rate (6 cm h^{-1}) than the values believed to affect nesting success over a season (5 mm day^{-1}). Our recession rate is comparable to values in coastal creeks, where tidally driven fluctuations in water level affect foraging decisions (Bryan et al. 2002).

Methods

Study area.—The experiments were conducted in a set of constructed ponds adjacent to the northern Everglades and described in detail in Gawlik (2002). The ponds were located on the northwest border of the Arthur R. Marshall Loxahatchee National Wildlife Refuge located in Palm Beach County, Florida. The ponds were part of a set of 15 replicate 0.2-ha impoundments embedded in a 1,545-ha constructed wetland. We manipulated aquatic vegetation so that ponds were similar in vegetation structure. There was no emergent vegetation, but ponds contained scattered patches of submerged plants. Prey were allowed to enter all ponds through a common inflow pipe.

We attempted to validate a key assumption that prey density was similar among ponds by examining ancillary data on the distribution of small fish collected during a previous experiment at the site (Gawlik 2002). In that experiment, small fish (<2 cm) passed through a screen designed to exclude larger fish from the intake pipe. We found that small fish density ($\bar{x}$ = 1.1 fish m^{-2}, SD = 3.1, n = 192) was variable within ponds, and there was no significant difference in density among ponds (analysis of variance [ANOVA], F = 1.01, df = 11 and 191, P = 0.44). There was little chance for bird predation to reduce prey densities after our experiments began, because the experiments ran for only one hour per day. Also, because treatments were re-randomized and ponds were refilled with water daily, treatment type had little effect on prey density in a particular pond.

Water depth and decoy flock experiment.—We used eight ponds for the first experiment, which examined the influence of water depth and the presence of a decoy flock on foraging-habitat selection. The experiment was conducted on 22–26 October 1997. Each pond had a water depth of either shallow (10 cm) or deep (37 cm) and either had a flock of decoys present or it did not. A decoy flock was created by placing 15 plastic lawn flamingos, each painted white with a black bill and mounted on wire legs, ~1 m from each other in the center of the pond. Previous work using these flamingo decoys in this configuration showed that wading birds were attracted to the decoys and would land next to them as if they were a live foraging flock (Crozier and Gawlik 2003). In a previous experiment, it appeared that more wading birds arrived at the experimental site from the north and encountered the northern ponds first. Therefore, we used a randomized block design, with ponds separated into a northern and southern block of four ponds each. On each day of the experiment, we randomly reassigned the water-depth and decoy-flock treatment combinations within the blocks.

Water depth and water-level fluctuation experiment.—Six of the ponds were used for the second experiment, which examined the influence of water depth and fluctuating water level on foraging-habitat selection. This experiment was conducted on 3–7 November 1997. Each pond had a water-depth treatment of either shallow (10 cm) or deep (37 cm), and a fluctuating water-level treatment of increasing level (6 cm h^{-1}), decreasing level (6 cm h^{-1}), or no change. A completely randomized design was employed instead of a randomized block design, because we did not have enough ponds available for spatial replication. Thus, there were no distinct groupings of north and south ponds. On each day of the experiment, we randomly reassigned the water-depth and water-level-fluctuation treatment combinations among the six ponds.

In both experiments, the observation period began each day at dawn and ended 1 h later. Two observers were simultaneously stationed in separate towers ~5 m tall. Towers were positioned to provide each observer a clear view of half (three or four) of the ponds but far enough away to avoid disturbing the birds. Each tower was ~50 m from the nearest pond and had no obvious effect on bird behavior. Observers recorded the number, species composition, and time of arrival and departure for all wading birds that landed in the ponds as well as their subsequent behavior.

Analyses.—Statistical analyses were performed using SAS, version 9.1 (SAS Institute, Cary, North Carolina). In both experiments, we assumed that days were independent because treatments were re-randomized each day, thereby forcing birds to assess all treatments each morning. The dependent variable in both experiments was the number of wading bird flocks that landed per pond. The number of flocks was used rather than the number of birds because the behavior of individuals within a flock was not independent. However, most of the flocks consisted of only one bird. Species were pooled because of lack of independence and sample-size restrictions.

To eliminate the chance that birds could have gained information on the habitat quality of ponds from direct sampling, we included in the analyses only those birds initially arriving from outside the experimental site. Because the stimulus value of the ponds changed as birds arrived, flocks were included in the analyses only if they landed before any pond at the site had increased to more than three birds. Three birds was chosen *post hoc* as the cutoff, because it was a natural breakpoint in the data distribution.

In the water-depth and decoy-flock experiment, we developed a mixed model in PROC MIXED to compare the abundance of wading-bird flocks among treatments. The model contained terms for the fixed effects of water depth and decoy presence and for the random-block effect, as well as terms for the random interactions between the block and each treatment effect. Estimates of the random-block effect and its interactions were of no interest and are not presented. The variance-component covariance structure was most appropriate for the data based on Akaike Information Criteria (Littell et al. 1996).

In the water-depth and water-level-fluctuation experiment, we used an ANOVA in PROC GLM to compare the abundance of wading-bird flocks among water-depth and water-level-fluctuation treatments. Initially, we constructed a full fixed-effects model that contained the two main effects and the interaction term. The interaction term was eliminated because of its large *P* value, leading to a final reduced model containing only main effects. Inspection of residual plots indicated that the assumption of equal variances among treatments was met for both experiments.

RESULTS

Water-depth and decoy-flock experiment.—Over the five-day observation period, seven species of wading birds consisting of 318 individuals selected our experimental ponds as foraging habitat. Because each day we truncated the data when three birds occurred within a single pond, only flocks arriving within the first 17–19 min of the surveys (range: 4–8 flocks day^{-1}) were used in the analysis. Tricolored Heron (*E. tricolor*) and Little Blue Heron were the most common species in the analysis consisting of 19 and 11 individuals, respectively. One Snowy Egret and one White Ibis were also included in the analysis.

The model indicated that wading birds were significantly more attracted to ponds with a decoy flock present than to ponds without flocks (*F* = 6.2, df = 1, *P* = 0.02). Birds were also significantly more attracted to ponds with shallow water than to ponds with deep water (*F* =

6.2, df = 1, P = 0.02). When birds were faced with the intermediate treatment combinations of shallow water–decoy flock absent and deep water–decoy flock present, they selected the treatments equally (Fig. 1A), which suggests that flock presence and water depth had a similar potential for attraction.

Water-depth and water-level-fluctuation experiment.—Over the five-day observation period, six species of wading birds (total 121 individuals) selected ponds as foraging habitat. The truncated data set used in the analysis consisted of flocks arriving within the first 24–52 min of the surveys. Tricolored Heron was the most abundant species, with 26 individuals. White Ibis, Little Blue Heron, Glossy Ibis (*Plegadis falcinellus*), and Snowy Egret were the next most abundant species in the analysis, with 9, 8, 7, and 6 individuals, respectively. One Great Egret was also included in the analysis. The number of flocks selecting ponds during the first 24–52 min of the surveys ranged from 7 to 13 flocks.

The reduced model showed a significant effect of water depth, with more flocks selecting ponds with shallow water than deep water (F = 18.7, df = 1, P < 0.01), as was the case in the previous experiment. However, there was not a significant effect of water-level fluctuations on the selection of ponds by flocks (F = 0.7, df = 2, P = 0.52). All shallow-water treatments were selected more than deep-water treatments (Fig. 1B).

DISCUSSION

The results from the first experiment suggest that wading birds, which forage in habitat that is patchy and unpredictable, rely on a combination of social and environmental cues to select foraging habitat. The specific cues in the present study had about equal potential for attracting wading birds. The strength of the social cues is noteworthy, given that most habitat-selection studies focus on environmental variables. It was striking to see birds trying to land at sites with deep water that was obviously unsuitable for foraging, simply because a decoy flock was present. The effect of social cues may have been even stronger if we had observed more white-plumaged birds, because birds with dark plumage, which were the majority of birds in this experiment, are less attracted to white-plumaged decoys (Kushlan 1977, Green and Leberg 2005).
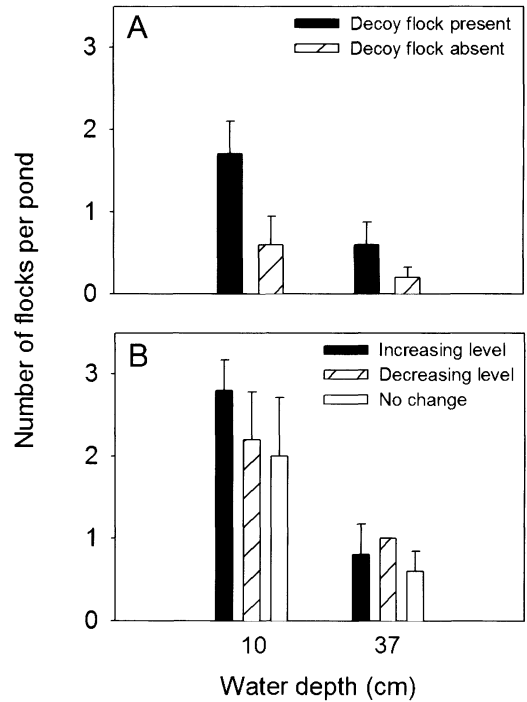

FIG. 1. (A) Number of flocks (mean ± SE) landing in eight experimental ponds with treatments of water depth (10 cm or 37 cm) and decoy flock (present or absent) over a 5-day period (n = 40). (B) Number of flocks (mean ± SE) landing in six experimental ponds with treatments of water depth (10 cm or 37 cm) and water-level fluctuation (increasing 6 cm h^{-1}, decreasing 6 cm h^{-1}, or no change) over a 5-day period (n = 30).

The searcher species are known to be highly social, which could be an effective strategy for exploiting food resources in an unpredictable environment such as a fluctuating wetland (Krebs 1974, Kushlan 1979). Several species have been shown to be most attracted to flocks of birds with white plumage (Caldwell 1981, Master 1992, Green and Leberg 2005) as well as to flocks with a larger number of birds (Krebs 1974). Prey intake rate can be higher in larger flocks (Krebs 1974), so the presence of large foraging flocks could be a cue for good foraging conditions (Gawlik 2002). Because this cue is visible from a distance in an open marsh, it could significantly reduce search time and thus allow birds to overcome one of the key obstacles of foraging in patchy, unpredictable environments.

In the second experiment, which compared the environmental cues of water depth and water-level fluctuation, only water depth had a significant effect on foraging-habitat selection. Water depth is an environmental cue that has been repeatedly shown to be an important determinant of habitat use (Kahl 1964, Kushlan 1976a, Hoffman et al. 1994, Ntiamoa-Baidu et al. 1998, Bancroft et al. 2002, Gawlik 2002, Maccarone and Brzorad 2005). Water depth may provide birds with information on how vulnerable prey are to capture. Water depth also may reflect the density of prey in a patch, particularly during the dry season, when low water levels often coincide with concentrated prey.

Our results showed that birds were more attracted to ponds with shallow water than to those with deep water; however, water-level fluctuation had no significant effect on foraging-habitat selection. A similar pattern was observed in tidal estuaries (Maccarone and Brzorad 2005). Wading birds used habitats based on water depth but did not use habitats based on the direction of the tidal change. In lakes, seasonal water-level fluctuations affect wading-bird habitat use through an interaction with habitat type (Smith 1995, Dimalexis and Pyrovetsi 1997). Birds are not responding to water-level fluctuation *per se* but rather to the spatial extent and suitability of different habitat types, which are ultimately a function of lake stage. This view of water-level fluctuation differs from the present study, where we tested for direct effects over shorter time-scales. Our study does not preclude the existence of indirect effects over longer time-scales.

In freshwater marshes, water-level fluctuation is an important ecological process for wading birds, because decreasing water levels makes prey available (Kushlan 1989). As water levels recede, aquatic organisms are forced into isolated pools of water within a drying marsh, producing concentrated patches of prey that are vulnerable to capture (Kushlan 1976a, Gawlik 2002). Our results suggest that the species we observed did not use water-level fluctuation as a cue for habitat quality, even though nesting success of some wading-bird species in the Everglades clearly depends on water-level fluctuations (Frederick and Spalding 1994). Because birds respond behaviorally to increasing water level by quickly abandoning their nests, they must be able to continuously assess the quality of their foraging habitat. We hypothesize that birds gauge changing habitat quality from water-level fluctuations by sampling prey captures directly (Dugan et al. 1986) rather than using fluctuations *per se* as the cue. This hypothesis is consistent with observations of Wood Storks returning to a foraging site the day after heavy rains had increased the water level and made the habitat unsuitable (D. E. Gawlik pers. obs.).

An alternative hypothesis for the lack of response to water-level fluctuation is that the cue does not reflect habitat quality for some species. Kushlan (1979) suggested that the White Ibis does not depend on a water recession to concentrate prey but instead select habitat with shallow water. Such habitat makes prey in the water column vulnerable to capture, and it allows White Ibis to probe below the water column into the sediment, where another set of prey animals may exist. The Tricolored Heron, the most common species in our study, similarly may not rely on water-level fluctuations to produce good habitat, because they select foraging habitat on the basis of water depth rather than prey density (Gawlik 2002). If water recessions function primarily to increase prey density, there is no reason to expect that the Tricolored Heron would perceive water-level fluctuation as a cue for habitat quality. Future tests of these hypotheses on a species-specific basis will improve our understanding of habitat selection and focus attention on ecosystem characteristics that are most likely to affect wading-bird populations.

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