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THE EFFECTS OF PREY AVAILABILITY ON THE NUMERICAL RESPONSE OF WADING BIRDS

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Abstract. Reduced prey availability has emerged as a primary hypothesis to explain population constraints on wading birds in numerous wetlands around the world. However, there is almost no understanding of which component of prey availability (i.e., prey density or vulnerability of prey to capture) is affecting populations and whether the relative effects of each component differ among species. In this study, I manipulated prey density and water depth (i.e., prey availability) in 12 0.2-ha ponds to determine their relative effects on the numeric response of eight species of free-ranging wading birds (White Ibis, *Eudocimus albus*; Wood Stork, *Mycteria americana*; Snowy Egret, *Egretta thula*; Glossy Ibis, *Plegadis falcinellus*; Great Egret, *Ardea alba*; Tricolored Heron, *Egretta tricolor*; Great Blue Heron, *Ardea herodias*; and Little Blue Heron, *Egretta caerulea*). The experiment was conducted in a constructed wetland adjacent to, and west of, the northern tip of the remnant Everglades, in Palm Beach County, Florida, USA. Each pond was set to a water depth of 10 cm, 19 cm, or 28 cm, and was stocked with golden shiners (*Notemigonus crysoleucas*) at a density of either 3 fish/m² or 10 fish/m². Total bird use (all treatments pooled) increased from day 1 (day after stocking) to day 6, stabilized for several days at ~280 birds, and then decreased until day 16, when bird use nearly ceased. Fish were depleted most rapidly in the shallow treatment and least rapidly in the deep treatment. The giving-up-density (GUD) of prey increased with increasing water depth. There was no significant difference among species in the slope of that relationship; however, a visual inspection of the data showed that differences in GUDs were becoming more apparent in the deepest treatment. At that depth, the White Ibis, Wood Stork, and Snowy Egret had higher GUDs than did the Glossy Ibis, Great Egret, Tricolored Heron, Great Blue Heron, and Little Blue Heron. Also, the first three species were affected significantly by both prey density and water depth, whereas the latter five species showed a decidedly weaker response to one or the other component of prey availability. The first three species were more abundant in the shallow treatments and the high prey density treatments, and they abandoned the study site before other species reached their maximum density. The feeding strategy of the first group appeared to be one of searching for new high-quality food patches rather than staying and exploiting food patches that were declining in quality. Species that employed a searching strategy also have shown the most severe population declines, suggesting that factors affecting bird density at feeding sites may also have affected population size.

Key words: Everglades; feeding experiment; feeding strategies; fish density; food availability; giving-up-density; numeric response; prey density; vulnerability; wading birds; water depth; wetland.

INTRODUCTION

Food availability plays a key role in theories of community structure (Hutchinson 1959, Hairston et al. 1960) and optimal foraging (Emlen 1966, MacArthur and Pianka 1966) that have been prominent in ecological thinking for some 20 yr. Food availability is a major evolutionary force with regard to avian life histories (Lack 1954, Martin 1987), and it is a mechanism by which global processes such as forest fragmentation (Zanette et al. 2000) and global warming (Sillett et al. 2000) influence avian population densities.

Despite the central importance of food (hereafter

used interchangeably with “prey”) availability, the term is frequently misused in the ecological literature. Simply put, prey availability does not always equal prey density (Wiens 1984, Boutin 1990). Most often, prey density is the variable measured in studies that make inferences about the availability of prey. Prey availability, however, is a composite variable consisting of prey density and the vulnerability of a prey item to capture. The prey availability (a) of a site or habitat can be expressed as

$$a = d_1v_1 + d_2v_2 + \dots d_iv_i$$

where i is the number of prey types at a site or in a habitat, d is the density of a particular prey type, and v is the vulnerability of a prey type to capture, which ranges from 0 to 1. Vulnerability is determined by characteristics of the prey, environment, and predator. Char-

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nov et al. (1976) recognized that the behavior of prey in response to a predator might alter, temporarily, the availability of the prey (i.e., "resource depression"). Also, position in the environment can alter the availability of food by putting a prey item physically out of reach of a predator. Zwartz and Wanink (1984) showed that a large percentage of clams buried in intertidal mudflats were out of reach of avian predators, depending on the length of their bills. Examples of predator characteristics that determine prey vulnerability include the wing shape of raptors, which determines the probability of capturing prey in either forested or open habitats (Gamauf et al. 1998), and the leg length of wading birds (Ciconiiformes), which reportedly restricts their access to prey at certain water depths (Kushlan 1976, Powell 1987).

Given the diversity of possible interactions among prey items, predator, and environment, it is not surprising that the relationship between prey availability and prey density varies. In the particular case in which prey are exposed and vulnerable to a predator, the relationship between density and availability may be direct and positive. In the other extreme, prey density will have little bearing on availability. In cases in which predators are constrained by their ability to capture prey, it is the vulnerability of prey that determines availability. Without considering both components of prey availability, it is not possible to determine whether the predator is actually responding to density per se or to changes in the vulnerability to capture. Furthermore, the circumstances under which one component or the other is driving a species' response to prey availability may illuminate linkages between ecosystem processes and animal populations. One such example is the effect of wetland metabolism on feeding success. When water conditions are anoxic, often in early morning, fish are driven to the water surface where they become vulnerable to capture by wading birds. In that circumstance, wading birds can have high prey capture rates and, ultimately, high nesting success (Kersten et al. 1991), despite the occurrence of deep water.

Hydrologically pulsed wetlands (Kushlan 1989) are a type of ecosystem in which the distinction between prey density and vulnerability to capture may be particularly acute for predators. Long periods of inundation increase the production of prey (i.e., fishes and aquatic macroinvertebrates; Loftus and Eklund 1994). However, because water depth and duration of inundation (hydroperiod) are often correlated, piscivorous birds may have limited access to their prey under such conditions (i.e., prey are not vulnerable in deep water).

In the Florida Everglades, a large subtropical fluctuating wetland, numbers of breeding wading birds (Ciconiiformes) have had high interannual variation, with generally decreased population sizes for some species since the 1930s (Ogden 1994). Occasional years with large numbers of nesting birds have been related to particular surface-water patterns such as uninterrupted

receding water levels during the dry season (Kahl 1964, Kushlan 1979, Frederick and Collopy 1989) or water depths below a certain threshold (Kahl 1964, Kushlan 1976). These relationships, and evidence that reproduction of Great White Herons (*Ardea herodias*) was limited by prey abundance (Powell 1983, Powell and Powell 1986), led to the suggestion that hydrologic conditions are somehow driving prey availability, which is limiting wading bird population sizes (Kahl 1964, Kushlan 1986, Kushlan and Frohling 1986, Frederick and Collopy 1989, Powell et al. 1989, Frederick and Spalding 1994, Ogden 1994). This hypothesis, which states that prey availability limits wading bird population sizes, is termed here the "prey availability hypothesis." Decreased prey availability also has been hypothesized to constrain populations of wading birds in a variety of wetlands around the world (see reviews in Butler 1994, Hafner 1997). An underappreciated point is that not all species of wading birds in the Everglades have declined at the same rate since the 1930s, even though all species frequently nest and feed sympatrically. Several species may, in fact, be more abundant now than historically (Crozier et al. 2000). These disparate population trends suggest that either prey availability has not decreased for all species or that species have responded in an individualistic fashion to reductions in prey availability. In either case, a test of this hypothesis must be species specific.

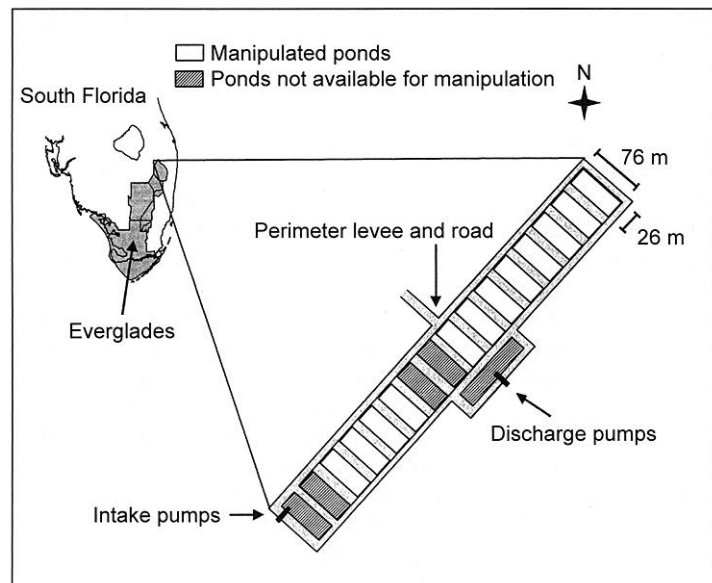
In this study, I sought to test the prey availability hypothesis on a species-specific basis by determining the relative constraints of prey density and vulnerability to capture on feeding site use by an assemblage of picivorous wading birds. The density of birds at a feeding site was used as a surrogate for a population level response because factors affecting feeding aggregation size of wading birds also affect reproductive output (e.g., Kersten et al. 1991, Hafner et al. 1993), and only bird density is amenable to controlled experimental tests. The experimental approach was to measure bird density and prey density, and control for characteristics of the prey and environment. Thus, any species-specific response to prey availability was a function of variability in predator characteristics. Specifically, I manipulated water depth (i.e., prey vulnerability) and prey density in 12 ponds and quantified the response by eight species of free-ranging wading birds in the Everglades. The null hypothesis for each species was that neither prey density nor vulnerability of prey to capture affected bird density.

METHODS

Experimental facility

The experiment was conducted in a set of 15 replicate 0.2-ha ponds (12 were used for this experiment) directly adjacent to, and northwest of, the Arthur R. Marshall Loxahatchee National Wildlife Refuge in Palm Beach County, Florida, USA (Fig. 1). The ponds were

FIG. 1. Study site adjacent to the northern Everglades in western Palm Beach County, Florida, USA.



built within a 1545-ha wetland constructed as a prototype for a large-scale nutrient removal project. Ponds were rectangular, with a peat substrate, and were arranged in a row adjacent to one another. Ponds had no emergent aquatic vegetation, but did contain sparse submergent plants and submerged portions of dead cattail (*Typha domingensis*) stems as a result of pre-experiment site preparation. Cattail stem density averaged 2.5 stems/m² among the nine ponds in which vegetation was sampled. During site preparation, great effort was made to create ponds with vegetation that was structurally similar to that of open sloughs in the Everglades (i.e., sparse submerged vegetation with little emergent vegetation). This habitat is used heavily by wading birds for foraging (Hoffman et al. 1994), but it does not represent the only habitat in which birds occur. The results of the experiment should be interpreted with that limitation in mind. A different vegetation structure could affect the response of birds to the treatments.

To remove naturally occurring fishes that might have confounded prey density treatments, ponds were drained prior to the experiment and were allowed to stand without water for one week. A 1-cm² mesh screen was placed over the water supply pipe so that only fish that were smaller than sizes preferred by wading birds could pass back into the ponds. Similar screens were also placed over the outflows to ensure that stocked fish could not escape ponds. Ponds were then refilled at treatment depths and were allowed to stand for three days before they were stocked with fish.

Water depths in each pond were controlled with a gravity flow system maintained by electric intake and discharge pumps. Each pond had a 5-cm inflow valve that allowed water to flow from the supply pipe into the pond basins. A small amount of water flowed out

of each pond over a series of horizontal boards covering an outflow pipe, thus regulating maximum water depth.

Design and analysis

The experiment was conducted for 16 days, from 5 March 1996, one day after ponds were stocked with fish, to 21 March 1996, when bird use nearly ceased. All statistical analyses were conducted on replicated data. Only the temporal pattern of bird use throughout the experiment was unreplicated. Thus, these data were visually inspected and discussed. The fish species stocked in ponds was the golden shiner (*Notemigonus crysoleucas*), a species common in the Everglades (Lofus and Kushlan 1987) and available commercially in large quantities and uniform sizes. These last two characteristics are essential for conducting such a large-scale experiment. However, they impose a constraint in that the experimental prey community is necessarily less diverse than the naturally occurring prey community. I attempted to mediate for this by allowing a natural community of very small fishes to co-occur in the ponds with the stocked prey species, but it is not known whether the experimental fish community elicited the same response from birds as the natural one.

Experimental treatments were water depth (10 cm, 19 cm, and 28 cm) and fish density (3 fish/m² and 10 fish/m²). Water depths were chosen based on mean leg length of the target bird species. The 19 cm depth treatment was near the maximum foraging depth for the White Ibis, *Eudocimus albus*; Glossy Ibis, *Plegadis falcinellus*; Snowy Egret, *Egretta thula*; Tricolored Heron, *Egretta tricolor*; and Little Blue Heron, *Egretta caerulea* (Powell 1987, Bancroft et al. 1990). The 28 cm depth was near the maximum for the Great Egret, *Ardea alba*, and well below that of the Great Blue

Heron, *Ardea herodias* (Powell 1987) and Wood Stork, *Mycteria americana*. The initial fish density treatments represented "average" and "high" densities for fish >2 cm in length (the size typically taken by wading birds), based on samples taken (F. Jordan, *unpublished data*) in the adjacent section of the Everglades in Arthur R. Marshall Loxahatchee National Wildlife Refuge. Small herons in the Everglades take prey averaging 0.5 g (Bancroft et al. 1990), whereas Great Egrets may take fish up to 70 g (Frederick 1994). To provide a range of prey sizes for the diverse bird assemblage, each pond was stocked with 75% small fish ($n = 46$; wet mass 3.2 ± 0.5 g, mean ± 1 SD; total length 7.5 ± 0.5 cm), and 25% large fish ($n = 34$; wet mass 8.5 ± 0.3 g; total length 10.0 ± 0.3 cm). Using these numbers to estimate fish biomass density produces initial fish density treatments of 45 g/m² and 13 g/m². These are within the range of values reported for sites in the southern Everglades (Loftus and Eklund 1994) and could be characterized as "very high" and "high" densities, respectively. Because prey densities in all ponds went to very low levels by the end of the experiment, birds were presented with a wide range of prey conditions that were very comparable to what is found in the natural Everglades.

I randomly assigned three water depth and two fish density treatments among 12 ponds in a 3×2 factorial arrangement with two replicates. Although ponds were initially stocked at known fish densities, those densities decreased quickly as a result of bird predation. Thus, in the analysis, I treated fish density as a continuous variable. I determined fish densities with 1-m² throw-trap samples (Kushlan 1974a) during four sampling periods. Individual ponds were sampled a maximum of four times each, but sampling ceased in a given pond if no golden shiners were captured in any of the throw-trap samples during the previous sampling period. A throw-trap is similar to a nylon mesh box with an open top and bottom. The trap was tossed into the water so that the walls of the trap enclose a known volume of the water column with associated fish and invertebrates. A rectangular seine with an aluminum frame slightly less than 1 m in width was then passed through the enclosed water column until five passes were made without catching a stocked fish. The number of golden shiners in each size class and the number of small "naturally" occurring fishes were recorded for each throw. Throw-trap samples were distributed evenly within a pond by dividing each pond into 16 10×8 m plots and sampling each plot once during each sampling period. All fish density values reported here are uncorrected for throw-trap sampling bias. A pilot study indicated that fish density estimates from throw-trap samples were ~55% of the actual stocking density.

The density of golden shiners in each pond during each day of the experiment was estimated from linear regression models fitted to the throw-trap data transformed as $\ln(y + 1)$. All data analyses were done with

SAS for Unix or NT operating systems (SAS Institute 1990a, b). The predicted values were then back-transformed (Flewellling and Pienaar 1981) as

$$y = \exp\left(\hat{y} + \frac{S^2}{2} - \frac{S_y^2}{2}\right) - 1$$

where y is the estimated fish density (number of fish per square meter), $\exp$ is the natural log, $\hat{y}$ is the predicted fish density ($\ln[y + 1]$), S^2 is the pooled variance, and S_y^2 is the variance of predicted fish density ($\ln[y + 1]$). I imposed the additional constraint that no back-transformed value of fish density could be less than zero.

The primary response variable was bird density (number of birds/0.2 ha), which was measured twice per morning from censuses that were separated by at least one hour. Censuses were conducted from a vehicle along one side of the set of ponds. A pilot study demonstrated that censuses from a vehicle disturbed birds less than did an observer walking, and it allowed the observer to stay ahead of any birds that did flush from a pond. If any birds were flushed, they would typically return to the pond after the vehicle had passed. As the vehicle moved past each pond, the abundance of each species present was voice-recorded into a cassette tape recorder. Tape recordings were subsequently transcribed to data sheets immediately following each census. Censuses within a day were not considered to be independent because birds did not move much among ponds after mid-morning. Therefore, mean density from two censuses for each day was used in the analyses. Censuses were assumed to be independent among days because it appeared that birds were assessing the foraging conditions of each pond each day, and fish density changed within ponds at approximately that time scale. During about the first hour of daylight each morning, birds of all species moved extensively among ponds, usually staying at a pond for only a few minutes before moving to another. Birds gained direct information on the quality of the site through short-duration foraging bouts, and apparently by the escape response of fish as they darted away from birds. Birds would fly low over the water surface of one pond, then crest the levee and surprise any fish on the other side, producing a sudden rippling of the water surface by escaping fish. After the early morning movements, birds tended to congregate in a few ponds, at which time the first census was conducted.

To determine the relative effects of water depth and fish density on prey availability for each species, general linear models were constructed using the GLM procedure in SAS (SAS Institute 1990b), with day-since-stocking and water depth as categorical variables and fish density as a covariate. Days were excluded from the analyses of each species if no birds were present. Because an ANOVA is influenced by violations of the assumption of equal variances, several transfor-



FIG. 2. Mixed-species flock of wading birds feeding in a 19-cm water depth treatment.

mations of bird density were evaluated that reduced or eliminated the dependence of the variance on the mean response. Slopes of the linear regression of $\ln$ variance vs. $\ln$ mean indicated that the appropriate transformation of bird density was $\ln(y + 1)$ (Box et al. 1978). For each bird species, an initial full model was specified that contained a term for fish density, water depth, day-since-stocking, and all two- and three-way interactions. Interactions were eliminated based on a lack-of-fit test. If statistical differences among treatments were detected at $\alpha \leq 0.05$, multiple comparison tests were conducted on the least square means. To assess whether other flock members influenced the use of treatments by a species, the degree of association for each species pair was measured using Pearson correlation coefficients.

A second way in which I evaluated the effects of water depth (i.e., prey vulnerability) on prey availability was by measuring the perceived foraging costs by birds. Giving-up density of prey (GUD; Brown 1988) is the density of food items remaining in a patch after an animal quits feeding in it. If animals are foraging optimally, then GUD is an indirect estimate of those costs, because an animal will leave a patch when their foraging costs equal their gains. This relationship has been demonstrated experimentally for birds (Kohlmann and Risenhoover 1996) and mammals (Brown and Alkon 1990, Brown et al. 1992). For social-for-

aging birds, the GUD of a flock can be measured at any time between when the first and last animal in the flock abandons the patch. In this study, the GUD was reported for each species at each pond on the day that bird density for a given species decreased below 50% of the maximum for a given pond. This measure was equivalent to the median GUD of the flock over the entire time that the patch was used by a given species. Standard deviations reflect the variation among ponds within a depth treatment. The relationship between water depth and GUD was compared among species with an ANCOVA, using water depth as a covariate and species as the class variable.

RESULTS

The morning after fish were stocked (i.e., day 1), a single Great Blue Heron, Little Blue Heron, White Ibis, Glossy Ibis, and Great Egret visited the site. Even though prey availability was at its highest point on that morning, the White Ibis left within an hour (before the first census), and the Great Blue Heron left within two hours. On the second morning, 17 birds of five species arrived at the site. All departed by 0930 hours. Thereafter, numbers of birds and amount of time they remained at the site increased. Over the course of the 16-d experiment, use of the site (Fig. 2) by birds was temporally dynamic (Fig. 3), much like the use of drying sloughs in the Everglades. When pooled across all

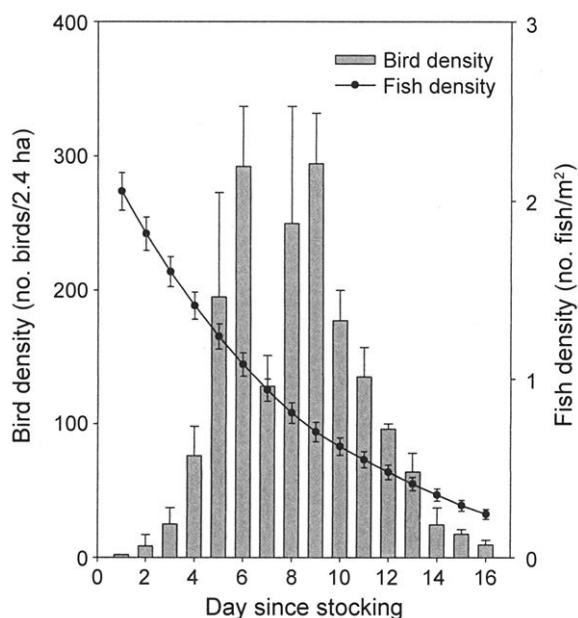


FIG. 3. Daily mean bird density (all species and treatments pooled) and fish density (all treatments pooled), by days since fish-stocking. Error bars are ± 1 SE. Daily mean bird density was calculated from two censuses per day.

treatments, bird density increased quickly during the first five days of the experiment, then numbers stabilized for several days at ~ 280 birds, except for a decrease on day 7 due to rain, and finally on day 10, bird density began to decrease (Fig. 3).

Individual species exhibited considerable variation on this basic pattern, with no single species exhibiting a pattern representative of the "average" for all species pooled (Fig. 4). White Ibises were numerically dominant for the first eight days of the experiment. They increased and decreased in numbers very quickly, and abandoned the site altogether before the densities of other species had peaked. Wood Storks exhibited a similar pattern, but they first appeared midway through the experiment after most White Ibises were gone. Although Wood Storks were present in the assemblage for only a few days, they were the second most abundant species during that period. In contrast, Great Egrets were present for most days of the experiment, but they increased in numbers more slowly and persisted longer than did the Wood Stork or White Ibis. The Great Egret was numerically dominant during the second half of the experiment. Snowy Egrets also were present for most days of the experiment, but they never reached densities near those of the White Ibis or Great Egret. Snowy Egrets increased in density at a slower rate than did White Ibises, and they peaked in numbers after White Ibises but before Great Egrets. The Glossy Ibis, Tricolored Heron, Little Blue Heron, and Great Blue Heron also occurred at relatively low densities, but they peaked in numbers earlier in the experiment than did the Great or Snowy Egret.

The temporally dynamic pattern of bird density was concurrent with changes in fish density. When pooled across all treatments, fish density decreased rapidly until day 9, when total bird abundance was at its peak,

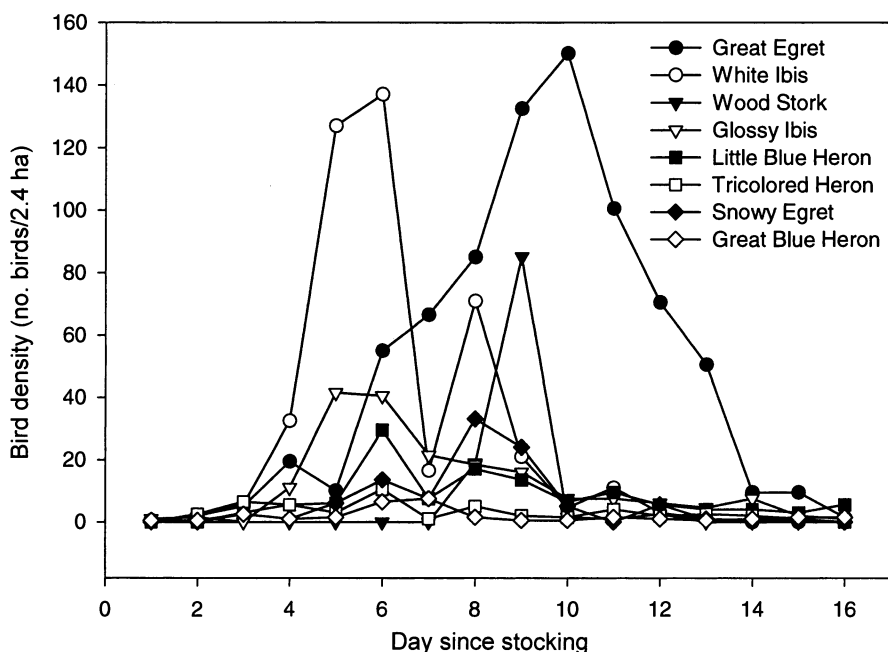
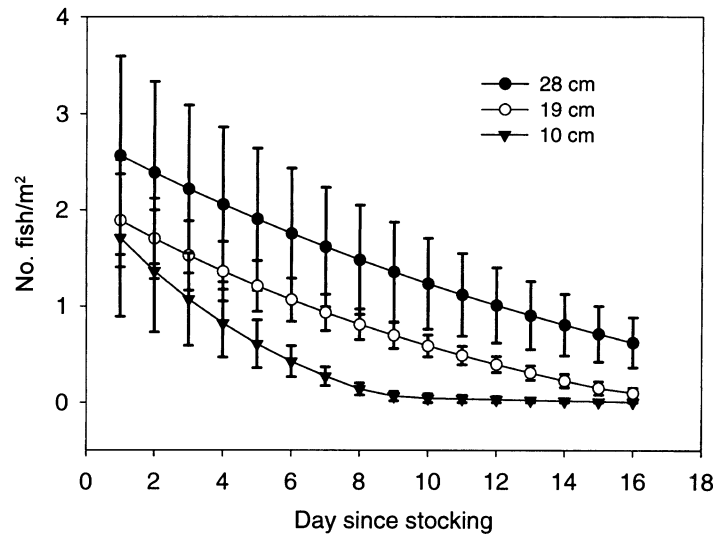


FIG. 4. Daily mean bird density over time varied by species (all treatments pooled). Density was low on day 7 because of rain.

FIG. 5. Daily estimated fish density decreased differentially among water depth treatments of 10 cm, 19 cm, and 28 cm. Error bars represent ± 1 SE.



and then decreased more slowly as bird abundance declined (Fig. 3). However, there were noticeable differences among water depth treatments in the rate of decrease in fish density and in the number of fish remaining in ponds after bird use ceased (Fig. 5). Fish density decreased most rapidly in the shallow-water treatments, which were depleted by day 12. "Depleted" is defined as a fish density estimate of 0 fish/m². Hereafter, fish density treatments are referred to as "high" and "low," and water depth treatments are referred to as "shallow," "medium," and "deep." Because of the sampling bias, it is likely that there were still a few fish present when the estimated density was zero, at least in the medium-depth treatment. In the shallow treatment, a thorough visual inspection indicated that birds did indeed deplete the fish. The medium-depth treatments were not depleted until the final

day of the experiment, and the deep treatments were never depleted. This pattern suggests that vulnerability to capture was negatively related to water depth. Also, it suggests that a water depth threshold between 19 cm and 28 cm provides refugia for fish in open-water habitats. Presumably, the depth threshold would be lower in more heavily vegetated habitats that provide cover for fish.

GUDs provided additional evidence that the vulnerability of fish to capture was negatively related to water depth and that birds did incur a foraging cost with increasing water depth. For all species, GUD was positively related to water depth (ANCOVA, Type I sums of squares, $F_{1,83} = 63.74$, $P < 0.001$; Fig. 6). At any given water depth over the range considered here, there was no difference in GUDs among species ($F_{7,83} = 0.92$, $P = 0.50$), nor did slopes differ among species ($F_{7,76}$

FIG. 6. Giving-up density for eight bird species preying upon fish increased with increasing water depth treatments of 10 cm, 19 cm, and 28 cm.

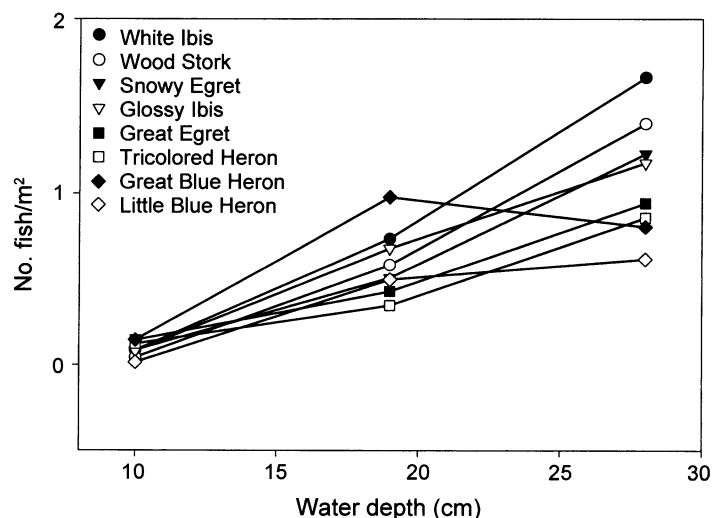


TABLE 1. Type III General Linear Model ANCOVA for densities of eight species of wading birds in the Florida Everglades, USA, in relation to day-since-stocking, water depth, and the covariate, fish density.

Source	df	MS	F	P
White Ibis				
Day	11	1.84	2.19	0.020
Depth	2	4.23	5.02	0.008
Fish density	1	6.09	7.24	0.008
Depth $\times$ Day	22	0.59	0.70	0.826
Snowy Egret				
Day	11	1.08	4.63	<0.001
Depth	2	1.36	5.84	0.004
Fish density	1	4.07	17.38	<0.001
Depth $\times$ Day	22	0.14	0.59	0.924
Wood Stork				
Day	4	3.43	8.22	<0.001
Depth	2	1.61	3.85	0.029
Fish density	1	5.72	13.71	<0.001
Depth $\times$ Day	8	0.12	0.30	0.963
Little Blue Heron				
Day	13	0.61	3.55	<0.001
Depth	2	0.67	3.94	0.022
Fish density	1	1.03	6.03	0.015
Depth $\times$ Day	26	0.32	1.89	0.011
Great Egret				
Day	15	1.23	2.22	0.009
Depth	2	0.01	0.02	0.981
Fish density	1	3.38	6.10	0.015
Depth $\times$ Day $\times$ Fish density	47	1.50	2.70	<0.001
Glossy Ibis				
Day	14	0.68	1.66	0.071
Depth	2	2.43	5.99	0.003
Fish density	1	1.52	3.75	0.055
Depth $\times$ Day	28	0.32	0.78	0.774
Tricolored Heron				
Day	13	0.09	0.95	0.507
Depth	2	1.07	11.75	<0.001
Fish density	1	0.25	2.79	0.097
Depth $\times$ Day	26	0.18	1.94	0.009
Great Blue Heron				
Day	15	0.13	2.47	0.003
Depth	2	0.11	2.13	0.123
Fish density	1	0.02	0.42	0.517
Depth $\times$ Day	30	0.06	1.25	0.198

= 0.99, $P = 0.45$). However, a visual inspection of the data (Fig. 6) indicated that differences among species were becoming more apparent as water depth increased. In the shallow treatment, all species converged on the ponds until the fish were depleted. In the medium treatment, the range of GUDs was only slightly greater. However, in the deep treatment differences were more apparent, with White Ibises, Wood Storks, Snowy Egrets, and Glossy Ibises, respectively, having the highest GUD.

The density of White Ibises differed significantly (Table 1) both among water depth and fish density treatments and days (see Appendix, Fig. A1). Bird density was positively related to fish density, holding the effects of water depth constant. Multiple comparison tests showed that, after accounting for effects of fish density, White Ibises were significantly more abundant in the shallow (LSM $\ln[y + 1] = 0.74$ birds/0.2 ha, P

= 0.003) and medium treatments (LSM $\ln[y + 1] = 0.55$ birds/0.2 ha, $P = 0.01$), respectively, than in the deep (LSM $\ln[y + 1] = 0.06$ birds/0.2 ha) treatment (LSM = least squares mean). There was no significant difference in the density of White Ibises between shallow and medium depths ($P = 0.33$). Despite the similar effects of water depth and fish density on mean bird density, large numbers of birds only occurred in the high-density, shallow and medium treatments (see Appendix, Fig. A1).

Snowy Egrets were similar to White Ibises in that their density differed significantly among water depths and days, and was positively affected by fish density (Table 1). Also, Snowy Egrets only formed large numbers in the high-density treatments (see Appendix, Fig. A2). Snowy Egrets were more abundant in the shallow (LSM $\ln[y + 1] = 0.48$ birds/0.2 ha, $P = 0.001$) and medium (LSM $\ln[y + 1] = 0.34$ birds/0.2 ha, $P = 0.01$)

treatments than in the deep ($\text{LSM } \ln[y + 1] = 0.07$ birds/0.2 ha) treatments, but the former two treatments did not differ significantly ($P = 0.19$). Snowy Egret density differed more as a function of fish density than water depth.

Wood Stork density also differed significantly as a function of fish density, water depth, and days (Table 1). Storks occurred in largest numbers in the shallow-low-density and two high-density treatments (see Appendix, Fig. A3). The strong response to the shallow low treatment is somewhat misleading in the figure, which depicts fish density as a categorical variable, because Wood Storks did not arrive at the study site until midway through the experiment after fish densities in the shallow and medium treatments had already been severely reduced. The true response to fish density was accounted for in the model because fish density was estimated for each pond each day and was treated as a covariate. Storks were significantly more abundant in the shallow ($\text{LSM } \ln[y + 1] = 0.74$ birds/0.2 ha, $P = 0.01$) and medium ($\text{LSM } \ln[y + 1] = 0.56$ birds/0.2 ha, $P = 0.02$) than in the deep ($\text{LSM } \ln[y + 1] = 0.003$ birds/0.2 ha) treatments. There was no significant difference between the shallow and medium treatments ($P = 0.43$). Wood Storks were unusual in that they apparently spent two nights (days 9 and 10) roosting and feeding in the ponds. This is common behavior for storks, particularly when they are not nesting or when they are nesting but foraging at great distances from their colony (Kahl 1964, Bryan et al. 2001). No other target species was observed feeding nocturnally, but several Black Skimmers (*Rynchops niger*) regularly did so.

Little Blue Heron density differed significantly as a function of fish density, water depth, and days (Table 1), but it did not appear to be constrained by deep water as were the preceding species. A significant depth $\times$ day interaction showed that this species used the shallow and medium treatments during the first portion of the experiment, but switched to the deeper treatments during the last few days (see Appendix, Fig. A4). Overall, Little Blue Herons were significantly more abundant in the shallow ($\text{LSM } \ln[y + 1] = 0.53$ birds/0.2 ha) than the deep ($\text{LSM } \ln[y + 1] = 0.26$ birds/0.2 ha, $P = 0.006$) treatments. Another characteristic that set this species apart from the previous three was that there was no clear depth threshold. There was no significant difference in density between the shallow and medium ($\text{LSM } \ln[y + 1] = 0.38$ birds/0.2 ha, $P = 0.07$) treatments, nor between the medium and deep ($P = 0.17$) treatments. The effect of fish density was most evident in that the largest numbers of birds occurred in the shallow and medium high-density treatments (see Appendix, Fig. A4).

Great Egret density responded to fish density, depth, and days (Table 1), but in a more complicated way than for the preceding species. The three-way interaction indicated that Great Egrets were similar to Little Blue

Hérons in that they foraged in the deep water, but their initial preference was for the shallower treatments (see Appendix, Fig. A5). For the first five days of the experiment, the highest densities were in the shallow-high treatment. At day 5, bird density started to increase in the medium-high treatment. On day 7, density increased on the deep-high treatment and on day 9, density increased on the medium-low treatment. At this point in the experiment, Great Egret density was at its highest, and the species was present in all of the treatments. This was in marked contrast to Wood Storks, White Ibises, Snowy Egrets, and Glossy Ibises, which almost never occurred in the deep low treatment. Starting on day 11, Great Egrets began to abandon the study site (all other species had earlier reached their peak density), and they were no longer present in large numbers in the shallow-high treatment. By day 14, birds had nearly abandoned the study site altogether. After this point, the remaining birds moved frequently among treatments. Overall, Great Egrets were more abundant in the shallow ($\text{LSM } \ln[y + 1] = 6.27$ birds/0.2 ha) than the medium ($\text{LSM } \ln[y + 1] = 0.91$ birds/0.2 ha, $P = 0.05$) or deep treatments ($\text{LSM } \ln[y + 1] = 0.73$ birds/0.2 ha, $P = 0.04$). There was no significant difference between the medium and deep treatments ($P = 0.56$).

Density of Glossy Ibises responded strongly to depth and less so, but positively, to fish density (Table 1). Glossy Ibises were significantly more abundant in the shallow ($\text{LSM } \ln[y + 1] = 0.55$ birds/0.2 ha, $P < 0.001$) and medium ($\text{LSM } \ln[y + 1] = 0.38$ birds/0.2 ha, $P = 0.02$) than the deep ($\text{LSM } \ln[y + 1] = 0.08$ birds/0.2 ha) treatments. There was no significant difference between the shallow and medium depths ($P = 0.15$; see Appendix, Fig. A6).

The density of Tricolored Herons was affected by water depth, but not consistently among days (Table 1). The significant depth $\times$ day interaction showed that this species used only the shallow treatments early in the experiment, but eventually moved into the medium- and deep-water treatments, regardless of fish density (see Appendix, Fig. A7). Overall, Tricolored Herons were significantly more abundant in the shallow ($\text{LSM } \ln[y + 1] = 0.35$ birds/0.2 ha) than the medium ($\text{LSM } \ln[y + 1] = 0.07$ birds/0.2 ha, $P < 0.001$) or deep treatments ($\text{LSM } \ln[y + 1] = 0.12$ birds/0.2 ha, $P = 0.001$). There was no significant difference between the medium and deep treatments ($P = 0.48$).

There were no significant negative correlations among species within ponds (Table 2) that would have suggested that some species were avoiding sites based on the presence of heterospecifics. There were 17 positive pairwise correlations out of a possible 28, suggesting that individuals were either attracted to the same environmental conditions or they were attracted to each other.

In summary, White Ibises, Snowy Egrets, and Wood Storks responded strongly to both fish density and wa-

TABLE 2. Pearson correlation matrix (r values) for densities of eight species of wading birds within ponds in the Florida Everglades.

Species	Wood Stork	White Ibis	Snowy Egret	Glossy Ibis	Little Blue Heron	Tricolored Heron	Great Egret	Great Blue Heron
Wood Stork								
White Ibis	0.05							
Snowy Egret	0.35*	0.35*						
Glossy Ibis	0.02	0.93*	0.27*					
Little Blue Heron	0.10	0.61*	0.53*	0.56*				
Tricolored Heron	0.01	0.21*	0.08	0.17*	0.33*			
Great Egret	0.32*	0.24*	0.56*	0.27*	0.43*	0.06		
Great Blue Heron	-0.03	0.09	0.12	0.18*	0.22*	0.11	0.11	

Notes: Raw data for this test were the mean densities from two censuses per day. For all pairwise tests, $n = 192$; 12 ponds $\times$ 16 days.

* $P < 0.05$.

ter depth treatments with no interactions from other variables. For those species, there was a depth threshold between 19 cm and 28 cm that seemed to constrain the use of foraging sites. Little Blue Herons and Great Egrets responded primarily to fish density, with a weaker response to water depth. In both cases, birds did not avoid the deep-water treatments; they simply foraged there after they had fed in the shallower treatments. Glossy Ibises responded more strongly to water depth than to fish density, but effects from both variables were evident. Tricolored Herons only responded to water depth. Finally, the density of Great Blue Herons was relatively constant throughout the experiment (see Appendix, Fig. A8), and this species showed no significant response to either treatment at the levels provided (Table 1).

DISCUSSION

Components of prey availability

This experiment demonstrated that changes in either prey vulnerability or density did not produce similar responses among the eight species of wading birds examined here. Densities of six of the eight species were strongly related to fish density, holding the effects of water depth constant. Tactile-feeding wading birds (storks and ibises) are thought to respond to density closely (Kahl 1964), and probably more so than visual feeders (Kushlan et al. 1985, Frederick and Spalding 1994). It is evident here that tactile feeders responded strongly to prey density, as did Snowy Egrets and, to a lesser extent, Great Egrets and Little Blue Herons. A response to prey density by visual-feeding wading birds has been observed in a variety of ecosystems (Hafner and Britton 1983, Draulans 1987, Feunteun and Marion 1994). In this study, even when bird density and prey density were positively related, the response to prey density did not equate directly with prey availability because the relationship was also affected by water depth. A similar pattern emerged in an experiment with Sanderlings (*Calidris alba*), small shorebirds that consume primarily invertebrates (Myers et al. 1979). Incorporating a response to prey vulnerability can im-

prove predictions from optimal foraging theory models, as was the case in an experiment on prey selectivity with predatory fishes and crayfish (*Orconectes propinquus*; Stein 1977). Departures from model predictions were largely a function of overlooking the increased searching costs due to decreased vulnerability of prey to capture.

Evidence for the influence of prey vulnerability has sometimes been inferred simply from a weak or non-existent effect of prey density. In wetlands of Yucatan, Mexico, food density did not influence the density of Flamingos (*Phoenicopterus ruber ruber*), leading to the suggestion that water depth and prey quality are what determine prey availability (Arengo and Baldassarre 1999). Similarly, in North American wetlands, crayfish abundance and capture rates by White Ibises were not correlated, leading to the suggestion that prey vulnerability, rather than density, makes prey available (Kushlan 1979, 1989). Prey vulnerability probably also produces diet selectivity in Wood Storks (Ogden et al. 1976, Kushlan 1979). Storks are tactile feeders and therefore lack the ability to discriminate among prey once they are encountered. Yet, storks are highly selective for particular fish species, suggesting that prey are differentially vulnerable to encounter. In the Camargue, France, prey capture rates of Little Egrets were higher in early morning when fish were near the surface because of anoxic conditions in the water (Kersten et al. 1991). As anoxic conditions subsided, prey capture rates decreased and the large feeding aggregations of birds dispersed. Each morning, large aggregations of birds reoccurred at the same site and prey capture rates were once again high (Kersten et al. 1991), suggesting that overall fish density was less important than vulnerability to capture. It is possible, however, that birds were also responding, to some extent, to fish density at very small spatial scales, because fish were also concentrated in openings between vegetation patches when they were more vulnerable.

Here, where prey vulnerability was manipulated directly, density of Tricolored Herons was unrelated to fish density, but was strongly affected by water depth.

Also, GUDs for all species suggested that there was an increasing cost for each progressively deeper treatment between 10 cm and 28 cm. This pattern differed from the water depth effect on the numeric response, which (except for the Little Blue Heron) suggested that water depth created a threshold of site use. The GUD is therefore reflecting an additional foraging cost that was not detected by changes in bird density. The effect of water depth on wading birds is more complex than being a simple correlate of leg length. It appears that species have an upper threshold for water depth, which may reflect morphological constraints like leg length (Meyerrieks 1962, Hom 1983, Brandl and Utschick 1985, Powell 1987, Ntiamoa-baidu et al. 1998) or bill length, in the case of tactile feeders. Below that threshold, there are costs that increase as a function of water depth. Potential costs include decreased locomotion of the predator because of increased resistance or drag from increased surface area in contact with the larger water column. Also, strike efficiency may be reduced because prey have the added ability to escape vertically in the water column in addition to the horizontal escape options available in shallow water (e.g., moving to dense vegetation patches). Finally, deeper water may reduce strike rate because prey simply are not detected as easily when they have a deeper water column in which to conceal themselves. This would be particularly acute in turbid water, where light may not penetrate the entire water column. A prediction from this model of water depth effects is that all species should have a higher net energy intake in shallow water than deep water, holding the effects of prey density and relative position in the water column constant.

Feeding tactics in response to prey availability

Feeding constraints for wading birds in this assemblage can be viewed as a continuum with White Ibises, Wood Storks, and Snowy Egrets (hereafter termed "searchers") on one end, Great Blue Herons and Great Egrets on the other, and Glossy Ibises, Little Blue Herons, and Tricolored Herons between the two extremes. Hereafter, the latter five species are referred to as "exploiters." The searchers were the most constrained in their selection of feeding sites. They abandoned the study site within a few days of their arrival when prey density in the shallow and medium (but not deep) treatments began to decrease, and they never used the deep treatment in large numbers. The tactic of this group was to select the highest quality patches and abandon them quickly, in essence, "high-grading" the experimental landscape. The density of the searchers at a feeding site tracked prey density in shallow water depths closely. This was also the case in the llanos of Venezuela, where Wood Stork flock size was closely related to the occurrence of high-quality patches that were isolated pools with high densities of prey created during the seasonal water level recession (González 1997). Empirical observations indicate that Snowy

Egrets or White Ibises are often the first to locate food patches, and they are frequently the catalyst for mixed-species feeding aggregations (Caldwell 1979, 1981, Master 1992, Smith 1995). Until this study, there was little evidence to show that these species were also selecting the highest quality patches.

For the searching strategy to be adaptive, the costs of moving to a new food patch vs. staying in a rapidly degrading patch must be lower for searchers than for exploiters, or the benefit of staying must be lower for searchers than for exploiters. Lower costs of searching could come from reduced search time or reduced flight costs. Wood Storks are known to have low flight costs relative to other species because storks rely more heavily on thermals and nonflapping flight to reach feeding sites (Kahl 1964). Decreased benefits of staying would be a more rapid decline in capture rate with decreased prey densities than that of the exploiters. Indeed, it has been suggested that successful tactile feeding, as used by storks and ibises, is particularly dependent on high prey density (Kahl 1964, Kushlan et al. 1985, Frederick and Spalding 1994).

Two notable characteristics of the searcher species are that they are highly social and have white plumage. There is good evidence that social feeding and white plumage are characteristics that reduce search time (Krebs 1974, Kushlan 1976, Willard 1977, Pulliam and Caraco 1984) and are especially advantageous when food resources are clumped and ephemeral (Kushlan 1981, Erwin 1983, Clark and Mangel 1984), as they are in the Everglades. Although the primary advantage of social feeding for birds is to reduce search time, flock members also may increase their capture rate (but not necessarily capture efficiency) once they are in a food patch by flushing prey toward one another (Willard 1977, Kushlan 1978; but see Krebs 1974). Flock members may also reduce their individual risk of being preyed upon (Caldwell 1986) and imitate the successful feeding behavior of conspecifics. I observed the latter during the first few days of the study. White Ibises probed in the sediment, which is typical feeding behavior for capturing invertebrates, but inefficient for capturing fish in the water column. The birds left the site after feeding for only a short time. After the flock size increased to ~50 birds, individuals spent more time foraging at the study site, were more successful at capturing fish, and had largely switched to sweeping the water column rather than probing the sediment. In this case, the intraspecific interactions appeared to be commensal rather than competitive.

At the other end of the continuum were species (exploiters) that persisted at the study site because of adaptations that mitigated the effects of decreasing fish density. Although Great Egrets foraged in all water depths, they indicated a preference for the shallower treatments by selecting them first. Those birds remained at the site until fish were depleted or in low densities in all treatments, and they foraged in the entire

range of water depths. The Great Blue Heron was the extreme example because it never responded to changing fish density and was not constrained by any water depth presented here. Adaptations for exploiting low-quality feeding sites include morphology, diet, behavioral plasticity, and perhaps physiology (Maurer 1996), although the latter was not examined here. A morphological adaptation such as long leg length allows birds to exploit a wider range of water depths and thus habitats. A morphological adaptation such as thick bill size is related to diet in that it allows individuals to capture a wider range of prey items (Kushlan 1978) and therefore makes more resources available at any given feeding site than for species with thinner bills. For example, Little Blue Herons and Great Egrets, which possess thicker bills than Tricolored Herons and Snowy Egrets, switched prey types as hydrologic conditions changed at a site, whereas the latter two species did not (Smith 1997). Behavioral plasticity such as feeding from floating vegetation in deep water, which is frequently done by Tricolored Herons (Smith 1995), may allow birds to exploit a wider range of water depths that might otherwise be unavailable because of morphological constraints such as short legs. Behavioral plasticity allows birds to readjust their foraging tactics as habitat conditions change. In a variable environment, neither morphology nor behavior alone, but rather their combination (i.e., foraging apparatus; Maurer 1996) determines resource use patterns.

In a fluctuating wetland with varied microtopography, high-density patches of fish occur primarily at the edge of drying surface water (hereafter, termed a dry-down), which form isolated pools. Thus, at any one time a relatively small area of a wetland has high-quality feeding sites, and they are highly clumped. At any point in space, the quality will be high for brief periods only. Bird species that can exploit low-quality patches will be less dependent (i.e., they have a wider niche breadth) than searchers on a seasonal drydown because they use morphological (e.g., long tarsus or large bill) and behavioral adaptations to increase their net energy intake at low prey availability. Thus, their densities are not likely to track prey density closely. Furthermore, searchers will require a larger spatial area to meet their nutritional needs over an entire year because only a small fraction of the landscape has high-quality sites at any one time.

Patterns from comparative studies suggest that differences between searcher and exploiter species are robust across ecosystems. In coastal North Carolina, Little Blue Herons used a wider range of habitats than did either Snowy Egrets or White Ibises (Custer and Osborn 1978). Snowy Egrets had a narrower niche breadth than Great Egrets and Great Blue Herons in California salt marshes (Hom 1983) and than Tricolored Herons in the southern Everglades (Strong et al. 1997). In coastal New York, Great Egret abundance and capture success were not correlated with water depth, but abun-

dance of Snowy Egrets and Glossy Ibises was significantly and negatively correlated with water depth (Maccarone and Parsons 1994). In New Jersey and northeast Florida, Great Egrets did not follow predictions from optimal foraging theory as closely as did Snowy Egrets (Erwin 1985).

There is also good evidence from field studies that the differences between searchers and exploiters in response to food availability ultimately lead to differences in reproductive output. Within the Everglades ecosystem, increases in water levels during the dry-down have a greater negative effect on Snowy Egrets, Wood Storks, and White Ibises than on Little Blue Herons, Tricolored Herons, and Great Blue Herons (P. Frederick, *personal communication*). In one instance, an abrupt increase in water levels during the drydown led to massive abandonment of Snowy Egrets, whereas Tricolored Herons and Little Blue Herons in the same colony at the same stage of nesting did not abandon their nests and eventually had excellent reproductive success (P. Frederick, *unpublished data*). Although Roseate Spoonbills (*Ajaia ajaja*) were not examined in this study, their nesting success also appears to be closely tied to the occurrence of shallow water with high densities of fish (i.e., high-quality food patches). When water levels during the drydown stayed above 12 cm, nesting usually failed (Lorenz 2000). Repeated sampling of fish densities over time showed that 12 cm was the water depth at which fish were becoming highly concentrated (Lorenz 2000). Data here suggest that, in addition to the fish density effect, spoonbills may have responded to the shallow depths because of prey vulnerability.

There is considerable disagreement among studies of sympatric wading birds regarding the degree to which species segregate along niche axes of habitat (Jenni 1969, Kushlan 1976, Willard 1977, 1985, Hom 1983, Kushlan et al. 1985, Kent 1986, Frederick and Bildstein 1992, Ramo and Busto 1993, Fasola 1994, Chavez-Ramirez and Slack 1995, Smith 1995, Strong et al. 1997), water depth (Meyerriecks 1960, Kushlan 1976, Willard 1977, 1985, Custer and Osborn 1978, Hom 1983, Powell 1987, DuBow 1996, Dimalexis et al. 1997), prey type (Willard 1977, Kushlan et al. 1985, Kent 1986, Frederick and Bildstein 1992, Ramo and Busto 1993, Fasola 1994, Smith 1997), prey size (Willard 1977, 1985, Kushlan 1981, Hom 1983, Kushlan et al. 1985, Kent 1986, Frederick and Bildstein 1992, Ramo and Busto 1993, Fasola 1994, Trexler et al. 1994, Smith 1997), and behavior (Kushlan 1976, Willard 1977, 1985, Kushlan et al. 1985, Kent 1986, Frederick and Bildstein 1992, Dimalexis et al. 1997). Interpretations include a wide range of hypotheses such as resource partitioning to reduce competition, predator avoidance, morphological mechanisms to structure communities, and resource complementarity. What is unambiguous from this body of literature is that wading birds commonly occur in highly disturbed systems with

fluctuating resources levels, which are rarely measured directly (Butler 1993).

The simplest interpretation of the disparate patterns among studies is that the degree of resource partitioning for any given niche axis is dependent on prey availability levels (e.g., Hafner and Britton 1983), which varied among studies (i.e., in space and time). Under the controlled prey availability conditions in this study, the wading bird assemblage was opportunistic when resources were highly available (e.g., Fasola 1994), and birds tolerated extensive overlap in water depth, habitat, and prey type for at least short periods of time. All species used the shallow- (see also Willard 1985) and medium-depth treatments when prey were abundant. The Great Blue Heron and Tricolored Heron did not select sites based on prey density and water depth, in contrast to the other species, but all species nevertheless occurred sympatrically at feeding sites. Only after prey were depleted did species show habitat partitioning based on water depth. Resource partitioning occurred as a result of some species having the behavioral flexibility and morphological traits to exploit a wider range of environmental conditions (i.e., increased niche width) as patch quality decreased. This pattern is one of the main predictions of niche theory (Wiens 1989), suggesting that processes structuring wading bird communities may indeed be more generalized than is apparent from the existing literature. Also of interest is that, under conditions of high overlap, foraging theory predicts that food is unlimited. Thus, with wading birds, the presence of large multispecies flocks may signal conditions of unlimited food, which should correspond to increased reproductive output.

Does the prey availability hypothesis account for historical population changes?

The differential effect of prey availability on wading bird species in this study provides the first hint as to how the prey availability hypothesis (Fig. 7) could account for species-specific population responses. Wood Storks, White Ibises, and Snowy Egrets were the only species constrained by both water depth and prey density. These also are the species that have shown the most severe declines in breeding populations in the Everglades since the 1930s (Ogden 1994, Crozier et al. 2000). Conversely, the Great Egret and Great Blue Heron, which showed little sign of feeding constraints, appear to be more abundant now than during historic times (1930s for Great Egrets and 1960s for Great Blue Herons; Crozier et al. 2000).

Based on the concordance between the experimental results and long-term population data, I hypothesize that an important change in the Everglades ecosystem has been the pattern by which high prey densities and shallow water (i.e., high-quality patches) co-occur. Either the overall frequency of their co-occurrence has been reduced or the spatial and temporal pattern of their co-occurrence has been altered. This is distinct from

the suggestion that average prey availability levels have declined or that overall prey population levels have decreased, because this hypothesis focuses on the high-quality patches (Fig. 7). Only one component of availability (i.e., high prey density or shallow water) needs to change to influence the occurrence of high-quality patches, illustrating the delicate balance between them. There may be additional factors that further enhance the quality of food patches for individual species. For example, large fish size may be particularly important for large-bodied birds like Wood Storks (Ogden et al. 1976). Even then, because large fish tend to occur in deeper water, the relationship between prey density and vulnerability is germane.

The temporal pattern of high-quality patches is important because these patches must occur prior to breeding so that adults have time, which probably varies among species, to accumulate sufficient energy reserves to meet their energy threshold for breeding (Butler 1993). High-quality patches must continue throughout the entire breeding season as the energetic demands of nestlings increase. Nest failure reportedly occurs when the seasonal drydown is too rapid (Bancroft et al. 1994) and presumably the duration of patches with highly available prey is too short, or when it stops completely due to rising water levels (Frederick and Collopy 1989).

The spatial pattern of high-quality patches is important because food must be predictable in space in order to reduce search time and thus foraging costs. Topographic variation over a range of scales affects the occurrence and predictability of high-quality patches. Macrotopography (spatial extent of hundreds of kilometers) in the Everglades consists of a gentle slope to the landscape of ~ 1.6 cm/km (Holling et al. 1994). During the dry season, water depths recede at a rate on the order of 0.5 cm/day. The gradually sloping land surface, coupled with a slow water recession rate, ensure that the location of good foraging patches will remain in the same general region for at least several days. Wading birds follow these slow-moving patches and use a progression of habitats (and elevations) as water recedes and food patches move across the landscape (Robertson and Kushlan 1974, Kushlan 1979, 1986). Short-hydroperiod portions of the landscape (i.e., high elevations) provide foraging habitat early in the dry season and may provide the only suitable foraging habitat during years with large amounts of rainfall. Long-hydroperiod portions of the landscape (i.e., low elevations) provide foraging habitat late in the dry season and during particularly dry years. Macrotopographic variation is necessary to produce a continuous seasonal drying pattern, thereby illustrating the linkage between topographic variation at the landscape scale and the temporal pattern of food availability (DeAngelis 1994, Holling et al. 1994).

Microtopographic variation (spatial extent of tens of meters) also contributes to the formation of high-quality

Everglades prey availability hypothesis

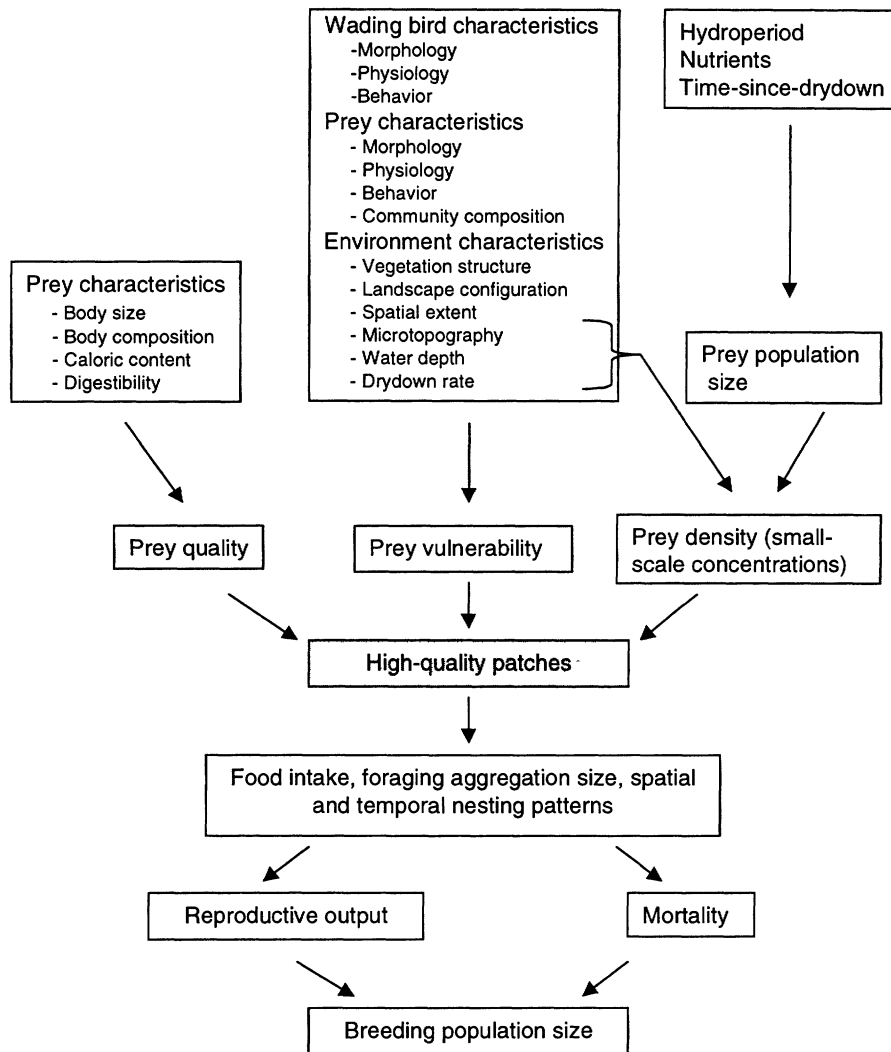


FIG. 7. Conceptual model of the prey availability hypothesis for wading birds in the Everglades. It identifies the pathways by which breeding populations could be limited by changes in prey availability, which is a function of prey density and prey vulnerability. This hypothesis is distinct from previous ones in that it focuses on the occurrence of high-quality patches rather than overall prey population size. The list of predator, prey, and environment characteristics is not exhaustive.

ity patches. As water recedes across the landscape, small depressions in the soil surface allow prey to become concentrated into small pools rather than to become stranded as individuals at low densities. In oligotrophic wetlands like the Everglades, microtopographic variation may well be the primary mechanism that produces patches with high densities of prey. Much of the total topographic relief in the Everglades can be found over very short distances. Zaffke (1983) reported an average range in surface elevation of 30 cm over 100-m transects. Microtopographic variation may also reduce search time because it renders a portion of the habitat obviously unsuitable for aquatic prey when no water is present. Further, because the depressions where fish are eventually stranded tend to be in open sloughs

rather than in higher ridges of dense sawgrass (*Cladium jamaicense*), they produce patches with highly vulnerable as well as dense prey. The net effect of microtopographic variation in a drying wetland is an increase in the density of vulnerable prey concurrent with a reduction in the total number of patches that must be searched to find prey.

The earlier suggestion, that species with higher GUDs (i.e., Wood Storks, White Ibises, and Snowy Egrets) require a larger spatial extent of marsh than do other species when water depths are deeper than optimal, supports the notion that overall loss of spatial extent (Robertson and Kushlan 1974) could have contributed to observed population declines (Fleming et al. 1994). Also, it provides an explanation for why

those declines would differ among species. Because differences in GUDs were only apparent in deep water, the loss of short-hydroperiod wetlands (Fleming et al. 1994), which are used by wading birds early in the dry season and during very wet years, may have had particularly serious consequences.

Another consequence of a reduced spatial extent of marsh is that now a relatively narrow range of hydrologic conditions will result in movement of high-quality patches across the entire landscape. The hydrologic conditions that maximize the spatial extent and seasonal duration of high-quality patches are to have all short-hydroperiod marshes inundated at the start of the dry season, followed by a large decrease in water levels over the course of the drydown. In other words, there should be large seasonal fluctuations in water levels (Kushlan 1989), with a key point being that water levels should be very high at the start of the dry season. Under historic conditions when the spatial extent and elevation gradient were larger, almost regardless of the amount of rainfall, high-quality patches would form and persist throughout the dry season somewhere in the landscape. From year to year, the exact location of those patches might shift up or down the elevation gradient, but the patches would still be available to such mobile animals.

There is considerable circumstantial evidence that the Everglades ecosystem has changed in ways that would affect prey availability, but less evidence exists to indicate specifically the loss of high prey density and shallow-water conditions. Ecosystem processes that produce high-quality patches are productivity, hydroperiod, and the seasonal drydown. It has been suggested that the productivity of the estuary has decreased due to reduced freshwater flow (Powell et al. 1989, Walters et al. 1992, McIvor et al. 1994), and this, in turn, could be responsible for lower fish densities. There are no historic productivity data for the estuary region to compare, but there are data on the response of the fish community to anthropogenic increases in nutrient levels. Elevated phosphorus levels in the freshwater marsh produce a 4- to 20-fold increase in fish density compared to unenriched sites (Turner et al. 1999). For comparison, increased hydroperiods also produce a higher fish density (Loftus and Eklund 1994), but the magnitude of the increase is small (2–4 fold) relative to the 20- to 150-fold increase produced during a seasonal drydown (Carter et al. 1973, Kushlan 1974b, 1976, Loftus and Eklund 1994, Howard et al. 1995).

Changes in the spatial and temporal pattern of the seasonal drydown would therefore have the greatest effect on the formation of high-quality food patches. Because birds follow a progression of habitats across the landscape throughout the dry season, the location of high-quality patches at the time of nest initiation is probably a key determinant of where or whether birds ultimately nest. Over the last 50 yr, sea level rise and the resulting shift in the edge of the coastal mangroves

to 3.3 km inland (Ross et al. 2000), a reduction in the total volume of flowing water (Fennema et al. 1994), and the fragmentation of the northern Everglades into impoundments (Light and Dineen 1994) have clearly changed the location and timing of formation of high-quality patches. During the same time period, nesting colony locations have shifted inland from the coastal estuaries (Ogden 1994).

The processes of hydroperiod, productivity, and the seasonal drydown are not mutually exclusive, and an increase in overall fish population size followed by a strong water level recession would produce very high-quality patches. However, patches with high prey densities produced by the seasonal drydown are fundamentally different from fish population increases as a result of increased hydroperiod or nutrient inputs, because seasonal drydowns produce small-scale shallow-water patches that are clumped in space and that move across the landscape over time. If this attribute of the ecosystem is restored, it is likely that the species currently most constrained in their choice of feeding sites will be the ones that benefit most. It should be emphasized that restoring this ecosystem attribute to a greater frequency does not require that optimum hydrologic conditions for searchers occur each year. Indeed, it is the interannual variation in hydrologic conditions, coupled with species-specific feeding constraints, that will sustain the entire complement of the Everglades' wading bird species for the long term.

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APPENDIX

A series of figures (A1–A8) showing daily mean bird density of eight species of wading birds in response to treatments of fish density and water depth is available in ESA's Electronic Data Archive: *Ecological Archives* M072-005-A1.