RESOURCE USE STRATEGIES OF WADING BIRDS

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Ciconiiform wading birds possess several characteristics that make them useful as subjects for ecological studies. They are relatively large birds, ranging from the Least Bittern (*Ixobrychus exilis*), 28 cm long, to the Goliath Heron (*Ardea goliatha*), 140 cm long, (Hancock and Elliott 1978). They are widespread, with some superspecies ranging from the temperate zone through the tropics. They represent a diversity of variations on a general avian theme, that of a long-legged aquatic predator. Their relatively high energy demands and locally large populations make them important components of aquatic ecosystems. Interspecific differences in size, habitat use, sociality, distribution, responses to seasonal environmental pressures and food habits provide the fabric for natural experiments in the elaboration of resource use strategies in aquatic environments.

In this paper, I present a selective review of the current state of knowledge of resource use strategies in wading birds. This report and its companion paper, a review of foraging ecology (Kushlan 1978a), have as their common goal the stimulation of further use of this group of birds for ecological study.

PHYSICAL FACTORS

Short-term weather conditions, such as extreme temperature or rainfall, often constrain resource use in birds (Anderson 1965, Robins 1970). Most adult wading birds appear to be relatively immune to the direct stresses of excessively hot or cold conditions, compared with smaller birds, by virtue of behavioral and physiological adaptations (Kahl 1963, Hafez 1964, Steen and Steen 1965), not the least of which is their relatively large body mass (Calder 1975). Rainfall and cool temperatures may have indirect effects such as delay or interruption of feeding schedules. Consistently cold weather may have the long-term energetic cost of reducing availability of the poikilothermic prey that are commonly consumed by wading birds (Kushlan 1978a), by lessening the prey's activity level, or by driving them into deeper water. Rainfall increases turbidity in waters used by visually foraging birds, which can influence habitat choice and feeding rates (Krebs 1974, Custer and Osborn 1978a, Thompson 1978) and may affect nestling mortality (Owen 1960).

Seasonality, particularly seasonal variation in resource availability, is a dominating feature in the evolution of many species and communities (Beals 1970, Fogden 1972, Leck 1972). The importance of seasonal vari-

ation in weather conditions on wading birds has been conclusively dem-
onstrated for the temperate Grey Heron (*Ardea cinerea*). Mortality, par-
ticularly of first-year birds, and resulting population trends of this heron
are determined in part by the severity of winter conditions (Lack 1966,
Stafford 1971, Reynolds 1979, North 1979).

Seasonal rainfall patterns affect prey availability by causing water levels
to fluctuate in shallow-water habitats. Relationships between water level
changes and wading bird foraging have been demonstrated for a number
of species (Kushlan 1978a). However, most information available is for the
Wood Stork (*Mycteria americana*). Kahl (1964) found in the Big Cypress
Swamp of Florida that Wood Storks began to nest at a specific water level.
Kushlan et al. (1975) found a mathematical relationship between the timing
of Wood Stork nesting and the rate of water level decline in the Florida
Everglades. A similar relationship was later confirmed in a separate sys-
tem in central Florida (Clark 1978). The existence of such precise rela-
tionship between seasonal hydrologic conditions and nesting phenology of
the Wood Stork suggests that seasonal fluctuations in the physical envi-
ronment may also play a crucial role in the availability of resources to
other species of wading birds.

GEOGRAPHY

Geography affects resource use, especially as it influences population
size and diversity along latitudinal or continent-to-ocean gradients. For
example, the richness of the wading bird guild increases with decreasing
latitude in eastern North America (Fig. 1). The data figured are for coastal
regions but, as wading birds are primarily coastal in distribution over much
of the area, this constraint does not much affect regional species richness.
Richness declines rapidly north of 40° N, probably because of adverse
climate for wading birds and a decrease in the amount of coastal marshes
along the east coast. It has been clearly demonstrated that the amount of
habitat available is correlated with both population size (Custer and Os-
born 1977, Kushlan 1978a) and colony site location (Lack 1954, Kushlan
1976a, Fasola and Barbieri 1978). Changes in wading bird species richness
affect interactions among foraging wading birds, particularly among
species that feed aggregately, because the diversity of foraging aggrega-
tions increases from temperate to tropical latitudes (Kushlan 1978a).

The drop in species richness between 20 and 25° N in eastern North
America (Fig.1) is an exception to the general temperate to tropical pat-
tern. This particular drop occurs on the Florida Keys, an island chain off
the lower Florida coast. Such oceanic environments appear to have a lower
resource base actually available to a bird that feeds by wading than do
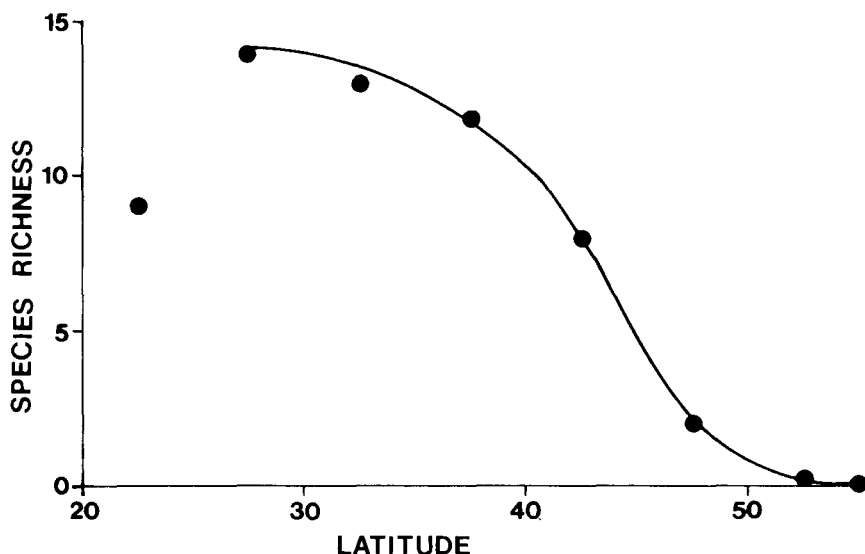extensive, shallow inland or coastal marshes (Kushlan and Robertson

FIG. 1.   The relationship between latitude and wading bird species richness in eastern North America. Data analyzed in 5° blocks. Data on nesting species from Custer and Osborn (1977), supplemented for high latitudes by Palmer (1962) and at low latitudes by Green (1946) and Kushlan and Robertson (1977). Isolated point corresponds to the Florida Keys, an oceanic environment.

1977). Recher and Recher (1972) have shown that only a single wading bird, the Reef Heron (*Egretta sacra*), can exist on the Great Barrier Reef, an area of low resource availability to herons, despite its high productivity overall.

POPULATION MOVEMENTS

Movements of individuals and entire segments of populations are tactics commonly employed by wading birds in response to fluctuations in resource availability. Wading birds use up to 3 types of population shifts: migration, dispersal and intraregional movement (Fig. 2).

Seasonal migrations, which may be intercontinental in extent, are well known among wading birds, including such diverse species as the White Stork (*Ciconia ciconia*), White-faced Ibis (*Plegadis chihi*), Green Heron (*Butorides virescens*), Cattle Egret (*Bubulcus ibis*) and other temperate herons (Meyerriecks 1960; Ryder 1967, 1978; Kahl 1972; McClure 1974; Siegfried 1978).

Dispersal of juveniles and adults occurs at the end of nesting. Such dispersal probably results in movement of birds from areas where re-
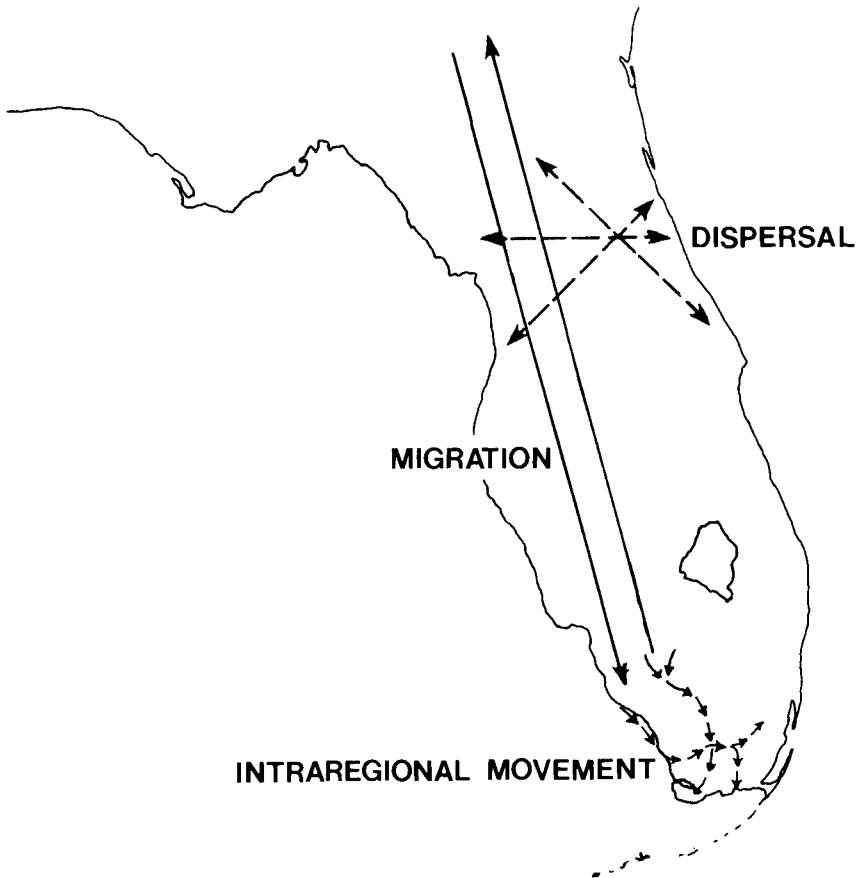
FIG. 2.   Movement tactics of wading birds as illustrated by the situation in Florida.

sources are scarce or unavailable to more favorable areas (Byrd 1978). For example, after completing nesting in Florida, birds tend to disperse northward into temperate marshes (Kushlan and Robertson 1977), where food may be approaching its seasonal maximum. As a result, the annual resource base available to the population is increased.

Intraregional movement is a less appreciated component of wading bird foraging tactics (Kushlan 1978a). Such movements have been well documented for species such as the Cattle Egret in Africa, Sacred Ibis (*Threskiornis aethiopica*) in Africa and Australia, Strawnecked Ibis (*T. spinicollis*) in Australia, and White Ibis (*Eudocimus albus*) and Wood Stork in Florida (Carrick 1962, Craufurd 1966, Urban 1974, Ogden et al. 1978, Clark and Clark 1979, Kushlan 1979a).

The relation of the 3 types of population movements to environmental conditions can be illustrated by the pattern shown by the Wood Stork in southern Florida (Kushlan et al. 1975, Ogden et al. 1978). After nesting is completed in spring and early summer, Wood Storks migrate northward, spending the summer and early autumn in north Florida and other coastal plain areas. Return migration takes place later in the fall. On their return to south Florida, storks forage initially in coastal marshes and then begin intraregional movements, moving through a succession of coastal and inland foraging sites throughout the nesting period. These movements correspond with the timing of seasonal drying of various marshes and resulting concentration of fish on which the storks depend (Ogden et al. 1976). Should water levels rise instead of fall, storks abandon their feeding pattern and disperse to scattered sites.

PREDATION

Avoidance of or alertness for potential predators may consume time and energy and may affect the types of foraging activity in which a bird can engage. Healthy adult wading birds are preyed upon rarely and, concomitantly, specific antipredator adaptations appear to be poorly developed (Milstein et al. 1970). For adult wading birds, passive awareness of possible predators generally suffices, supplemented by simple responses such as alert posture, freezing, bill thrusts, bittern stance, ducking and flight. Characteristics such as cryptic coloration, which may serve antipredator functions in other groups, appear most readily explainable as foraging adaptations in wading birds (Kushlan 1978a). Social foraging, common among wading birds, may confer an extra measure of group vigilance through feeding vocalizations that can communicate that "all is well" (Kushlan 1976b). Available reports of successful predation on adult wading birds are often circumstantial (Bent 1937, Monson 1951, Cottrille and Cottrille 1958, Blaker 1969, Milstein et al. 1970, Callahan and Carey 1979). Bayer (1979) presented the best account of a predator, a Bald Eagle (*Haliaeetus leucocephalus*), attacking wading birds, Great Blue Herons (*Ardea herodias*). Although unsuccessful, the eagle's attack and its presence altered the foraging behavior of the herons, leading to the formation of temporary groupings. It appears that the threat of predation is usually not a major determinant of foraging patterns in most wading birds, but this is an aspect of wading bird foraging about which much more information is needed.

Predation threat to nestlings has critical effects on resource use tactics of the parents. A number of predators eat wading bird eggs and nestlings (Baker 1940, Owen 1960, Teal 1965, Dusi and Dusi 1968, Dickerman and Gavino 1969, Blaker 1969, Milstein et al. 1970, Taylor and Michael 1971).

Black-crowned Night Herons (*Nycticorax nycticorax*) may prey on other species of wading birds nesting in the same colony (Beckett 1964, Teal 1965, Kale 1965, Blaker 1969, Wolford and Boag 1971). Sibling cannibalism also occurs (Dusi 1968). Because of the long growth period and exposed nesting sites, adult wading birds guard chicks past the post-hatching brooding period (Milstein et al. 1970). The need for such nest attendance affects resource use in 2 major ways. During the guarding period, growth rates are relatively rapid until biomass growth and organ development are such as to permit the chicks to be left alone (Kushlan 1977a, b; Werschkul 1979). Adult nest-guarding also requires that the burden of early food gathering fall to the non-guarding adult, which in Wood Storks may also feed the attending parent (Kahl 1966). The female White Ibis tends to forage during the middle of the day while the larger male guards the nest (Kushlan 1976c, 1977c). If such a schedule imposes time and energy constraints on the adults, the need for effective foraging may become increasingly critical during this period of nesting. When young achieve the size and locomotor maturity that permits independence of parental guardianship, both parents can forage at the same time, which should increase the amount of food available to young (Owen 1955, Siegfried 1972, Kushlan 1977b) or decrease stress on adults (Werschkul 1979).

FORAGING SOCIALITY

Wading birds forage alone or in groups of varying size. Large aggregations of wading birds form at sites of high prey availability (Kushlan 1976a). By foraging in an aggregation, wading birds probably decrease search time between food patches, increase the likelihood of foraging in a suitable location, decrease risk of obtaining no food and perhaps have more potential food available (Kushlan 1978a). Some species have characteristics, such as white plumage, that aid in establishing aggregations by attracting other birds to feeding sites (Kushlan 1977d).

Aggregated foraging permits efficient use of the ephemeral resources that characterize many wading bird habitats. The amount and distribution of resources and their availability change markedly on a daily or seasonal basis such that wading birds may be able to feed on these resources for only relatively short periods at a time. By aggregating, birds find and use these locations as they become available. In south Florida, seasonal changes in prey availability cause aggregations to form daily at newly suitable sites and, as a result, the birds sequentially use much of the habitat available over the annual drying cycle (Kushlan 1976b, 1979a).

Aggregative foraging also brings birds into close proximity and increases social interactions (Grubb 1976, Woolfenden et al. 1976, Kushlan 1978b, Russell 1978). Wading birds reserve a feeding space within an aggregation

by continuing to defend individual distances. The amount or types of re-
sources consumed within aggregations could increase, decrease, or be
unchanged depending on the circumstances. I have proposed (Kushlan
1978a) that within an aggregation some wading birds gain a net energy
benefit with increasing aggregation size up to some maximum. Such an
increase may possibly be due to a subtle commensal benefit derived from
nearby birds, similar to that noted below. The point of maximum com-
mensal benefit may be determined by increasing interference among the
birds. The influence of the 2 effects depends on the number of birds
present, feeding tactics employed by each species and prey availability.
An increased return from aggregative foraging has been demonstrated for
Little Blue Herons (*Florida caerulea*) foraging with White Ibis (Kushlan
1978b) and for Snowy Egrets (*Leucophoyx thula*) and Great Egrets (*E.
alba*) foraging with Roseate Spoonbills (*Ajaia ajaja*) (Russell 1978). Many
other possibly commensal associations have been reported in wading birds
(Kushlan 1978a). Krebs (1974) studied the intake of Great Blue Herons
feeding within and outside of aggregations in an attempt to determine
whether aggregating was beneficial. Unfortunately, his results were equiv-
ocal. DesGranges (1978) found higher feeding rates when Great Blue Her-
ons fed in larger than in smaller groups. This result supports the possibility
that there may be a commensal advantage to feeding in aggregations.
Interference phenomena have been documented by Goss-Custard (1970)
for shorebirds, but their occurrence in wading birds requires study. Rus-
sell (1978) suggested that the subordinate position of Snowy Egrets in
mixed aggregations reduced their potential increase in net energy gain.
Similarly, piracy, such as Great Egret piracy on White Ibis (Kushlan
1978c), adversely affects foraging efficiency and presumably energy gain
of the victim.

The relationship between aggregation size and energy gain should differ
among wading bird species. A species with a foraging repertoire composed
of behaviors that are effective within aggregations could increase its en-
ergy intake with increasing aggregation size. Other species, such as stand-
ing-feeders or active-feeders whose behavior brings them into conflict with
larger standing-feeding birds, would have the effectiveness of their for-
aging decreased as aggregation size increases. Such species may, how-
ever, "parasitize" aggregations of other birds by using them to find patches
of abundant prey and then feeding near, but not within the aggregation
(Kushlan 1977d).

COMPETITION

The role of indirect competition in channelling resource use patterns in
wading birds is unclear. Considering an entire regional wading bird com-

munity, species can be shown to partition resources through a combination of characteristics, including habitat, time of feeding, general feeding strategy (visual or tactile), size of bird and feeding behavior (Kushlan 1978a). Studies of more compact species groups, such as sympatric herons or ibis, have shown that species differ by size, food, feeding location, or behavior (Carrick 1959, Meyerriecks 1962, Jenni 1969, Kahl 1972, Kushlan 1976b, Willard 1977, Custer and Osborn 1978a, Thompson 1978, Hoffman 1978). However, it remains useful to consider the degree of overlap among sympatric species. Resources generally appear to be divided with a low degree of overlap among herons of different sizes (Willard 1977) and between ibis and storks using similar feeding behavior (Kushlan 1979b). However, overlap in food and habitat among certain, similarly-sized herons has been found to be high in specific instances (Jenni 1962, Willard 1977, Custer and Osborn 1978a). Such overlap need not imply competition in itself, as little is known about the resource state in these cases, but it does suggest the desirability of additional study to determine whether any competition may be involved.

The effect of direct competition on resource division may be especially critical within a feeding aggregation; there have been no studies that clearly show how resources are actually shared or whether competition occurs in such situations. Kushlan (1976b) showed that 7 species (Great Blue Heron, Great Egret, Snowy Egret, Little Blue Heron, Louisiana Heron [*Hydranassa tricolor*], Wood Stork and White Ibis) differed by location, water depth or behavior while feeding together. These differences suggest, although do not prove, that in this case the birds were taking different segments of the available resource spectrum. Competition certainly does occur at times. In the above example, Black-crowned Night Herons, which overlapped in foraging characteristics with Snowy Egrets, did not use the site while the aggregation fed there, probably because of dominance by Great Egrets (Kushlan 1973a). When resources are limited, competition among Cattle Egrets clearly resulted in differential resource allocation to older, more competitively dominant birds (Woolfenden et al. 1976). These results suggest that direct interference competition may be widespread among wading birds.

FORAGING TACTICS

Where to search.—An important consideration in understanding wading bird searching tactics is that habitat and prey for most species are distributed in spatial and temporal patches (Kushlan 1976a). As a result, wading birds need to sample potential patches to decide where to forage. For species such as the White Ibis, choice of foraging patch may in some cases be a primary factor in foraging optimization (Kushlan 1979a). The

energy penalty for wrong choices may be rather severe, because of the relatively high costs incurred by large birds in moving from place to place. Thus, there is probably considerable pressure for wading birds to sample foraging patches efficiently.

Several tactics are employed by wading birds in patch selection. A number of species typically travel and forage in single species flocks. Cattle Egrets (Siegfried 1971, 1978) and White Ibis (Kushlan 1979a) are notable examples. Custer and Osborn (1978b) found that these 2 species often flew in interspecific groups to feeding sites in contrast with 8 other wading bird species. It has been proposed that information regarding the location of food patches is transferred among wading birds at colony and roost sites (Krebs 1974). At least some cirumstantial evidence supports this hypothesis (Krebs 1974, Custer and Osborn 1978b, DesGranges 1978). Information is no doubt transfered in flight lines and at foraging sites as 1 bird sees another feeding. Species that feed in aggregations typically choose sites where other birds are foraging (Kushlan 1977d).

Other tactics used to decrease the frequency of wrong sampling choices include trial and error, learning, return to previously used patches, territoriality and sequential sampling. The dynamics of wading birds foraging in a temporally changing patch demonstrated the role of trial and error (Kushlan 1976a). A few wading birds regularly visited the feeding site for short periods when prey abundance was low. As prey became more abundant, feeding time increased and number of wading birds increased until a large aggregation formed. This succession of events suggests that birds were sampling by trial and error. Length of stay in a patch may have been determined by how much food a bird was able to obtain. Similarly, habitat use in the White Ibis appears to be determined in part by the energy value of the food located there (Kushlan 1979a).

Learning probably plays an important role in feeding site selection. The importance of learning to forage effectively is demonstrated by atypical foraging sites being chosen by juveniles (Kushlan and Kushlan 1975) and also by the lowered foraging effectiveness of young birds (Recher and Recher 1969a, Cook 1978a).

Wading birds return to a previously used patch provided its profitability continues to be sufficient (Owen 1955, Bateman 1970, Kushlan 1976b, Cook 1978b). This means that a given patch will be used for a period of time determined by the rates of resource depression and renewal. Prey availability in some patches, such as reef crests used by the Reef Heron (Recher and Recher 1972), may be renewed daily. Daily renewal in some cases permits the development of permanent territory holding systems. A single species of wading bird can use several tactics in its use of foraging patches. Great Blue Herons, for example, in different situations can hold

permanent territories (Bayer 1978), switch between intertidal and terrestrial foraging (Krebs 1974), or show temporal variability in feeding sites used around a colony (DesGranges 1978).

When resource status changes gradually, patches may be sampled sequentially as they become available. As south Florida swamps dry seasonally, birds can use 1 patch until it is depleted and then move to a nearby patch where prey become available later. Intraregional movements exhibited by many wading birds, discussed previously, result from repeated shifts in foraging sites.

The search.—The effectiveness of a wading bird's search for prey is determined in part by the foraging behaviors used. These behaviors, which I have cataloged elsewhere (Kushlan 1978a), can be expected to be chosen to increase net energy gain. Snowy Egrets, for example, apparently select feeding behavior in relation to prey availability (Kushlan 1972). When dissolved oxygen is low, such as in the early morning, fish may have to come to the surface where diffusion provides a higher oxygen concentration (Kushlan 1974). Under these conditions Snowy Egrets feed by standing, a behavior of relatively low cost. However, as oxygen levels increase during the day and fish become less available at the surface, the egrets may have to resort to more energy intensive behavior, such as foot-dragging. Thus, when resources were easily obtained, egrets used an energetically efficient behavior. Use of passive, low cost behaviors for abundant, conspicuous and easily captured prey or use of active, more variable behaviors when prey are less available may be characteristic of wading birds. In one such case, when standing-feeding was the least successful behavior for Snowy Egrets, success was about inversely related to energy expenditure (Kushlan 1973b). If energy gain is proportional to success, then the net energy gain may be about equivalent for each behavior. Birds using various behaviors may all forage effectively, perhaps because individuals may specialize in different behaviors (Kushlan 1973b).

Prey location, selection and pursuit.—The location, pursuit and selection of prey have been the subject of considerable discussion. MacArthur (1972) suggested that if a bird chooses the diet that minimizes average pursuit and search time per gram of prey, a species should be more specialized in a productive environment than in an unproductive one. In support of this hypothesis, MacArthur (1972) used Recher's (unpubl.) data on the Great Blue Heron, which showed that birds took a narrower food size range in a more productive tropical habitat (south Florida), than in a less productive temperate habitat (New York). However, in using this example MacArthur overlooked 2 confounding factors, that the birds of the 2 populations are not the same size and that the ranges of prey available to the 2 populations may not be similar. The Great Blue Heron population resi-

dent in Florida consists of larger birds than in New York. Because they can handle larger prey the larger birds may be expected to take a wider size range of prey in Florida, rather than the smaller range predicted by the productivity hypothesis. Also, the types and sizes of prey available undoubtedly differ between a subtropical marine site and a temperate freshwater site. Should a more limited range of prey exist in 1 site, irrespective of total productivity, the heron should not be expected to take a wider range of prey there.

There are, however, other examples from wading bird studies that may be useful in assessing the relationship of productivity to food selection. When food is most available diet breadth should be restricted (MacArthur 1972). Thus prey taken in a single location in summer, when availability would be high, should be less diverse than in winter when productivity presumably declines. However, Willard's (1977) data on Great Egrets, Great Blue Herons and Snowy Egrets suggest that, during the spring-summer period of higher food availability, prey sizes were more diverse than in fall-winter. Similarly, a greater diversity of prey was taken by White Ibis in presumably more productive coastal habitats than in inland habitats (Kushlan 1979b). These results are not in accord with predictions and are particularly puzzling for searching predators such as Great Egrets and Great Blue Herons, because these birds would minimize search time by taking additional prey when food is scarce. Such apparent discrepancies from predicted results merit further study.

Smaller species should have a more restricted diet because of shorter search times for smaller more abundant prey, while a larger forager should have a longer search time and eat a wider range of prey (MacArthur 1972). In support of this, it appears that large herons do tend to take a wider size range of prey than small herons (Willard 1977).

A species that searches for its prey should be a generalist, whereas a species that pursues its prey should be a specialist (MacArthur 1972). Jenni (1969) showed that for 2 herons of similar size in north Florida the Snowy Egret, the pursuer, was relatively more specialized than the Little Blue Heron, the searcher. Thus, in the same foraging area, the searcher had a more diverse diet, probably because taking each prey encountered decreased search time between prey items. However, the distinction between searcher and pursuer is often not easy to make, because most species can use either tactic at different times or in different habitats.

Pursuit time has been reduced to zero for those wading birds that forage by tactile detection of prey, a strategy that apparently has evolved at least twice in ciconiiform wading birds (Kushlan 1978a, 1979b). The American White Ibis and the Wood Stork are examples of such species (Kahl and Peacock 1963, Kushlan 1977e). Pursuit is nonexistent because the first

contact with prey is the moment of capture. This, of course, makes the decision of where to search and how to search critical to such foragers.

Other species appear to specialize in pursuit strategies. These active foragers, including the Reddish Egret (*Dichromanassa rufescens*), Louisiana Heron and Snowy Egret (Kushlan 1978a), are species that typically run down prey, especially schools of fish. The Reddish Egret appears to specialize in pursuing schooling fish in shallow water. There has been no test of the relative efficiencies of various types of tactics used by wading birds specializing in active pursuit.

MacArthur and Pianka (1966) predicted that a predator should rank prey types according to their energy value per handling time. For the White Ibis in south Florida, handling time for most prey actually consumed is small and, in general, energy content appears to have minimal relevance to prey selection (Kushlan 1979a). This is because, as a tactile forager, the ibis should accept any prey it catches and can consume quickly. Thus, ibis should encounter their environment in a fine-grained way; and, since prey density should control search time in this completely searching predator, ibis should take prey in proportion to the prey's density. However, density is also, in many cases, irrelevant to the ibis, which selectively consume certain species of prey even at very low density (Kushlan 1979a). Prey selection is made in large part on the basis of a potential prey's catchability, that is, the ability of ibis to effect its capture (Kushlan 1979b). Visually foraging wading birds, on the other hand, at least have the potential to rank prey before capturing. However, there is currently little evidence that they do so.

Capture and handling.—The motor patterns associated with capturing, handling and swallowing prey have been summarized elsewhere (Kushlan 1978a). The maximum possible size of prey for a wading bird is not easily determined, since, given sufficient time and freedom from robbing, a wading bird can eat even very large prey, piece-by-piece. Recher and Recher (1969b) suggested that a heron is capable of seizing and holding a fish at least 25% longer than its bill. Smaller birds take more time to handle prey per gram of prey than do larger birds (Kushlan 1978a). Thus, ease of handling may be an important factor in the wider prey size taken by large wading birds.

Schoener (1971) predicted that handling time would be constant below a certain prey size, but for larger prey it becomes an exponential function of prey size. This appears to be so for the White Ibis (Kushlan 1979a). Handling time increases drastically with increasing prey size to the point where the predator becomes satiated or where it becomes uneconomical to eat the prey because of other considerations. In the White Ibis, capturing of large prey by individual birds increases the probability of an

attack by robbers, particularly Great Egrets. This robbing could restrict the diet of the victim, since some typical prey items are lost through robbing and handling time is increased by avoiding the pursuit of the potential robbers. The White Ibis, when feeding in an aggregation, will often drop newly caught large prey rather than attempt handling (Kushlan 1979a). Similarly, Great Blue Herons drop struggling fish (Recher and Recher 1969b).

Recher and Recher (1969b) showed that defensive structures and behavior increase handling time, increase the likelihood of prey escape and decrease the average net energy value of a captured prey item. In the prey of wading birds, structures appear more effective in defense than behavior alone. A prey that has a high handling time should not be added to the diet if its value per time exceeds the mean of previous prey taken in the diet. Great Blue Herons, however, at times take prey requiring high handling time. Recher and Recher (1972) showed that the average weight of food gained by Great Blue Herons for each minute spent subduing and swallowing a puffer (Tetradontidae) was considerably less than the average weight of food obtained for each minute of foraging time. It would be advantageous for herons to ignore fish such as puffers. Some individual Great Blue Herons, however, have learned to subdue puffers by piercing them and consume them even though it is apparently relatively inefficient for them to do so.

Foraging maximization.—Wading birds may prove useful in studies of the tactics used by animals to increase food intake or energy gain. Present information on wading bird foraging suggests areas that merit particular attention. For example, components of prey other than energy may restrict a wading bird's ability to maximize energy at any given time. Marabou Stork (*Leptoptilos crumeniferus*) chicks require calcium, which is obtainable from natural prey but not from the normal marabou food, carrion, (Kahl 1966) which probably could be gathered more efficiently.

Feeding may not be performed in a maximally efficient manner in some cases, such as when it interferes with a wading bird optimizing its entire activity pattern. During pair formation wading birds spend long hours in territorial defense (Burger 1978) and thereby may need to shorten their feeding time, perhaps by choosing poor feeding sites near the colony. Similarly, social dominance interactions in flocking or aggregating wading birds (Woolfenden et al. 1976, Grubb 1976) may decrease the possibility of using the most efficient foraging behavior or feeding site.

Wading birds usually respond dramatically to short-term availability of easily-obtained prey, such as at fish kills where they can feed with high efficiency (Hoffman 1978, Dombe and McFarlane 1978). However, a long-term strategy of optimizing energy return may require ignoring such short-

term energy bonanzas. Great Blue Herons that hold territories during nesting may not be as likely as nonterritorial birds to take advantage of foraging opportunities at such ephemeral food sources (Bayer 1978).

On a long-term basis, an animal must maintain a positive or neutral energy balance. Thus, a wading bird must obtain sufficient energy to offset its energy expenditure. During nesting and feeding young, high foraging efficiency may be required. On the other hand, non-rigorous foraging may be possible when constraints on time or energy budgets are not great (Kushlan 1978c).

Thus, wading birds appear to demonstrate important factors impinging on energy maximization such as non-energetic foraging requirements, complex activity patterns, long-term considerations and short-term behavioral choices. All can affect approaches to increasing net energy gain and as such can provide considerable insight into resource use strategies.

SUMMARY

Wading birds, because of their large size and diversity, appear to offer some promise for unraveling of certain aspects of foraging ecology and resource use strategies. This paper presents a selective review of the current status of knowledge of resource use strategies in ciconiiform wading birds.

Because of their large size, adult wading birds appear to be relatively immune to direct adverse effects of inclement weather, although indirect effects of weather on prey availability are important. Seasonal variation in resource availability can limit population levels of temperate species and is also a dominating influence in tropical populations, where seasonal fluctuation of surface water conditions determine in large part the nature of resource use. Wading bird species richness increases latitudinally toward the tropics and decreases away from continental areas. Population movements, including seasonal migration, radiative dispersal and intraregional movement, are adaptations to variable resource conditions. Predation pressure on nestlings may influence the evolution of growth patterns and time budgets of nesting adults.

Foraging sociality, especially aggregative feeding, is an important aspect of resource use, and may involve commensalism, competitive interactions and interference. Differently-sized wading birds appear to forage differently, but similarly-sized species may show considerable overlap in foraging parameters. Territoriality and aggregative feeding can decrease search time, or increase or decrease foraging effectiveness. Foraging behavior is diverse and variable, and responds to prey availability. Prey selection of wading birds require study, particularly with respect to factors associated with effectiveness of prey choices.

ACKNOWLEDGMENTS

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Erratum.— Vol. 92, No. 4, "Intersexual niche partitioning in Downy Woodpeckers" by Joseph B. Williams. Fig. 3, p. 446, should be disregarded and the figure appearing on p. 444 substituted. Fig. 3 caption remains the same. The figure printed below should be substituted for Fig. 2, p. 444. Fig. 2 caption remains the same.