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Food Habits of 4 Species of Wading Birds (Ardeidae) in a Tropical Mangrove Swamp

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Abstract.—The food habits of wading birds in the tropics are poorly known, particularly in coastal systems. We documented the food habits of Tricolored Herons (*Egretta tricolor*), Great Egrets (*Ardea alba*), Snowy Egrets (*E. thula*) and Little Blue Herons (*E. caerulea*), and assessed the degree of similarity among their diets in a mangrove swamp in southwestern Puerto Rico. Thirty-five birds were collected during the winters of 1994 and 1995 to examine their stomach contents. Eleven prey groups, comprised of 7 families of fish, 2 genera of crustacea (*Xiphocaris*, *Uca*), a lizard (*Anolis* spp.) and one group of insecta (i.e., Orthoptera), were identified. Great and Snowy Egrets fed mainly on shrimps (*Xiphocaris* spp.) and guppies (*Poecilia* spp.), while Little Blue Herons fed exclusively on Fiddler crabs (*Uca* spp.), and Tricolored Herons fed mainly on guppies (*Poecilia* spp.) and snooks (*Centropomus* spp.). Three dietary groups were identified on the basis of a percentage overlap index. Snowy and Great Egrets exhibited the highest degree of dietary overlap (54%) owing to their high consumption of shrimps. Fish contributed to the intermediate overlap values (22-24%) among Tricolored Herons and Snowy and Great Egrets. Little Blue Herons overlapped the least (i.e., < 1%) with Tricolored Herons and Great Egrets, and not at all with Snowy Egrets. Our data underscored the ability of wading birds to prey upon a variety of resources across their range. This capability is advantageous when exploiting coastal systems which might exhibit spatio-temporal fluctuations in prey availability. Received 5 November 1996, accepted 24 June 1997.

Key words.—Ardeidae, dietary overlap, estuaries, egrets, food habits, foraging, herons, mangroves, Puerto Rico, wading birds.

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Wading birds serve important ecosystem functions such as accelerating nutrient cycling at feeding grounds (Morales and Pacheco 1986) and regulating fish populations (Kushlan 1976, López *et al.* 1988, Miranda 1995). Our understanding of these functions is facilitated by information on the species' food habits and the extent of their dietary similarities (Kushlan 1978). In temperate and sub-tropical wetlands such information is readily available (e.g., Jenni 1969, Kushlan 1976, Custer and Osborn 1978, Kent 1986). Parallel data in the tropics, however, are scant. Of the available information, Kushlan *et al.* (1986) and Morales and Pacheco (1986) focused on fresh water habitats. To our knowledge, only Ramo and Busto (1993) have documented the food habits of wading birds in a tropical mangrove forest, which they also considered one of the most important feeding habitats for wading birds in coastal tropical environments.

In Puerto Rico, mangrove swamps are particularly prevalent along the southern

and western coasts (Cintrón *et al.* 1978, Cardona and Rivera 1988). Unfortunately, information on the foraging ecology, including food habits, of wading birds is lacking. Wetmore's (1916) is the only available work on wading bird food habits in Puerto Rico. His work, while important, was based on casual collections with no mention of the habitats where birds were collected. We studied the foraging ecology and potential impact of wading birds on fish populations in a coastal mangrove in southwestern Puerto Rico during the winters of 1994 and 1995 (Miranda 1995). Here we report the food habits of Tricolored Herons (*Egretta tricolor*), Great Egrets (*Ardea alba*), Snowy Egrets (*E. thula*) and Little Blue Herons (*E. caerulea*), and the degree of similarity among their diets.

STUDY AREA

Field work was conducted at the Boquerón Wildlife Refuge located in southwestern Puerto Rico (18°00'N, 67°08'W) (Fig. 1). The refuge is about 3 km² and is comprised of shallow water lagoons bordered by red (*Rhizo-*

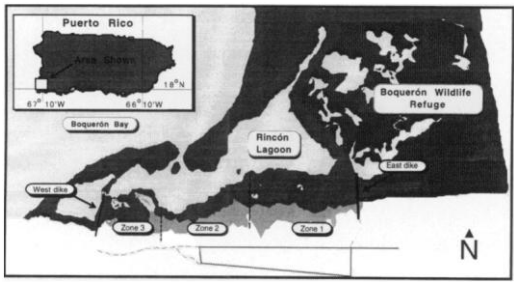


Figure 1. Map of the Boquerón Wildlife Refuge showing the study area encompassed between the east and west dikes (i.e., zones 1, 2 and 3). The location of the study area in Puerto Rico is shown in the insert.

phora mangle), black (*Avicenia germinans*) and white mangrove (*Laguncularia racemosa*). Data were collected in the southwestern portion of the refuge (i.e., zones 1-3), on a 83 ha of mangrove forest demarked on the east and west by man-made dikes. Thirty percent of the area was open water with an average depth of 11 cm (max. = 25 cm). Open water pools ranged between 5 to 510 m² in size (\bar{x} = 292 m²). More than 170 species of birds use the refuge as breeding or wintering grounds, including 10 species of wading birds (Cardona and Rivera 1988).

METHODS

Thirty-five birds were collected between December and May of 1994 and 1995. Of those, 13 were Great Egret, 8 Snowy Egret, 7 Little Blue Heron and 7 Tricolored Heron. Birds were collected using an air gun after being observed feeding for approximately 10 minutes. After collecting a bird, the stomach was removed and put in ice as quickly as possible (usually in less than 10 minutes) to slow down the digestion process. To minimize biases caused by changes in volume, stomach contents were analyzed the same day of collection. Stomach contents were sorted using a dissecting microscope, and recognizable food items were identified and classified to the lowest taxonomic level (e.g., family, genera). Remains of prey found in the heron's proventriculus were classified as unidentified items. All prey, except unidentified items, were counted, weighed (nearest g) with a OHAUS analytical scale model TS400D, and their volume was estimated by water displacement in a 50 cm³ volumetric beaker to the nearest cm³. Data were reported in two ways: 1) as percentage (i.e., prey items/total prey items tallied per wading bird species), and 2) using an importance index (Ashmole and Ashmole 1967, Harrison *et al.* 1983). The index is a composite value which takes into account prey volume, number of items of a given prey type and frequency of occurrence (i.e., number of times a prey item was identified in stomachs). Its use is advantageous because it avoids possible biases associated with using only 1 metric (e.g., volume, numbers) when ascertaining the relative importance of a prey item in a diet (Duffy and Jackson 1986). To calculate the importance index, each prey item was ranked by volume, number and frequency of occurrence. For example, a prey item with the highest volume in a sample of 10 different prey items (i.e., different types) would get a value of 10, the next highest would get 9, and so on until all prey items are ranked. The same procedure is

repeated for number and frequency of occurrence. Ranks are then summed to give each prey item category an importance value (i.e., index). To assess the degree of diet similarity among wading bird species, we used the Percentage Overlap index (Renkonen or Schoener overlap index; Krebs 1989). This index is easy to interpret (e.g., it assess actual area of overlap under the resource utilization curves) and is not sensitive to how one divides up the resource states (Krebs 1989). The percentage overlap measure is given by:

$$P_{jk} = [\sum (\text{minimum } P_{ij} \bullet P_{ik})]100$$

where P_{jk} is the percentage of overlap between species "j" and species "k", $P_{ij}P_{ik}$ is the proportion of resource "i" of the total resources used by species "j" and species "k", and "n" is the total number of resource states.

Prey abundance was estimated using a modified 1 m² throw-net (Miranda and Collazo In press). Modifications consisted of substituting most of the heavy, box-like frame used by Kushlan (1981) except for the bottom pipes, which delineates the 1 m² sampling unit. We attached a 50 cm long, 3.2 mm mesh size nylon net, opened on the top and bottom to 1 side of the 1 m² frame. This net was fitted with 40 foam floaters, which create a square enclosure when thrown in the water. To the other side frame, we attached 25 cm long nylon net, of the same mesh size, extending or hanging from the frame forming a "veil." This veil is flexible and capable of blocking fish irrespective of most bottom contours. Prey was sampled at a total of 88 sampling sites. Of these, 39 were used sites and the remaining were selected randomly. An used site was defined as a location where 2 or more wading birds were actively feeding. To select random sites, we used a random numbers table to select a compass bearing (i.e., 0-360°). We followed this bearing for 50 m when the starting (reference) point was an used site to ensure sampling independence (i.e., not affected by prey abundance at used site). A randomly selected distance, between 0-50 m, was chosen when we started from randomly selected points along a transect that bisected the study area on an east to west axis. Two to 6 throw-net samples were taken from each sampling site, depending on its size. Once the net was secured, all prey enclosed within the throw-net were collected using a 300 mm (1 mm mesh) dip net. This process ended when we got 3 empty dip nets in a row. Captured prey were held in buckets, identified, counted, measured to the nearest mm, and released. Data were expressed as the mean number (\pm SE) of prey/m².

RESULTS

Eleven prey groups were identified in wading bird stomachs (Table 1). Fish prey were represented by members of seven families. There were also crabs (*Uca* spp.), shrimps (*Xiphocaris* spp.), lizards (*Anolis* spp.) and insects (Order Othoptera). Prey proportions for the 4 species of wading birds combined were 24.1% fish, 74.8% crustaceans and 1.5% for other items (e.g., insects, lizards). The size of fish in stomachs ranged from 16.5 to 109.5 mm, with an average of

Table 1. Importance index, percent of total items (%) and frequency of occurrence for each prey group identified in the stomachs of wading birds collected in the mangrove swamps of the Boquerón Wildlife Refuge, Puerto Rico during the winters of 1994 and 1995. Importance index is a composite value based on prey volume, frequency of occurrence and number of prey items. Mean number (\pm SE) of fish and *Xiphocaris*/m² are presented. n/e = not estimated.

Prey Item	Great Egret N = 13			Snowy Egret N = 8			Little Blue Heron N = 7			Tricolored Heron N = 7			Prey/m ² N = 88
	Impor. Index	%	Freq. Occur.	Impor. Index	%	Freq. Occur.	Impor. Index	%	Freq. Occur.	Impor. Index	%	Freq. Occur.	$\bar{X} \pm$ SE
Centropomidae	9.6	2.7	4	0	0	0	0	0	0	12.2	4.1	4	0.06 \pm 0.03
Elopidae	7.4	0.4	1	0	0	0	0	0	0	9.3	2.7	1	1.77 \pm 0.47
Gobiidae	7.9	0.4	1	0	0	0	0	0	0	11.1	2.7	2	0.23 \pm 0.06
Gerridae	8.5	1.3	2	19.8	1.3	3	0	0	0	9.6	3.4	3	2.82 \pm 0.56
Mugilidae	9.6	5.9	1	0	0	0	0	0	0	9.3	3.4	1	6.02 \pm 1.17
Poeciliidae	10.4	19.8	2	20.9	18.3	3	0	0	0	15.0	66.9	4	48.28 \pm 8.03
Cichlidae	6.8	0.4	1	0	0	0	0	0	0	0	0	0	0.19 \pm 0.09
Unident. Fish	6.8	0.9	1	18.2	0.4	1	0	0	0	9.0	0.7	1	0.19 \pm 0.09
<i>Uca</i> spp.	6.5	0.4	1	0	0	0	100	100	7	7.3	0.7	1	n/e
<i>Xiphocaris</i> spp.	11.5	4.0	9	22.5	78.4	7	0	0	0	9.7	13.5	2	13.21 \pm 2.89
<i>Anolis</i> spp.	6.8	0.4	1	0	0	0	0	0	0	0	0	0	n/e
Orthoptera	8.2	1.8	2	18.6	1.3	1	0	0	0	0	0	0	n/e
Unident. items	0	0	0	0	0	0	0	0	0	0	2.0	2	n/e
Total Items		222			223			406				148	

41.5 ± 9.2 mm (N = 240). Members of Poeciliidae (i.e., guppies) were the most abundant of the sampled prey items, followed by shrimps (Table 1). The least abundant were members of Centropomidae (e.g., snooks). The availability of fiddler crabs was not estimable because they burrowed as we approached sampling areas. We did not estimate the abundance of *Anolis* or Orthoptera.

Little Blue Herons fed exclusively on fiddler crabs (*Uca* spp.; Table 1). Tricolored Herons were mainly fish eaters, with guppies and snooks (Centropomidae, *Centropomus* spp.) as their most important prey items. Guppies were their most important food item due to their high number in stomachs. Snooks were not as numerous, but emerged as an important prey item due to their higher volume (snooks = 4 cm³, guppies = 1 cm³). Snooks were also taken in greater proportion (i.e., 4%) than were available in the environment (i.e., 0.1%). Another relatively important item for the Tricolored Heron were Gobiidae (Table 1). Shrimps and crabs were prey of relatively low importance. Crabs occurred only in 1 stomach while shrimps occurred in 2 (Table 1).

Great Egrets fed mainly on fish and crustaceans (Table 1). Almost all the crustaceans found in Great Egret stomachs were shrimps, their most important prey item. Members of all 7 fish families were present in their stomachs, making fish the most important prey group. Among these, guppies and snooks were the 2 most important fish prey. Other prey items (e.g., insects, lizards) were consumed, but were less important (Table 1). Snowy Egrets fed on 4 prey families, all of which were relatively important in their diet (Table 1). Shrimps were the most important food item followed by guppies. Great and Snowy Egrets were the only 2 species in which we detected grasshoppers (i.e., Orthoptera) as food items.

Snowy and Great Egrets had the highest dietary overlap (i.e., 55%) (Fig. 2). Shrimps were the overriding item contributing to the overlap. Tricolored Herons overlapped with Snowy and Great Egrets, but to a lesser extent (i.e., 22-24%). Overlap between Tricol-

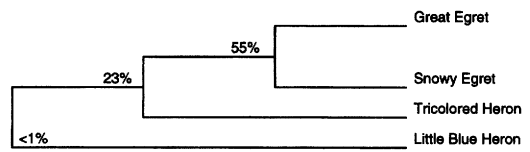


Figure 2. Dendrogram depicting percent of dietary overlap (Renkonen Index) among 4 species of wading birds collected in the mangrove swamps of the Boquerón Wildlife Refuge, Puerto Rico during the winters of 1994 and 1995.

ored Herons and Snowy Egrets was due mainly to the presence of guppies. Tricolored Herons and Great Egrets were the only ones documented to prey on snooks. Little Blue Herons did not overlap with Snowy Egrets, but did so with Tricolored Herons and Great Egrets. The degree of dietary overlap, though, was poor (i.e., < 1%), caused by a single fiddler crab in one Tricolored Heron and Great Egret stomach.

DISCUSSION

Little Blue Herons were the most specialized feeder in the study area, keying on fiddler crabs. The importance of crustaceans in the diet of Little Blue Herons was also reported by Wetmore (1916), who reported only 1 fish item, belonging to Gobiidae, in his samples. Little Blue Herons, however, are known to feed upon on a great variety of prey elsewhere (Rodgers 1983, Kent 1986, Master *et al.* 1993). Jenni (1969) concluded that Little Blue Herons were generalists and fed mainly on amphibians and fish. Kent (1986) found that Little Blue Herons were generalists, but crabs were important in their diet. It appears that in our study area, the species took advantage of an abundant resource, behaving like a specialist among generalists (Greenberg 1990).

The most abundant prey items for which field estimates were obtained, guppies and shrimps, were also the most abundant prey items found in stomachs of wading birds, except for Little Blue Heron. Similar results were reported by Jenni (1969), who found that mosquito fish (*Gambusia affinis*, Poeciliidae) was both the most abundant prey and important food item in wading bird diets in Florida. Members of Centropomidae (e.g.,

snooks), on the other hand, were the least abundant of all fish captured in the study area, but represented 2.7 and 4.1% of the total prey items in stomachs of Great Egrets and Tricolored Herons, respectively. Since prey selection is not dependent only on abundance, it is possible that the higher volume per individual made snooks a very profitable prey item (Moser 1986).

The food habits of Great and Snowy Egrets were very similar. Wetmore's (1916) report also suggest that both species shared a number of prey items including fish, grasshoppers and crabs. In contrast to our findings, these species rely almost exclusively on fish elsewhere (e.g., Ramo and Busto 1993). We believe that differences across the species' range are more a reflection of availability patterns and profitability, rather than a unique trait of the population observed in southwestern Puerto Rico or that sampled by Wetmore (1916). Tricolored Herons' similarity with Great and Snowy Egrets was not as high. The intermediate similarity values exhibited by this species probably has its basis on the fact that Tricolored Herons fed almost exclusively on fish. This is consistent with what is known about their food habits elsewhere. Jenni (1969) reported that their diet, based on volume, was made up of about 95% fish. In Mexico, the species' diet was also almost entirely comprised of fish (Ramo and Busto 1993). In both studies, fish species belonged most often to Poeciliidae. Although Wetmore (1916) examined only 1 Tricolored Heron, all prey items found were fish. Of these items, 94% were guppies.

We identified 3 foraging groups on the basis of percent diet overlap. The most conspicuous was the Little Blue Heron owing to its preference for fiddler crabs. The second group was comprised of Tricolored Herons, an almost strict piscivore. The third group was comprised of Great and Snowy Egrets, sharing nearly all prey items in their diets. Our results lend support to the possibility that resource partitioning among mixed-species foraging flocks may occur through dietary differences (see Kent 1986, Ramo and Busto 1993). In our study area, all 4 species of wading birds were observed foraging in

the same locations and time (Miranda 1995). Feeding aggregations formed early in the morning, just before sunrise, but none were recorded late in the morning or in the afternoon (i.e., after 1100 h.). The average size of wading bird aggregations was 24, ranging from groups of 4 to 70 individuals. Dietary differences may have contributed to the low percentage of interspecific aggressive interactions recorded during the study. Most (i.e., 91.7%) were directed towards conspecifics (Miranda op. cit.). The demographic implications to prey items also emerge from these data. The relative abundance of foraging wading bird species and their flocking patterns will likely influence the predation pressure they can exert on selected prey groups (e.g., fish vs. crabs). Finally, this work augmented our knowledge about the food habits of all 4 species in the tropics, where is poorly documented. It also underscored the ability of each species to exploit various prey items across their range (Kushlan 1978, Fasola 1994). This behavioral trait is advantageous when dealing with spatio-temporal fluctuations of habitat and prey availability that characterize many coastal systems (Kushlan 1978).

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