FORAGING IMPLICATIONS OF FOOD USAGE PATTERNS IN YELLOW-CROWNED NIGHT-HERONS[1]

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Abstract. Prey utilization by Yellow-crowned Night-Herons (*Nycticorax violaceus*) was examined during 1986 and 1987 in the lower Chesapeake Bay of Virginia. Nine crab species were identified in the diet with only three (*Uca pugnax, U. minax, Rithropanopeus harrisii*) representing 94% of the prey items collected. Habitat associations of the major prey species along with their high incidence in the diet suggest that these species may form highly profitable prey complexes in localized areas and that these areas represent important foraging centers in Virginia. The usage patterns of the minor prey species seem to be related to their degree of habitat overlap with the major prey species. A comparison of Virginia samples to those reported from New York and New Jersey (Riegner 1982a) reveals a discrepancy between the two sites in the occurrence of mud crabs in the diet. This discrepancy is suggested to reflect a geographic shift in the species composition of important prey complexes.

Key words: Yellow-crowned Night-Heron; Nycticorax violaceus; *diet; Chesapeake Bay; prey complex.*

INTRODUCTION

Yellow-crowned Night-Herons (*Nycticorax violaceus*) forage by using a series of slow stalking walks separated by motionless periods of visual searching (Rodgers 1983). During half- to full-tide periods yellow-crowns typically use these tactics along the edges of shallow protected bays and often stalk through partially submerged marsh vegetation. During periods of low tide they may wade through exposed muddy basins and patches of intertidal vegetation, and occasionally forage in the surf on sandy beaches (pers. observ.).

Although these herons are known to be dietary specialists on crustaceans (Palmer 1962, Hancock and Kushlan 1984), their reported use of different crab species and genera varies widely between regions (Bowdish 1902, Price 1946, Harris 1974, Niethammer and Kaiser 1983). Riegner (1982a) compared food remains collected from under 10 nests located in New York and New Jersey to the stomach contents of 120 birds collected from areas scattered over the southeastern and southcentral U.S. (Cottam and Uhler 1945). Small crabs were shown to be handled faster and more effectively than were larger crabs (Riegner 1982b), possibly explaining the

preponderance of small crab species in the diet. This suggests a mechanism for size-dependent prey selection, but does not address the preferential inclusion or exclusion of similar-sized crab species in the diet.

In this paper, I report on food remains collected from under 63 nests located on the lower Chesapeake Bay and suggest possible explanations for usage patterns. These samples are compared to samples collected from New York and New Jersey and possible explanations for the differences are discussed.

METHODS

During the breeding season, adult yellow-crowns with young use their crop to transport small crabs and other prey, which they regurgitate directly onto the nest platform for the young to consume. Several times a day, young regurgitate a bolus of crab claws (which are nearly always intact), swimming legs, and pieces of carapace. Intact claws may be identified to species and used to indicate food used by adults to rear young (see Riegner 1982a for a discussion of potential biases associated with this technique). It is assumed here that food used to rear young is reflective of adult diet.

As part of a larger study on the breeding biology of residential Yellow-crowned Night-Herons, over 2,500 crab claws were collected and identified to species from 63 nests located on five separate drainages (the Lafayette River, the

TABLE 1.   Crab claws identified from refuse samples collected from 25 stations from 1986–1987. n = total number counted, PT = percent of total, PS = percentage of stations where the species was collected, MP = mean percentage ± standard deviation—an estimate of importance breadth, calculated from the percentage of each sample represented by the species.

Species	Size (mm)[a]	n	PT	PS	MP
Uca pugnax	23	825	38.6	100.0	35.1 ± 18.14
U. minax	38	424	19.9	100.0	20.2 ± 15.28
U. pugilator	26	3	0.1	12.0	1.9 ± 1.03
Rithropanopeus harrisii	21	758	35.5	100.0	39.0 ± 21.40
Panopeus herbstii	62	14	0.7	32.0	2.1 ± 1.26
Callinectes sapidus	140	85	4.0	100.0	4.7 ± 3.53
Ocypode quadrata	50	16	0.7	8.0	9.6 ± 2.55
Hyas coarctatus	35	4	0.2	4.0	2.4 ± —
Emerita talpoida	20	7	0.3	8.0	2.4 ± 0.65

[a] Number indicates mean carapace width of large males (taken from Williams 1984).

southern branch of the Back River, the eastern branch of the Elizabeth River, Little Creek, and the Indian River) along the lower Chesapeake Bay. All nests sampled were built in 40- to 60-year-old loblolly pines (*Pinus taeda*) and positioned over or within 30 m of a residence in a heavily populated area. Claws were identified using species descriptions (Ryan 1956, Crane 1975, Williams 1984) and/or by comparison to preserved reference specimens. Claws of each species were sorted according to orientation (right or left). In species with equal-sized claws, right or left claws were used to indicate individuals depending on which were more numerous. In species with recognizable differences in claw size or structure, one claw type was chosen to indicate individuals. This procedure eliminated nearly 500 claws, resulting in a final sample of 2,136 claws which was used to assess the relative utilization of the crab species.

All claws were collected from each station in July or August of 1986 and 1987. To insure sampling consistency between nests, all claws were collected from each nest only once and as soon as possible after young had fledged. The 63 nests sampled were grouped into 25 stations according to their location. A station was comprised of a cluster of nests (ranging from one to eight) which because of their proximity would likely encounter the same foraging situations. Stations were separated by at least 3 km so that many different foraging areas were represented.

RESULTS

CRAB SPECIES UTILIZED

Nine crab species were identified from refuse samples as shown in Table 1. Ninety-four per-

cent of all claws collected were found to be from *Uca pugnax*, *U. minax*, and *Rithropanopeus harrisii*. Claws of these three species were collected from every sample station. The Atlantic blue crab was also collected from all stations but only represented 4.0% of the claws recovered, and did not account for more than 10.0% of those recovered from any station.

The five remaining crab species collectively represented only 2.0% of the total items collected. Their inclusion in the diet was inconsistent between both drainages and stations. None of these crab species was collected from more than eight stations nor represented more than 12.0% of the individuals at any station.

SPECIES CHARACTERISTICS AND MICROHABITAT PREFERENCES

The crab species that are utilized vary considerably in size as shown in Table 1. Riegner (1982b) has shown that handling time for yellow-crowns varies directly with prey size. All three of the principal prey species (*U. pugnax*, *U. minax*, *R. harrisii*) as well as *U. pugilator*, *Hyas coarctatus*, and *Emerita talpoida* are in the size category shown to be handled most efficiently. Crabs the size of *Ocypode quadrata* and *Panopeus herbstii* were handled less efficiently and species the size of *Callinectes sapidus* were handled least efficiently of those observed. Crabs of the latter size were shown to take 40 times longer to handle and were 10 times more likely to be dropped than were those of the smallest group.

Of the three crab species most collected, the substrate preferences of the two fiddler crabs overlap considerably, both preferring solid muddy sand sheltered by marsh grass within the in-
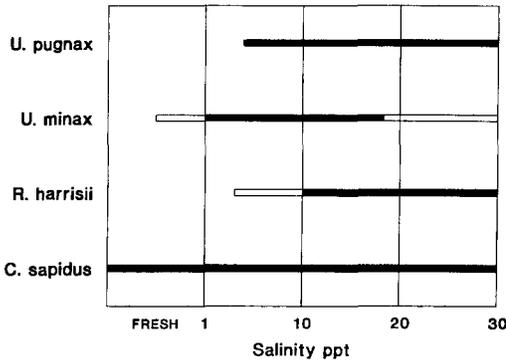
FIGURE 1. Known salinity tolerances for the principal prey species. Shaded regions represent general distribution and open regions represent marginal distribution (modified from Lippson and Lippson 1984).
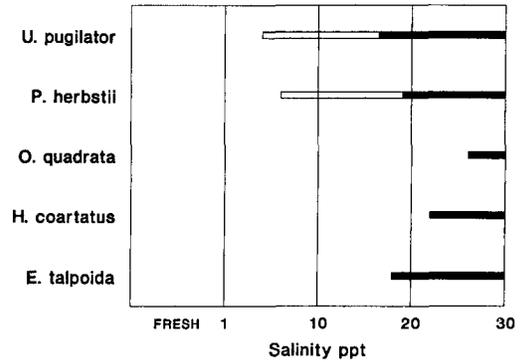

FIGURE 2. Known salinity tolerances for the minor prey species. Shaded regions represent general distribution and open regions represent marginal distribution (modified from Ryan 1956, and Lippson and Lippson 1984).

tertidal zone (Teal 1958, Crane 1975, Williams 1984). The mud crab prefers muddy bottoms with scattered debris at water depths ranging from 0–9 m (Ryan 1956). Figure 1 shows the known range of salinity tolerances for these three crab species in the bay, as well as that of the Atlantic blue crab. Clearly, the range of most intense overlap occurs between 10 and 18 ppt. All three of these species are known to be abundant in localized areas throughout the bay, but because of their habitat preference overlaps, they co-occur in small muddy-bottomed bays containing water of 10–18 ppt salinity and bordered by tidal marshes. The blue crab is abundant throughout the bay (Williams 1984) and was observed in large numbers on all drainages. Because of their abundance and wide range of habitat use, it seems that these crabs are likely to be available in all feeding areas, but that their low profitability may protect them from becoming selected prey items.

The common mud crab (*P. herbstii*) has much the same substrate requirements as the white-fingered mud crab and so likely is present in microhabitats utilized by the three major food species. This crab was collected in very low numbers from over 30.0% of the stations sampled. During a life history study of the Chesapeake Bay mud crabs, Ryan (1956) found this species to be rare in salinities from 13.95–19.04 ppt which possibly explains its widespread but infrequent occurrence in the yellow-crown diet. Figure 2 shows the known salinity tolerances for the minor prey species which together accounted for 2.0% of the total individuals (Ryan 1956, Lippson and Lippson 1984). The toad crab (*Hyas*

coarctatus) also utilizes areas overlapping those of the three crabs most collected, but its normal use of deeper water (Williams 1984) and preference for more coastal areas make it inaccessible to wading birds.

Even though the sand fiddler (*U. pugilator*), the mole crab (*E. talpoida*), and the ghost crab (*O. quadrata*) are within the size class shown to be handled most efficiently by yellow-crowns (Riegner 1982b), they were collected from only three stations. Ghost and mole crabs are found exclusively in open sandy beach habitats, and were collected from the same two stations, both of which were within 0.5 km of open beaches. The sand fiddler is considered to be very common along the Atlantic coast (Crane 1975) but only accounted for 0.1% of the diet. Colonies of this species were observed within 1.5 km of several stations but clearly prefer sandy substrates (Teal 1958, Crane 1975, Williams 1984). Although these three species may be common or abundant locally, their preference for high salinities and sandy substrates makes it unlikely that they frequently co-occur with the three principal prey species.

DISCUSSION

The high incidence of the mud fiddler (*U. pugnax*), the red-jointed fiddler (*U. minax*), and the white-fingered mud crab (*R. harrisii*) in food samples from all stations suggests that these three species are of widespread importance to Yellow-crowned Night-Herons in the lower Chesapeake Bay. The fact that these crab species differ somewhat in their microhabitat and salinity prefer-

ences (Ryan 1956, Teal 1958, Crane 1975, Williams 1984), along with their consistent importance in widely separated areas, further indicates that yellow-crowns selectively nest near and forage in areas where these three different tolerance ranges overlap. The data presented does not exclude the possibility that the herons nest near different habitats which host the crab species independently and so exploit them at different times. However, if the herons were moving between exclusive habitats and exploiting single species, then one would expect more utilization of the available sand fiddlers (assuming that they are equally profitable).

The time available for foraging in yellow-crowns is constrained by tide height. Fiddler crabs are only available to herons during a 3- to 4-hr period at low tide when they emerge from their burrows to forage and interact socially. Mud crabs are also only available at this time, when the water overlying muddy basins is shallow enough that they may be reached. In areas with muddy substrates these three species exist side by side (pers. observ.) and so together likely provide a prey-rich foraging site at low tide. The sand fiddler is found more frequently on sandy substrates in relatively high saline areas and so is not typically adjacent to large white-fingered mud crab populations.

COMPARISONS TO NORTHERN SAMPLES

Because of prey species differences between the two sample areas, it was only possible to make general comparisons. Species from both areas were grouped according to biotope from habitat descriptions by Williams (1984). Species were grouped as follows: marsh crabs—sand fiddler (*U. pugilator*), mud fiddler (*U. pugnax*), red-jointed fiddler (*U. minax*), marsh crab (*Sesarma reticulatum*); beach crabs—ghost crab (*O. quadrata*), mole crab (*E. talpoida*); mud crabs—white-fingered mud crab (*R. harrisii*), common mud crab (*P. herbstii*); bay to open water (swimming crabs)—Atlantic blue crab (*C. sapidus*), lady crab (*Ovalipes ocellatus*), green crab (*Carcinus maenas*), rock crab (*Cancer irroratus*), toad crab (*Hyas coarctatus*). These groupings are not meant to suggest that overlaps do not occur. Results of tabulations are shown in Table 2.

Although there is close agreement between the two regions as to the frequency of beach and swimming crabs in the diet, there is a clear discrepancy in the representation of mud crabs.

TABLE 2. Crab groups utilized in northern and Chesapeake Bay areas (see text). Species were grouped according to biotope from descriptions by Williams (1984).

Crab group	Chesapeake Bay		Northern	
	Number	%	Number	%
Marsh crabs	1,252	58.6	1,351	95.5
Beach crabs	23	1.1	—	—
Mud crabs	772	36.1	5	0.4
Bay to open water (swimming crabs)	89	4.2	58	4.1
Total	2,136		1,414	

Much of the nearly complete emphasis on marsh crabs evident in the northern areas has been replaced by the mud crab group in the Chesapeake Bay.

FORAGING IMPLICATIONS

Over a regional area, prey species are distributed in an orderly fashion according to the spatial distribution of individually preferred microhabitats. When many potential prey species are sympatric on a regional scale it is very likely that overlaps in the preferences for particular biotic and physical parameters will lead to the formation of regular and predictable prey assemblages on a local scale. If these assemblages are composed of species which are individually profitable to foragers, then the multispecies prey complex formed may be exceedingly profitable. When the occurrence of these complexes are regionally common and associated with a particular microhabitat such that they are easily located, the habitats may become "foraging centers" which are exploited extensively.

It appears from the habitat associations of the principal prey species and their disassociation with the habitats of relatively unimportant prey species that yellow-crowns are selectively feeding in foraging centers containing highly profitable prey complexes. If this is true, the inclusion of minor prey species in the diet may be more accurately predicted by their association with or proximity to the selected prey complex than by their individual profitabilities. This would seem to suggest that profitability is appropriate for considerations of within-habitat prey choice (see Pyke et al. 1977, Krebs et al. 1983, Stephens and Krebs 1987) but may be inappropriate on a spatial scale larger than that of the foraging center.

For predicting prey use and preferred feeding areas on a regional scale, emphasis should be shifted to the collective profitabilities of species forming prey complexes. In effect, when feeding areas are spatially disjunct, areas hosting highly profitable species assemblages should be utilized more often than areas containing less profitable assemblages. On a regional scale, this may lead to the exclusion of some of the most profitable species from the diet due only to their distribution relative to particular prey assemblages.

This would explain the diet patterns observed. The sand fiddler, which was locally available and nearly indistinguishable from the mud and red-jointed fiddlers in every way except distribution, was used less than any other species collected. The blue crab, thought to be the least profitable of the species utilized, was collected from every station. I suggest that the blue crab was included in the diet not strictly because of its own profitability, but because of its close association with the prey complex. The sand fiddler, which is most likely equally as profitable as the other two species in the genus, was not included in the diet because it was not associated with the proposed foraging center.

There is at present no reason to assume that species assemblages which are formed and maintained in one area will be stable over a wide geographic range. Differences in parameter preferences between species as well as geomorphological and community differences between regions would in fact suggest that this is unlikely. Species which associate with a particular group of species in one area may associate with a completely different set in another, leading to regional differences in the species composition of available prey assemblages.

One extension of the idea that the species complex is utilized as a unit is that a prey species may differ geographically in its relative importance in the diet not because of changes in abundance but because of differences in its species associations. The fact that the sand fiddler was an unimportant prey species in the bay does not eliminate the possibility that it may be utilized extensively further south where there are many more salt tolerant species with which it associates. In the bay the white-fingered mud crab and two fiddler crab species were important in the diet and suggested to be closely associated. Even though all three species range north to Canada, the mud crab was completely absent in the north-

ern samples although fiddler crabs represented 81.0% of the diet. Even if one assumed a drastic reduction in the abundance of this mud crab in the north, one would still expect some presence in the northern samples if in the north it remained as closely associated with the fiddlers as it appears to in the bay.

Foraging ecologists have typically utilized a reductionist approach to predict prey utilization, by considering prey communities to be aggregations of species existing independently. This simplifying assumption intuitively seems justified as long as the distributions of all potential prey species are either completely correlated or completely independent. When, however, the distributions of individual prey species are correlated with some but not all of the other potential prey species, herons may select foraging areas based on the presence of prey complexes rather than individual species. This may lead to the disuse of entire groups of desirable prey due to their lack of association with the prey complex. Further, when species correlations change between geographic regions, profound shifts in the importance of particular prey species in the diet may occur irrespective of their availabilities.

Herons in the Chesapeake Bay are faced with spatial foraging decisions limited by the distribution of water-dependent resources. Because of the fresh- and saltwater structure of the bay, habitats with very different characteristics may exist in close proximity. The complex of species which assemble within these habitats determines their value to foragers. I suggest that Yellow-crowned Night-Herons within the bay are selectively choosing from among a collage of possible feeding areas, to forage in areas containing the three-species complex evident in the diet. And further, I suggest that the location of other potential prey species relative to this complex largely determines their usage patterns. Certainly, other viable explanations exist which may explain the usage patterns observed in the bay as well as the discrepancies between the northern and bay samples. Detailed dietary observations for disjunct populations which encounter different potential prey groups are needed to address these questions more fully.

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