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Trophic Niche Breadth and Overlap of Three Egret Species in a Neotropical Mangrove Swamp

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Abstract.—Empirical studies testing the predictions of theoretical models on interspecific competition are scarce. The present study focused on the effects of competition on trophic niche by: (1) analyzing temporal changes in the diet of Snowy Egret (*Egretta thula*) on a Brazilian mangrove swamp before and after its breeding site was colonized by two congeners, Little Blue Heron (*E. caerulea*) and Tricolored Heron (*E. tricolor*); and (2) comparing spatial changes in the diet of the three egret species at the study site with six additional localities from the literature. Nestling boluses were analyzed in the 1993 and 1994 breeding seasons, when Snowy Egret was the only species in the area, and in 1995 and 1996, when the two other species were present. At the study site, although Snowy Egret consumed a greater proportion of molly fish (*Poecilia* spp.) than the two other egrets, all egrets fed mainly on mollies and shrimps, providing grounds for competition and trophic interference. However, contrary to the predictions of trade-off models, the Snowy Egret's trophic niche enlarged when the area was colonized by the other two egrets, suggesting that environmental variability is more relevant than competition in shaping trophic niche. The three egrets fed on similar resources to those found at other sites collated from the literature. Tricolored Heron appeared the most specialized species, showing a consistent, mangrove-related diet; Snowy Egret had a similar, but more variable diet, and Little Blue Heron showed the greatest trophic diversity, with a highly variable diet between sites. Overall, temporal and spatial variability in the trophic niches of egrets better match an independently-evolved pattern of resource use rather than predictions from competitive models of niche coevolution. *Received 5 July 2007, accepted 20 January 2008.*

Key words.—competition, *Egretta caerulea, Egretta thula, Egretta tricolor*, Little Blue Heron, niche breadth, niche shape, niche overlap, Snowy Egret, Tricolored Heron.

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Sympatric and closely-related species often occupy similar niches, providing opportunities for competition, which, in a classical view, could lead to the partitioning of their niches (Odum 1971; Arthur 1987; Pianka 2000). Whether interspecific competition of closely-related species may ultimately shape the trophic structure of animal communities has long been a major issue in ecology, but its role is still poorly understood. Different models have been proposed to explain whether and how niche structure and species assemblages relate to each other (Wiens 1992; Pianka 2000; Hubbell 2001; Tilman 2004). When two or more coexisting species overlap their niches, trade off models predict an active segregation of their niches (Pianka 2000), followed by an increase in niche overlap and relaxed competition in periods of greater resource abundance (Wiens 1992). Conversely, neutral models follow a different approach, based on dispersal-assembly instead of niche-assembly (Hubbell 2001). Under this paradigm, species do not shape each others niche, but occur in the ecosystems in a competitive-neutral way; the presence or absence of species depending mainly on their own strategy of survival and dispersal. Some of the current ecological debate points to the differences between these models (Tilman 2004), but other approaches are feasible, namely the role played by every species in the ecosystem (not merely its presence or absence, as neutral models do) may be studied from the pre-extant ecological strategies of this species when a new area is colonized.

Empirical studies testing predictions of these various models remain scarce. On an ecological scale, the effects of competition in natural environments can be approached by comparing the niche of a given species when competitors are present and when they are absent. This can be conducted in either the spatial or the temporal dimension. In a spatial dimension, we can compare the trophic niche of the species among areas in which competitors are present and others in which

they are absent. In a temporal dimension, we can compare changes in the trophic niche of the species before and after the competing species colonize the area.

In this study, I tested whether the occurrence of three closely-related egret species modified the structure of the trophic niche in the absence and presence of the congeners. Temporal changes in the diet of the Snowy Egret (*Egretta thula*) breeding in a Brazilian mangrove swamp were studied before and after the area was colonized by two other egrets, Little Blue Heron (*E. caerulea*) and Tricolored Heron (*E. tricolor*). From 1992 to 1994, the Snowy Egret was the only one of the three species to breed in the area; the two remaining species colonized the area in 1995 (Martínez and Rodrigues 1999; Martínez 2005) and all three species bred at the site until at least 2006 (pers. obs.). Also, I collated literature data on the diet of the three egret species from six localities in the Americas and compared changes in their diet (Jenni 1969; Miranda and Collazo 1997; Acosta 1998; Olmos *et al.* 2001; Maccarone and Brzorad 2002). Most egret species are gregarious and easy to observe, so various studies in the literature focus on their biology, and in particular the diet and trophic niche (Kushlan 1978; Kushlan and Hancock 2005).

METHODS

Study Site

Fieldwork was carried out on Cajual Island in the state of Maranhão, northeastern Brazil. The island is a 6,000 ha site (2°26'S; 44°30'W) in a region characterized by broad belts of mangrove forests and extensive intertidal mudflats. The complex includes freshwater ecosystems, forming a mosaic landscape with a strong saline gradient (see Martínez 2004 for details). Maximum tidal amplitude reaches 8.16 m (Mabesoone and Coutinho 1970). Rebelo-Mochel (1993) estimated mangrove vegetation cover in Maranhão at approximately 500,000 ha. The breeding egrets and herons forage in mangrove and freshwater areas, both on the island and the neighborhood. Snowy Egrets numbered approximately 600 breeding pairs from 1993 to 1996. The other two egret species, Little Blue Heron and Tricolored Heron, were absent in 1993-94, but there were approximately 100 to 150 pairs each in 1995-96 (Martínez 2005).

Sampling

Spontaneously regurgitated boluses from nestlings were collected twice a week on Cajual Island. Such boluses are the least biased food sample for diet studies (González-Solís *et al.* 1997). Overall, I analyzed 34 and 47 Little Blue Heron boluses, 34 and 46 Tricolored Heron boluses and 79 and 56 Snowy Egret boluses collected in 1995 and 1996, respectively. Previously, 26 and 61 Snowy Egret boluses were collected in 1993 and 1994, respectively, when the other two egret species were absent from the site. Prey items were identified and quantified by counting preserved pieces (Brown and Ewins 1996) and through comparison with specimens from reference collections. To estimate the biomass of the prey items, measurements of total or partial length of prey were taken and compared with length-mass regression functions calculated for every taxon.

Statistics

Prey items were classified according to the following three main categories: Taxon (at family level), Size and Habitat (Saltwater, Euryhaline, Freshwater, Terrestrial and Aerial). The frequencies of every prey class in the Taxon and Habitat categories over all the prey items were calculated as percentages. Classification by Size was defined in a logarithmic scale of prey biomass, since the prey biomass follows a lognormal distribution (Martínez *et al.* 1992). All the consumed prey fell into four classes, as follows: class A, 11 to 100 g.; B, 1.1 to 10 g.; C, 0.11 to 1 g; and D, 0.011 to 0.1 g.

Trophic niche breadth was estimated through the Brillouin's Index of Diversity, an unbiased estimator, with no assumptions about the sampling method; accumulated diversity functions were calculated in order to compare the diversity between species (Pielou 1975). These functions were jack-knifed (Zahl 1977), which allowed their statistic comparison (Hutcheson 1970). Spatial niche breadth was measured by using Levins' Index (Levins 1968; Krebs 1999). *t*-tests for comparison of means were performed to measure the confidence intervals of the differences between years and species regarding the mean biomass of prey. Niche overlap was estimated using Morisita's Index (Morisita 1959), the least biased index when studying prey items (Krebs 1999).

The frequencies of prey items for every class of the Taxon and Habitat categories were compared between years and species by using the *G*-test (Sokal and Rohlf 1995). When significant differences in the global analysis were found, the studentized residuals showed which prey classes produced the main effects. The values reported below are means ± SD.

RESULTS

Snowy Egret

The main prey consumed were mollies (*Poecilia* spp.), a small euryhaline fish (Tables 1 and 2). As the main prey predominated, diet diversity was low (Table 3). The mean biomass of prey items was 0.53 ± 1.33g; 82% of items fell into class D (0.11 to 1g) (Fig. 1).

Comparing the four sampling seasons, mollies were the most important item every

Table 1. Taxonomic classification of prey consumed by Snowy Egret, Little Blue Heron and Tricolored Heron on Cajual Island.

	Snowy Egret					Little Blue Heron			Tricolored Heron		
Prey	1993	1994	1995	1996	TOTAL*	1995	1996	TOTAL	1995	1996	TOTAL
CRUSTACEA											
Penaeidae	0,6	0,8	**7,0**	2,4	4,8	4,5	2,2	3,2	**16,5**	**6,3**	**10,3**
Alpheidae			0,1		0,1				1,1	2,2	1,8
Grapsidae		0,1	0,4		0,2		1,0	0,6	0,5	0,3	0,4
ARACHNIDA											
Araneae i.s.			0,5	0,2	0,4		2,5	1,4	0,1	0,9	0,6
INSECTA											
Odonata i. s.	0,2	0,5	1,4	0,4	0,9	0,3	0,6	0,4	1,1	0,9	0,9
Locustidae	0,6	0,3	0,1		0,1	0,1	0,3	0,2		0,1	0,1
Gryllidae				0,2	0,1						
Hemiptera i. s.			0,1	0,1	0,1		0,2	0,1			
Diptera i. s.		0,3	0,5	1,4	0,9	0,4		0,2	0,1	0,2	0,2
Lepidoptera i.s.							0,2	0,1			
Coleoptera i. s.		0,1	0,1		0,1	0,1	0,1	0,1			
TELEOSTEI											
Elopidae	0,1	0,5									
Clupeidae	0,8	0,3	0,1	1,7	0,8	2,7		1,2	0,1	0,2	0,2
Engraulidae		0,8	0,1	0,1	0,1		0,5	0,3			
Characidae		0,9	0,4	3,0	1,6	3,4	**12,3**	**8,7**	0,8	1,9	1,5
Erythrinidae						0,3	0,2	0,3			
Merluccidae		0,1		0,1	0,1	0,4	0,1	0,3	0,3	0,5	0,4
Soleidae										0,1	0,1
Poeciliidae	**97,7**	**94,7**	**85,0**	**90,2**	**87,5**	**76,4**	**77,5**	**77,0**	**62,1**	**72,6**	**68,5**
Rivulidae		0,5	4,1	0,4	2,3	7,2	1,0	3,8	2,7	7,7	5,7
Mugilidae		0,1	0,2		0,1	1,7	0,1	0,8	0,3		0,1
Cichlidae						0,9	0,5	0,7		0,2	0,1
Gobiidae						1,6		0,7	14,5	5,8	9,2
Leptodactylid.							0,2	0,1			
N	894	766	1844	1687	3531	708	884	1592	754	1165	1919

In bold, values over 5%.
*data only from 1995 and 1996.

year (Table 1), ranging from 85.0% (1995) to 97.7% (1993). Interannual differences were significant for the taxonomic prey study (G_{18} = 382, p < 0.001). Residual values show that differences were mainly due to mollies, which were more abundant in 1993 and 1994 compared to 1995. Also, diet composition by habitat showed significant differences (G_{15} = 199, p < 0.001); the residuals showed that freshwater prey was more abundant in 1995 and 1996 than in 1993 and 1994.

Diet diversity was significantly greater in 1995 than in 1996 (t_{133} = 6.16, p < 0.001) (Table 2). Mean prey biomass did not differ between years.

Snowy Egret Diets in 1993-94 versus 1995-96

In 1993-94, the main prey item was significantly more abundant in the diet composition than in 1995-96 (Table 1; G_9 = 124, p < 0.000001). Residuals show that in 1995-96 the consumption of shrimps, rivulids and characids increased, whereas mollies decreased. Overall diet diversity was significantly greater in 1995-1996 (0.42 ± 0.07) than in 1993-1994 (0.91 ± 0.12) (Table 3; t_{253} = 40.35, p < 0.001).

Tricolored Heron

The species fed mostly on euryhaline mollies (Table 1). However, other prey items were more also important, especially shrimps (Penaeidae and Alpheidae) and gobid fishes (*Gobionellus* sp.). Strictly marine animals accounted for 22.3% of all prey (Table 2). Diet diversity was higher than that of Snowy Egret (Table 3). The mean biomass of prey was 0.52 ± 0.71g. 82% of prey items belonged to class D (Fig. 1).

Interannual differences in prey taxa were significant (G_6 = 105, p < 0.001). Residuals showed that mollies and rivulids were more abundant in 1996 than in 1995, whereas shrimps and gobids were more abundant in 1995 than in 1996 (Table 1). Prey by habitat also showed significant differences (G_6 = 116, p < 0.001); freshwater prey was more abundant in 1996 than in 1995,and marine prey showed the opposite trend. Diet diversity was significantly greater in 1995 than in

Table 2. Habitat classification of prey consumed by Snowy Egret Little Blue Heron and Tricolored Heron on Cajual Island.

	Snowy Egret					Little Blue Heron			Tricolored Heron		
Prey	1993	1994	1995	1996	TOTAL*	1995	1996	TOTAL	1995	1996	TOTAL
Saltwater	1,6	2,6	7,7	4,2	6,0	9,2	3,9	6,2	**32,9**	**15,5**	**22,3**
Euryhaline	**97,7**	**94,8**	**85,2**	**90,2**	**87,6**	**78,1**	**77,6**	**77,8**	**62,3**	**73,5**	**69,1**
Freshwater	0,2	1,8	5,4	5,0	5,2	**12,4**	**15,4**	**14,1**	3,6	9,4	7,1
Terrestrial	0,6	0,3	0,7	0,6	0,6	0,1	2,9	1,7	0,1	1,0	0,7
Aerial		0,5	1,1		0,6	0,1	0,2	0,2	1,1	0,6	0,8
N	894	766	1844	1687	3531	708	884	1592	754	1165	1919

In bold, values over 10%.
*data only from 1995 and 1996.

Table 3. Brillouin's Diversity based on the taxonomic prey classification of the diet of three *Egretta* species from 1993 to 1996 on Cajual Island. Values report means ± Standard Error (n). SE was estimated from a jackknife technique.

Diet diversity	Snowy Egret	Little Blue Heron	Tricolored Heron
1993	0.22 ± 0.09 (894)	—	—
1994	0.48 ± 0.10 (766)	—	—
1995	0.98 ± 0.16 (1844)	1.53 ± 0.30 (708)	1.87 ± 0.26 (754)
1996	0.74 ± 0.15 (1687)	1.39 ± 0.27 (884)	1.66 ± 0.30 (1165)
TOTAL	0.91 ± 0.12 (3531)*	1.54 ± 0.22 (1592)	1.75 ± 0.21 (1919)

*Total results for the Snowy Egret were calculated from the 1995-1996 period only.

1996 (t_{78} = 3.34, $p < 0.005$) (Table 3). Mean prey biomass was slightly but significantly greater in 1995 (0.58 g) than in 1996 (0.48 g) (t_{1917} = 2.47, $p < 0.02$).

Little Blue Heron

The species fed mostly on mollies. Larger-sized characid freshwater fish accounted for a large proportion of prey. Diet diversity values were similar to those of the preceding species (Table 3). Mean biomass of prey was slightly greater than that of the other species (0.71 ± 1.20 g) and 72% of prey items belonged to class D (Fig. 1).

Interannual differences in the prey taxa were significant (G_8 = 172, $p < 0.001$). In this case, residuals showed that differences did not arise from the main prey (mollies), but from differences in shrimps, rivulids and mullets frequencies, which were more abundant in 1995, and characids in 1996 (Table 1). There were also significant differences by habitat (G_8 = 53, $p < 0.001$); as in the case of Tricolored Heron, freshwater prey were more abundant in 1996 than in 1995, and marine prey showed the opposite trend. The diversity of diet was significantly greater in 1995 than in 1996 (t_{79} = 2.16, $p < 0.05$) (Table 3). Mean prey biomass was 0.70 g. in 1995 and 0.71 g. in 1996.

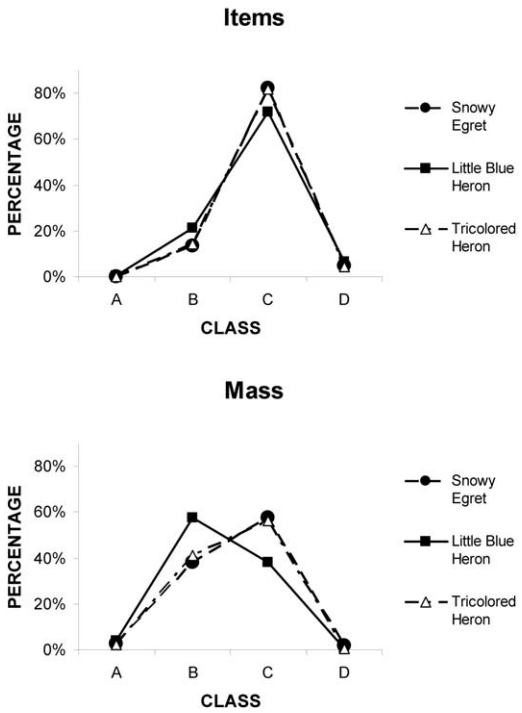

Figure 1. Percentages for each size class of prey in the diet of Snowy Egret, Tricolored Heron and Little Blue Heron on Cajual Island. Class A, largest prey items, from 11 to 100 g.; class B, from 1.1 to 10g.; C, from 0.11 to 1 g; and D, from 0.011 to 0.1 g. Graph above: percentage of every size class over the total number of prey items. Below: percentage of every size class over the total biomass consumed.

Interspecific Diets and Niche Comparison

Overall, the three egret species fed mostly on mollies of approximately 0.5 g, shrimps being the only additional item in relevant amounts for all the species. However, the diet composition of the three species differed significantly, both when the prey were grouped by taxonomic level (G_{24} = 4257, $p < 0.001$) and by habitat provenance (G_{18} = 3653, $p < 0.001$). Residuals showed that Snowy Egret consumed more mollies than the other species, Little Blue Heron more characid fish, and Tricolored Heron more shrimps and gobid fish (Table 1). Snowy Egret consumed more euryhaline prey, Little Blue Heron more freshwater prey, and

Tricolored Heron more saltwater prey (Table 2). Tricolored Heron showed the greatest niche breadth, which significantly differed from both Snowy Egret ($t_{433} = 40.59$, $p < 0.001$) and Little Blue Heron ($t_{159} = 6.19$, $p < 0.001$). The niche breadth for Little Blue Heron was also greater than Snowy Egret ($t_{334} = 28.33$, $p < 0.001$).

Little Blue Heron consumed larger prey than the other species. Mean prey biomass was significantly different from the other species (Snowy Egret, $t_{6939} = 4.991$, $p < 0.01$; Tricolored Heron $t_{3509} = 5.48$, $p < 0.01$). The Snowy Egret and the Tricolored Heron showed no significant differences in prey size ($t_{7266} = 0.49$, n.s.) (Fig. 1).

When results were compared annually, diet composition of the three species was consistently different, both in 1995 ($G_{12} = 522$, $p < 0.001$) and 1996 ($G_{14} = 477$, $p < 0.001$). Residuals showed that the prey categories accounting for the main differences were the same in both years, as well as in the global comparison. Niche overlap was high in all cases, but in 1996 was lower than in 1995 (Table 4). All egrets reduced their niche breadth significantly in 1996 (Table 3), and consumed more saltwater prey in 1995, and more freshwater prey in 1996.

DISCUSSION

All three egret species in this study inhabit mangrove swamps, although Tricolored Heron is the main specialist in coastal habitats. The Tricolored Heron and Snowy Egret feed mostly on small fish, but Snowy Egret may choose shrimps as the main prey; Little Blue Heron focuses its diet on, variously, fish, amphibians or crustaceans at different sites (e.g. Kushlan and Hancock 2005).

On Cajual Island, preliminary indications were that the three egret species consumed similar prey. That is, all fed primarily on mollies and secondarily on shrimps, and showed high niche overlap. Nevertheless, there were consistent differences between species, with Snowy Egret having the largest proportion of mollies in its diet, Tricolored Heron with a greater proportion of shrimps and other marine prey, and Little Blue Heron feeding on a greater proportion of freshwater and slightly larger prey than the other two species.

Snowy Egret, over the period 1995-96, when competitors were present, showed significantly greater diet diversity than in preceding years, when they were absent. Such a result is not consistent with classical trade-off models: these models may fit the observed overlap patterns, as they predict high overlaps and relaxed competition in periods of greater resource abundance (Wiens 1992) but they would predict a decrease (never an increase) in the niche breadth in such circumstances (e.g. MacArthur and Pianka 1966; Wiens 1992). The data suggest that changes in the Snowy Egret's diet between

Table 4. Morisita's Niche Overlap for three *Egretta* species on Cajual Island. Overlap in 1995 (above), 1996 (middle) and global analysis (bottom).

	Snowy Egret	Little Blue Heron	Tricolored Heron
1995			
Snowy Egret	1		
Little Blue Heron	0,866	1	
Tricolored Heron	0,743	0,728	1
1996			
Snowy Egret	1		
Little Blue Heron	0,840	1	
Tricolored Heron	0,784	0,806	1
TOTAL			
Snowy Egret	1		
Little Blue Heron	0,867	1	
Tricolored Heron	0,795	0,802	1

years could arise from minor environmental variations rather than competition. The interpretation is supported by a consistent change in the three species, from a greater consumption of saltwater prey and a greater diet diversity in 1995 to freshwater prey and lower diversity in 1996.

The common pattern shared by the three egrets in Cajual (mostly cyprinodontiforms, and secondly shrimps) was found for some of them at other sites in the Americas where the three species breed sympatrically, such as Florida (Jenni 1969), Puerto Rico for the Tricolored Heron and partially the Snowy Egret (Miranda and Collazo 1997) and Cuba for the Tricolored Heron and the Snowy Egret (Acosta 1998). Thus, Tricolored Heron showed a similar pattern in all sites (including this study) and Snowy Egret also showed a similar pattern in most sites, except that shrimps were more frequently eaten than cyprinodontiforms in Puerto Rico. Apparently, Tricolored Heron, rather than Snowy Egret could be the main predator of mollies and related fish along the different sites. As Tricolored Heron shows the most coastal pattern of distribution, being usually associated with mangroves, the true specialization of this bird could actually be in the use of mangrove resources, as opposed to a particular type of prey. In Puerto Rico, both mollies and shrimps were available, and yet Snowy Egret and Tricolored Heron showed different patterns of usage. Little Blue Heron showed the highest diversity of patterns between sites, changing from a diversity of fish (Cuba), only fiddler crabs (Puerto Rico) or a complex pattern similar to the other birds (Florida and this study).

In the USA, Maccarone and Brzorad (2002) studied Snowy Egret in New York City and Wichita, Kansas, where Tricolored Heron was absent and Little Blue Heron was rare as a breeding species (Alan Maccarone, pers. comm.); Snowy Egret fed on different amounts of fish and crustaceans (largely cyprinodontiforms and shrimps) at coastal and inland sites. In Southern Brazil, Olmos *et al.* (2001) studied Little Blue Heron: Tricolored Heron being extralimital and the Snowy Egret rare as a breeding species (Olmos and Silva 2003); Little Blue Heron consumed mainly grapsid crabs, compared to fiddler crabs in Puerto Rico, confirming a highly variable pattern between sites. Miranda and Collazo (1997) argued that this species behaved as a generalist elsewhere (Rodgers 1983; Kent 1986; Master *et al.* 1993) but focused on fiddler crabs in Puerto Rico as they were readily available. However, fiddler crabs are found in high densities both on the São Paulo coast (Olmos *et al.* 2001) and Cajual Island (Martínez 2004). In both Brazilian sites, the fiddler crabs were strongly sought after by Scarlet Ibis (*Eudocimus ruber*), and virtually ignored by the Little Blue Heron.

In summary, Snowy Egret seems to use a low diversity of food items, foraging in a high diversity of habitats, Tricolored Heron shows a narrow niche associated with mangrove forests, and Little Blue Heron shows an intermediate spatial niche breadth, and a greater diet diversity than the two other egrets. In general, changes along time and between sites in Snowy Egret diet seem more dependent on the site conditions than on the presence or absence of potential competitors. Thus, this species shows a general pattern of niche structure which locally adapts to particular conditions, rather than a competition-made niche shape.

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