Reproductive Success of Three Species of Herons Relative to Habitat in Southern Florida

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Abstract.—We compared numbers of nesting pairs, clutch size, nest success, and production of young of Tricolored Herons (*Egretta tricolor*), Little Blue Herons (*E. caerulea*) and Snowy Egrets (*E. thula*) breeding in freshwater, estuarine, and marine habitats of southern Florida between 1986 and 1989. Tricolored Herons were commonest in marine habitats, while Snowy Egrets and Little Blue Herons were most common in estuarine and freshwater habitats, respectively. Among Tricolored Herons, we found no evidence for consistent differences in laying date among the three habitats, and no relationship between clutch size and laying date. Among Tricolored Herons and Snowy Egrets, clutch sizes were larger in freshwater areas than in either of the two saline habitats, with no consistent differences in clutch size between marine and estuarine locations. Survival of nests was consistently higher in freshwater and marine than in estuarine habitat, an effect largely attributable to heavy egg predation by Common Crows (*Corvus brachyrhynchos*) in estuarine colonies during incubation. Fledging success of Snowy Egrets and Tricolored Herons also was consistently higher in freshwater habitats than in either of the saline habitats. Thus, freshwater habitats showed generally increased nesting success and productivity over saline ones. Potential explanations for these differences among habitats include increased nest predation in estuarine colonies, a degrading estuarine and marine food web in the region, and the energetic constraints of salt excretion. *Received 23 April 1992, accepted 3 September 1992.*

Key Words:—Ciconiiformes, *Egretta spp.*, Everglades, freshwater habitat, marine habitat, predation, reproductive success, salt tolerance, wading birds.

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Measures of reproductive success in long-legged wading birds (Ciconiiformes) are known to vary widely depending on species, location, degree of predation, and environmental conditions (Milstein *et al.* 1970, Kushlan *et al.* 1975, Ogden *et al.* 1980, Powell 1983, Shields and Parnell 1986, Frederick and Collopy 1989a,b, Bildstein *et al.* 1990). Among White Ibises (*Eudocimus albus*), one of the most consistently noted effects is a reduction in clutch size at colonies in marine or estuarine habitats compared with freshwater ones (Rudegeair 1975, Kushlan 1977, Frederick 1987). In addition, a comparison of a number of studies of both Tricolored Herons and Snowy Egrets suggests a similar trend towards reduced clutch size in marine habitats (Maxwell and Kale 1977, Rodgers 1978, Girard and Taylor 1979, Hammatt 1981, Black *et al.* 1984, Bjork 1986).

The cause of the differences in clutch size is not known. Kushlan (1977) suggested that increased energy expended in excreting salt reduced the energy available for egg formation in coastal-breeding White Ibises. Rudegeair (1975) felt that reduced clutch size in an offshore ibis colony was due to the additional flight energy expended in trips between a White Ibis colony and foraging grounds, and showed that coastal breeders made fewer feeding trips per day during the nestling period than did freshwater breeders.

While the comparisons to date suggest that depressed clutch size is associated with saline habitat, the confounding effects of timing of nesting, location, or predation upon clutch size have not been examined (Winkler and Walters 1983). It is also unknown whether other aspects of reproduction differ consistently between coastal and freshwater heronries, or whether the clutch size differences translate into differential production in the two types of habitats (Kushlan 1977). Bildstein *et al.* (1990) showed that the availability of freshwater habitats was critical to breeding success in White Ibises in coastal South Carolina because nestlings were intolerant of the salt load incurred by eating marine crustaceans.

Here we present a comparison of nesting numbers, clutch sizes, survival of nests, and numbers of young produced, in herons of the genus *Egretta* nesting in three wetland habitats with different salinities in southern Florida. The birds nesting in this region are largely migratory and show relatively little breeding site fidelity (Ogden 1978). Thus, choice of nesting habitat within southern Florida is not likely to be constrained by geography or philopatric tendencies. Because our measurements of reproductive success were recorded relatively synchronously, we can control for effect of year and timing of nesting, and investigate effects of location on reproductive performance.

METHODS

We monitored nesting by Tricolored Herons (*Egretta tricolor*), Little Blue Herons (*E. caerulea*) and Snowy Egrets (*E. thula*) in three ecologically distinct wetland zones of the southern Florida peninsula (Fig. 1). Freshwater areas are located in Water Conservation Area 3, and freshwater marsh sections of Everglades National Park, and are dominated by grasslands interspersed with tree islands. These habitats are seasonally inundated (up to 1.5 m) by fresh water. Estuarine colonies were located in a mosaic of wetlands fringing the southern tip of the Florida peninsula. These wetlands extended from the coastline 4 - 15 km inland, were dominated by mangroves, and lay entirely within the boundary of Everglades National Park. Marine colonies were located on islands in Florida Bay, a seasonally hypersaline embayment between the mainland tip of the Florida peninsula and the Florida keys. Studies of foraging dispersal suggest that birds nesting in freshwater habitat forage there almost exclusively, and that birds in marine and estuarine habitats feed primarily in the latter two habitat types (Frederick and Collopy 1988, Powell and Bjork 1990, Bancroft *et al.* 1990).

Within these areas, we monitored nesting dispersion through aerial surveys and ground counts. Colonies were located and total counts of nests were made at least once in any nesting season to estimate peak nesting numbers and fates of entire colonies. Not all habitats were monitored in all years, however, and we examine percentage usage only in those years during which all three habitats were monitored (see Table 1).

We also measured reproductive success by repeatedly visiting active nests marked individually with surveyor's flagging, along belt transects within a number of the largest colonies in each habitat. Nests were first visited within a week following the initiation of egg laying during the spring, and transects were oriented so that they included nests on the edge and in the center of each aggregation. If the colony was small, all nests were marked; if large, we marked all those we could reach in 1 h. Contents of all marked nests were noted during visits once every four to six days. All nests were monitored until they failed, or until at least one young reached an age of 14 d, at which point they were categorized as successful. While young *Egretta* herons may be dependent upon their parents in the colony for another 40 d, young began to leave the nest beyond this age, and could no longer be reliably censused (McVaugh 1972, Werschkul 1979, Frederick *et al.* in press).

We express nesting success as the probability of any nest remaining active through a given period (maintaining at least one egg during incubation, or producing at least one young to an age of 14 d during the nestling stage), as calculated using Mayfield's (1961, 1975) method, and combined period estimates according to Hensler and Nichols (1981). An incubation period of 22 days was used in all calculations (McVaugh 1972, Bjork 1986, Frederick and Collopy 1988).

Mean clutch size was calculated from those nests which had survived a minimum of 8 d and could be identified accurately to species. Fledging success was expressed as the number of young per successful nest.

We compared differences in reproductive parameters among habitats, keeping analyses separate by year and species. Since clutch size and fledglings per successful nest are neither continuous nor normally distributed, we compared these variables using Mann-Whitney U tests (Siegel 1956). We evaluated differences in nest success using Z - tests (Hensler and Nichols 1981).

In order to portray the results of these multiple tests, we looked at the number of tests that were significant in the expected direction divided by the total possible number of tests. In addition, the results of multiple tests of the same hypothesis in different years were combined to give a single probability ("combined probability", see Sokal and Rohlf 1981:780).

To see if clutch size was related to laying date, we analyzed the Tricolored Heron data, for which sufficient sample sizes were available. We ran separate ANOVA's for each colony, and also blocked the nesting date data by treatment (clutch size, colony, and habitat, all colonies in all habitats, unbalanced Type IV ANOVA).

Note that sample sizes and area-specific reproductive statistics are given by year in Appendix 1.

RESULTS

The Tricolored Heron was the only species consistently more numerous in marine colonies than elsewhere (mean of 59.3%, n = 3 years, see Table 1), and was much more numerous in saline (marine

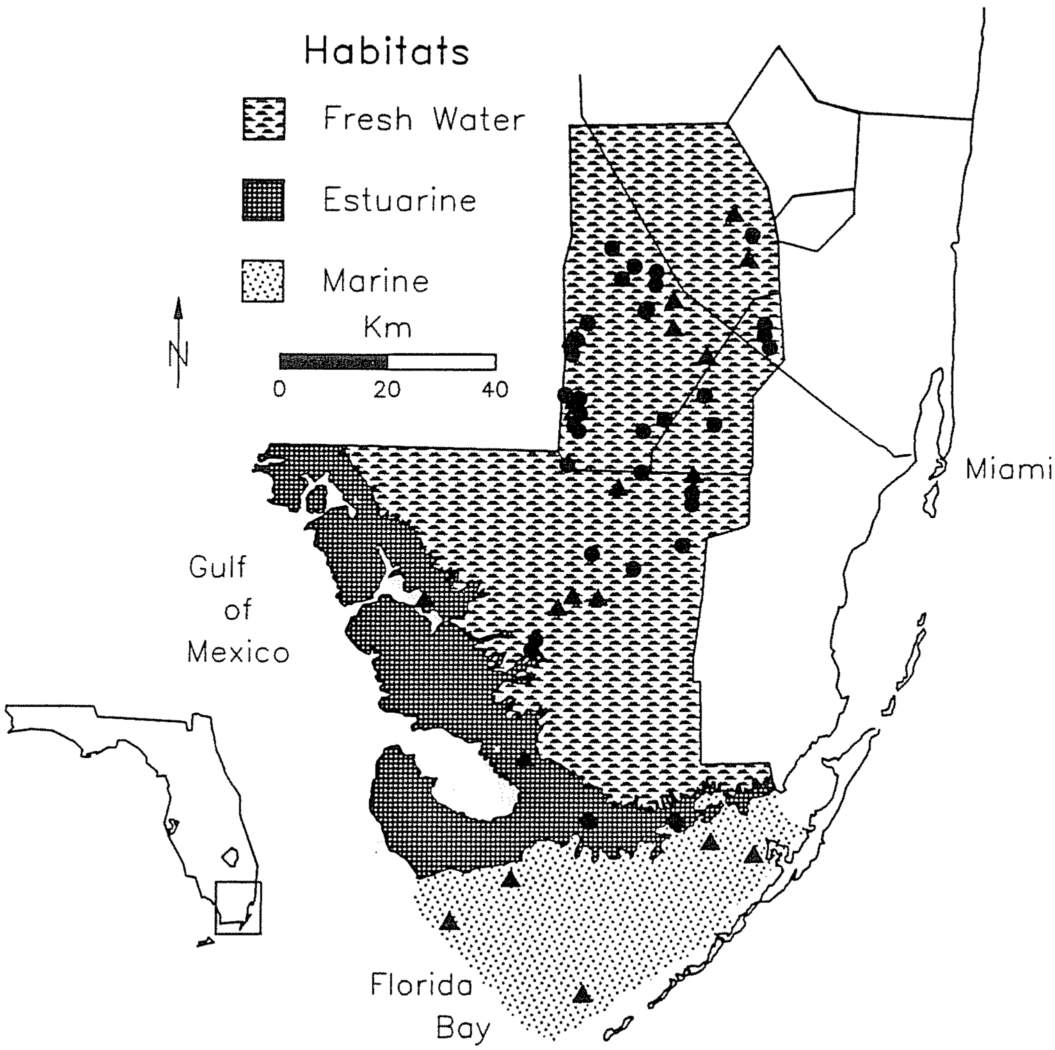

Figure 1. Map of southern Florida, showing locations of colonies found in freshwater, estuarine, and marine areas of the study area between 1986 and 1989. Colonies in which reproductive statistics were gathered are shown as triangles; all others are shown as dots.

and estuarine habitats combined), (75%) than in freshwater (25%). Little Blue Herons were found in very low abundances in marine colonies in the one year they were counted there (6.8%), and were consistently more common in freshwater habitats (annual mean of 89%, n = 4 years) than in estuarine habitats. Snowy Egrets were more numerous in estuarine habitat (48.9%) than either of the other two habitats during the two years in which all habitats were surveyed for this species. During the four years in which Snowy Egrets were surveyed in both estuarine and freshwater habitat, they were generally most numerous in estuarine habitat (annual mean of 68.7% of combined estuarine and freshwater nestings), although in one year they were more common in freshwater habitat.

Clutch size

Clutch size was generally larger at freshwater sites than at either of the saline sites (5/5 possible comparisons significant for Tricolored Herons, 2/3 for Snowy Egrets, 1/2 for Little Blue Herons, all combined probabilities significant, see Table 2). The trend of larger clutches in freshwater areas held during comparisons with both marine and estuarine colonies (3/3

Table 1. Numbers of nest starts of three species of *Egretta* herons in freshwater, estuarine, and marine habitats of southern Florida.

Year	Habitat	Tricolored Herons	Snowy Egrets	Little Blue Herons	Totals
1986	Freshwater	518	69	377	964
	Estuarine	615	1,250	49	1,914
	Marine	N.D.[1]	N.D.	N.D.	N.D.
	Total	1,133	1,319	426	2,878
1987	Freshwater	799	137	643	1,579
	Estuarine	501	400	40	941
	Marine	1573	527	50	2150
	Total	2,873	1,064	733	4,670
1988	Freshwater	583	400	129	1,112
	Estuarine	338	698	28	1,064
	Marine	1,392	60	N.D.	N.D.
	Total	2,313	1,158	N.D.	N.D.
1989	Freshwater	309	250	100	659
	Estuarine	241	176	35	452
	Marine	954	N.D.	N.D.	N.D.
	Total	1,504	N.D.	N.D.	N.D.
Composite Total (Mean annual % of total)[2]					
	Freshwater	1691 (24.5)	537 (23.7)	643 (87.7)	1579 (33.8)
	Estuarine	1080 (16.0)	1098 (48.9)	40 (5.5)	941 (20.2)
	Marine	3919 (59.3)	587 (27.3)	50 (6.8)	2150 (46.0)
	n (years)	3	2	1	1

[1]N.D. = No Data
[2]Calculated as means of years in which the species was surveyed in all habitats.

and 5/6, respectively). No consistent trends were apparent in clutch size differences between the two saline habitats.

Laying date

We found no evidence for a relationship between clutch size and date of laying. For Tricolored Herons, clutch size was not reliably dependent on date of clutch initiation within colonies (9 of 31 one-way ANOVAs were significant at alpha = 0.05, no trends seen within species). The Type IV ANOVA also showed no relationship between clutch size and date of laying, or between habitat and date of laying (Table 3).

Nesting success

Probabilities of nest starts resulting in at least one young of 14 d or older ("overall", Table 2) were generally significantly lower at estuarine colonies than they were elsewhere (5/6 possible comparisons significant for Tricolored Herons, 4/5 for Snowy Egrets, 1/1 for Little Blue Herons, all combined probabilities significant). Nesting success was also lower at marine sites than at freshwater sites (4/5 for Tricolored Herons, 3/3 for Snowy Egrets, and 1/2 for Little Blue Herons, all combined probabilities significant). During the incubation period, nest survival was significantly lower in the two saline habitats than in freshwater for

Table 2. Summary of annual pairwise comparisons of reproductive parameters of 3 *Egretta* species in southern Florida. Columns represent hypotheses being tested (example: FW>E = reproductive values from freshwater colonies are higher than in estuarine colonies; FW = freshwater, E = estuarine, M = marine, S = all saline combined).

	Combined Probabililty[1] FW>E	M>E	FW>M	FW>S
Tricolored Herons:				
Clutch size	<0.001 (3/3;0)	0.500 (1/3;2)	<0.001 (2/2;0)	<0.001 (5/5;0)
Nest Success:				
Incubation	<0.001 (3/3;0)	<0.001 (3/3;0)	<0.001 (1/2;0)	<0.001 (4/5;0)
Nestling	0.001 (1/3;0)	<0.001 (2/3;0)	0.071 (0/2;0)	<0.001 (2/5;0)
Overall	<0.001 (2/3;0)	<0.001 (3/3;0)	<0.001 (1/2;0)	<0.110 (3/5;0)
Fledgling Success	0.242 (1/3;0)	0.890 (0/3;0)	<0.001 (2/2;0)	<0.001 (3/5;0)
Snowy Egrets:				
Clutch size	<0.001 (1/2;0)	0.510 (0/2;0)	N.D.	<0.001 (1/2;0)
Nest Success:				
Incubation	<0.001 (2/2;0)	<0.001 (1/3;0)	0.0006 (1/1;0)	<0.001 (3/3;0)
Nestling	<0.001 (2/2;0)	<0.001 (2/3;0)	0.056 (1/1;0)	<0.001 (3/3;0)
Overall	<0.001 (2/2;0)	<0.001 (2/3;0)	0.0006 (1/1;0)	<0.001 (2/2;0)
Fledging Success	N.D.	0.006 (1/2;0)	N.D.	0.030 (1/2;0)
Little Blue Herons:				
Clutch Size	0.900 (1/1;0)	N.D.	0.014 (1/1;0)	0.070 (1/2;0)
Nest Success:				
Incubation	<0.001 (1/1;0)	N.D.	0.254 (0/1;0)	0.050 (1/2;0)
Nestling	<0.001 (1/1;0)	N.D.	0.368 (0/1;0)	0.080 (1/2;0)
Overall	<0.001 (1/1;0)	N.D.	0.880 (0/1;0)	0.090 (1/2;0)
Fledging Success	N.D.	N.D.	0.014 (1/1;0)	0.140 (0/1;0)

[1]Combined probability of all possible tests of significance, within years and species (see Sokal and Rohlf 1981;780). In parentheses, number of tests significant in hypothesized direction/number of tests possible; number of tests significant in direction oposite to H_1.

Tricolored Herons, Snowy Egrets, and Little Blue Herons (4/5, 3/3, and 1/2 possible comparisons, respectively, all significant). During the nestling phase, however, these differences were not as dramatic (1/5 for

Table 3. Results of unbalanced type IV ANOVA, examining effects of clutch size, colony, and area on laying date using records of individual Tricolored Herons in 1987, the only species-year combination in which all variables could be examined.

Source of Variation	df	F	P
Clutch	5	0.675	0.644
Habitat	2	0.810	0.468
Colony (habitat)[1]	9	18.67	<.0001
Clutch x habitat	5	0.885	0.499
Clutch x colony (habitat)	17	1.92	0.014

[1]Effect of colony, holding habitat constant.

Tricolored Herons, 3/3 for Snowy Egrets, 1/2 for Little Blue Herons, combined probability not significant for Tricolored Herons).

For both Tricolored Herons and Snowy Egrets, marine colonies produced consistently higher overall nesting success than estuarine ones (3/3 and 2/3 comparisons significant, respectively, Table 2).

Fledgling production

Saline colonies (both estuarine and marine) produced fewer 14-d old young per successful nest than did freshwater locations (3/5 comparisons significant for Tricolored Herons, 1/1 for Snowy Egrets, 1/1 for Little Blue Herons, all combined probabilities significant, see Table 2).

DISCUSSION

Tricolored Herons and Little Blue Herons appeared to be strongly associated with marine and freshwater breeding habitats, respectively. Snowy Egrets were not as consistently associated with a particular breeding habitat, but were much less often found in freshwater habitat than in estuarine or marine breeding colonies.

The decreased clutch size in saline (marine and estuarine) habitats relative to freshwater ones was consistent across years for Tricolored Herons, and while this difference was less consistent for Snowy Egrets, the difference was significant. Our results also suggest no consistent differences in clutch size between the two saline areas. The restricted size of the study area suggests that the clutch size differences are not the result of broader latitudinal gradients (Custer and Osborn 1981), and are likely to be truly local effects. The differences in clutch size are also not likely to have been an effect of differences in laying date between habitats, since we could establish no relationships between either habitat and laying date, or clutch size and laying date in Tricolored Herons. Since the other two species are close congeners and have similar foraging ecology and timing of breeding, it seems prudent to suppose that this conclusion also applies to them.

Rudegeair (1975) hypothesized that clutch size might be limited by the energetic costs of travel between feeding and nesting sites at the time of clutch formation. Although we have no information on flight distances during the pre-incubation period, birds at the estuarine and marine colonies we studied flew relatively short distances to foraging sites (7-10 km) during the nestling phase, and were similar to distances flown by birds from freshwater colonies (Frederick and Collopy 1988, Powell and Bjork 1990, Bancroft *et al.* 1990). This information suggests that increased costs of flight at coastal colonies is an unlikely explanation for reduced clutch size on the coast.

Energy available for clutch production might also be reduced by the need to excrete salt in marine environments. The observed pattern of clutch sizes is consistent with this hypothesis, but is far from conclusive evidence.

Clutch size might also be related to energy available in feeding habitats used during the pre-laying period (Ankney and McInnes 1978, Eldredge and Krapu 1988). While we cannot address this question directly from our studies, there is some evidence that food resources are currently depressed in Florida Bay and nearby coastal estuarine habitats. Powell (1983) found that clutch size in Florida Bay Great Blue Herons (*Ardea herodias*) was reduced by comparison both with historical records and with clutch sizes of food-supplemented birds. Ospreys (*Pandion haliaetus*) foraging in Florida Bay had significantly lower production of nestlings than those foraging in the nearby inshore waters of the Atlantic Ocean (Bowman *et al.* 1989), a result which was not confounded by substantial differences in salinity. Estuarine regions of the Everglades have become generally much more saline through reductions in freshwater flows (Walters *et al.* 1992) during the last 30 years, which directly affects recruitment of larval fish stages in the region (Tilmant *et al.* 1989, Rutherford *et al.* 1989). Certainly, the drastically reduced wading bird nesting effort in the estuarine zone during the last 30 years also is consistent with decreases in the availability of food resources (Ogden 1978, Kushlan *et al.* 1984).

Although survival of nesting attempts was generally lower in saline habitats, there were clearly differences among species, and within species among periods of the nesting cycle. Coastal-nesting Snowy Egrets had reduced nesting success in all periods, and in comparisons of both marine and estuarine colonies with freshwater ones. Tricolored Herons, however, only showed consistently reduced nesting success when estuarine and freshwater situations were compared; none of the comparisons between marine and freshwater sites was significant. This interspecific difference was underscored in 1990, when we noted generally weak and moribund Snowy Egret chicks in the estuarine Rodgers River Bay colony on the same date that same-aged Tricolored Heron chicks in that colony were healthy and well-fed. We also noted strong differences in nest predation among the three habitats that may explain the pattern of nesting success. In freshwater colonies, both aerial and terrestrial predators were quite rare, and nest predation accounted for a small proportion of total reproductive losses (Frederick and Collopy 1989b). Estuarine colonies experienced heavy egg and chick predation by Common Crows (*Corvus brachyrhynchos*, see Bancroft *et al.* 1990). Nest predation at marine colonies was generally low, and predators were varied, including small numbers of crows, Turkey Vultures (*Cathartes aura*) and in some cases nesting Southern Bald Eagles (*Haliaeetus leucocephalus*) (Powell and Bjork 1990, Frederick *et al.* in press). The fact that nesting success differences were most pronounced during the incubation period (a time of highest predation losses attributable to crows), and least during the nestling period suggests that egg predation by crows was an important contributor to the

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In sum, we find much support and little refutation of the hypothesis that clutch size, nesting success, and numbers of young per successful nest are lower in coastal than in freshwater Tricolored Heron and Snowy Egret colonies of southern Florida. Our results suggest that the reduction in clutch size is unlikely to have been the product of year effects, latitude, date of laying, or distance flown to food sources; the remaining explanations include energetic constraints of salt excretion, and quality of foraging habitat, between which we are unable to distinguish.

In light of the greater potential for reproduction in freshwater habitats, the apparent preference of Tricolored Herons and Snowy Egrets for coastal breeding is puzzling. The pattern might result from innate habitat preferences which are presently maladaptive as a result of recent estuarine habitat degradation in the Everglades. This seems unlikely, given that coastal reductions in clutch sizes have been observed in several other regions (Rudegeair 1975, Kushlan 1977, Maxwell and Kale 1977, Rodgers 1978, Girard and Taylor 1979, Hammatt 1981, Black *et al.* 1984, Bjork 1986, Frederick 1987). Several studies have found tradeoffs between egg production and nest survival among nesting habitats of aquatic birds, which ultimately result in similar production in "preferred" and "nonpreferred" habitats (Kushlan 1977, Pierrotti 1982). However, we could find no evidence of such tradeoffs, and the differences in production among our habitats seemed real.

Our final hypothesis to explain the nesting pattern is that coastal habitat is selected simply because the conditions are more predictable. While highly productive, freshwater marshes are comparatively ephemeral and unpredictable from year to year (Kushlan 1977, Ogden *et al.* 1980). This hypothesis would predict that the unpredictability of nesting in freshwater areas costs more in terms of lifetime reproductive success than does the lower production usually experienced in coastal breeding situations.

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Appendix 1. Combined reproductive statistics for three species of *Egretta* herons nesting in freshwater marsh, estuarine, and marine habitats.

Snowy Egrets:

	1986		1987		1988		1989			
Measure[1]	Estuarine	Freshwater	Estuarine	Marine	Estuarine	Marine	Estuarine	Marine	Freshwater	All Saline
Clutch Size	2.82 (0.603) n=11	2.67 (0.471) n=48	3.29 (0.726) n=14	2.80 (0.450) n=5	2.99 (0.662) n=98	3.50 (1.432) n=10	1.93[a] (0.829) n=14	N.A. N.A.	3.57[b] (0.590) n=23	N.A. N.A.
Incubation Nest success	0.4528[a] (0.01664)	0.8260[b] (0.07795)	0.7898 (0.02223)	0.7492 (0.03509)	0.7121 (0.01245)	0.7493 (0.03508)	0.0957[b] (0.01278)	0.4574[a] (0.05657)	0.7510[c] (0.01357)	0.1277[ab] (0.02462)
Nestling Nest success	0.5454[a] (0.05236)	0.8616[b] (0.09074)	0.3663[a] (0.05225)	1.0000[b] (0.0000)	0.8049[a] (0.01380)	1.00[b] (0.00)	0.2288[a] (0.17896)	0.3611[a] (0.08067)	0.9573[b] (0.01140)	0.3376[a] (0.16399)
Overall Nest success	0.2470[a] (0.09327)	0.7117[b] (0.09065)	0.0421[a] (0.04210)	0.7592[b] (0.02629)	0.5717[a] (0.01410)	0.7592[b] (0.01970)	0.0244[a] (0.05246)	0.1651[a] (0.07204)	0.7283[b] (0.07426)	0.0732[a] (0.05574)
Fledglings per successful nest	2.00 (0.00) n=5	2.78 (0.786) n=9	2.75 (0.126) n=4	2.00 (1.00) n=7	1.85[a] (0.667) n=13	2.47[b] (0.499 n=15	N.A.	N.A.	2.32 (1.04) n=22	N.A.

Tricolored Herons:

	1986		1987				1988		1989			
Measure[1]	Estuarine	Freshwater	Estuarine	Marine	Freshwater	All Saline	Estuarine	Marine	Estuarine	Marine	Freshwater	All Saline
Clutch Size	3.03[a] (0.642) n=59	3.29[b] (0.853) n=78	2.98[b] (0.580) n=89	2.68[b] (0.636) n=140	3.14[c] (0.513) n=209	2.78[ab] (0.639) n=228	2.68[a] (0.,650) n=22	2.19[b] (0.470) n=171	1.90[a] (0.520) n=44	2.00[a] (0.390) n=101	3.14[b] (0.900) n=35	2.00[a] (0.430) n=119
Incubation Nest success	0.4528[a] 0.01664	0.5527[b] 0.04376	0.5168[a] 0.09848	0.7379[b] 0.02643	0.7125[b] 0.02518	0.7382[ab] 0.02640	0.3511[a] 0.02818	0.7212[b] 0.03514	0.0957[a] 0.01278	0.4574[b] 0.05657	0.7510[c] 0.01357	0.2016[ab] 0.04669
Nestling Nest success	0.8563 0.01349	0.8347 0.03771	0.8636[a] 0.10564	0.9135 0.02520	0.9508[a] 0.01455	0.9135[b] 0.02519	0.5973[a] 0.04267	0.9093[b] 0.03321	0.5440[b] 0.02768	0.8754[b] 0.01075	0.8168[c] 0.02944	0.4513ab 0.01400
Overall Nest success	0.3877 0.06280	0.4730 0.48872	0.4460[a] 0.10499	0.6674[b] 0.030167	0.6610[b] 0.02812	0.6741[b] 0.03017	0.2079[a] 0.02256	0.6656[b] 0.03944	0.0520[a] 0.00866	0.4004[b] 0.3878	0.6134[c] 0.01718	0.1700[c] 0.02740

Fledglings per successful nest	2.28^{a} (0.665) n = 50	2.57^{b} (0.725) n = 71	2.42^{ab} (0.575) n = 19	2.29^{b} (0.681) n = 233	2.67^{a} (0.753) n = 201	2.30^{b} (0.684) n = 254	2.08^{a} (0.641) n = 13	1.93^{b} (0.664) n = 137	$2.00^{a,c}$ (0.378) n = 14	1.79^{b} (0.502) n = 94	$1.92^{a,c}$ (0.845) n = 26	1.81^{ab} (0.495) n = 107

Little Blue Herons:

	1986		1987	
Measure[1]	Estuarine	Freshwater	Freshwater	Marine
Clutch Size	3.67 (0.943) n = 15	3.44 (0.497) n = 18	3.53^{a} (0.570) n = 53	2.81^{b} (0.810) n = 36
Incubation Nest Success	0.1615^{a} (0.04007)	0.7200^{b} (0.06067)	0.7342 (0.03309)	0.8054 (0.05254)
Nesting Nest Success	0.00006^{a} (0.01461)	0.9018^{b} (0.03294)	0.9653 (0.02413)	0.8972 (0.07190)
Overall Nest Success	0.0000^{a} (0.0000)	0.6963^{b} (0.05289)	0.7164 (0.03775)	0.7297 (0.07724)
Fledglings per Successful Nest	N.D.	2.38 (0.073) n = 34	2.75^{a} (0.809) n = 60	2.15^{b} (0.670) n = 20

[1]All measures expressed as means, except nesting success, which is the probability of a nest producing at least one young to an age of 14 d. Standard deviations are given in parentheses. Different superscript letters indicate significant differences in reproductive parameters within years. Sample sizes are the number of nests studied, lumped across colonies within habitats. ND = No data.