Aspects of the Breeding Biology of the Cattle Egret (*Bubulcus ibis*) in Montserrat, West Indies, and its Impact on Nest Vegetation

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Abstract.—Aspects of the Cattle Egret's reproductive ecology and habitat use in an insular environment were studied on Montserrat, West Indies. Average size of 290 nests (17.9 cm) was smaller than sizes reported in the literature and was attributed to a paucity of available nesting materials. We measured 330 eggs to determine: egg volume (24,117.04 mm^3), fresh egg weight (24.4 g), egg weight loss during incubation (2.9 g), pipping egg ("star pips" only) weight (21.5 g), egg length (45.56 mm), egg breadth (32.22 mm), and a species-specific egg weight constant K_w (= 0.506) (where K_w is fresh egg weight divided by egg length times the square of the egg breadth or W/LB^2). Comparative data suggest that clutch-size in this species increases with latitude, but egg size does not.

Nest placement within the vegetation and within the colony (core vs. peripheral sites) was studied to compare differential habitat use by nesters. Four nest placement parameters were compared for core nests and peripheral nests: nest height (1.8 m vs 2.4 m), distance from trunk (0.4 m vs 0.6 m), distance from the distal end of the branch (0.89 m vs 0.77 m), and (nearest neighbor distance 52.4 cm vs 56.4 cm). We hypothesized that under keen interspecific competition for nest sites in mixed-species heronries, each species should be forced into a narrower habitat niche (narrower vertical stratification and horizontal partitioning of habitat) than if it nests in monospecific colonies but only nest height substantiated the hypothesis.

The Cattle Egret may be having a deleterious impact on the small tidal mangrove forest ecosystem found at Fox's Bay, Montserrat in conjunction with a multiplicity of environmental and ecological factors, including natural storms, wood-cutting, over-grazing by farm animals, reduced flooding, siltation, and soil compaction.

Key Words.—*Bubulcus ibis*, Cattle Egret, clutch size, competition for nest sites, ecosystem, egg, habitat destruction, habitat use, islands, Montserrat, Neotropics, reproductive ecology, vegetation, West Indies.

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The Cattle Egret (*Bubulcus ibis*) is native to Africa, southern Portugal, Spain, the humid Asian tropics from India to Japan, and northern Australia (Brown et al. 1982). The reproductive ecology of the Cattle Egret has been well documented in its traditional range, as well as its extended range in continental South, North, and Central America (Skead 1956, 1966, Lowe-McConnell 1967, Blaker 1969, Jenni 1969, Lancaster 1970, Siegfried 1971, 1972, Leber 1980, Brown et al. 1982). However, with the exception of a study by Delannoy (1976) in Puerto Rico, virtually nothing has been reported on the reproductive ecology or habitat use by Cattle Egrets in the West Indies, especially in the Lesser Antilles. We present here the results of a study of some of the aspects of the species' reproductive ecology (i.e., nest size and placement, egg size, volume, and weight) and habitat use. We also compare whether or not Cattle Egrets nesting in the absence of other ardeids show more variation in vertical stratification and horizontal partitioning of habitat in the selection of nest sites and nest placement than those nesting in mixed-species heronries.

We discuss the accelerated disappearance of the Fox's Bay tidal mangrove ecosystem and possible impact that nesting Cattle Egrets may be having on vegetation in nest sites. On Montserrat, for the last five years or so (1980-84), local residents in the vicinity of the Fox's Bay Bird Sanctuary have observed a steady die-off of mangrove vegetation at the long-established Cattle Egret colony. Some residents have blamed nesting Cattle Egrets for the apparent continual death of mangrove trees (Dennis Gibbs pers. comm.). This study was initiated as a result of the concern expressed by members of the Montserrat National Trust for the preservation of the Fox's Bay mangrove ecosystem.

STUDY AREA

The Greater Antilles (from Cuba to the United States and British Virgin Islands) and the Lesser Antilles (from Anguilla to Grenada) form a wide arc which curves for about 4,000 km from Florida to the north coast of Venezuela in the Caribbean Sea. Montserrat is one of 23 volcanic islands in a group known as the Leeward Islands, which form part of the Lesser Antilles Archipelago. Montserrat lies At

16° 40′ to 16° 50′ N latitude and 62° 9′ to 62° 15′ W longitude, about 43 km southwest of Antigua and about the same distance from Guadeloupe, its closest neighbor to the southeast. Montserrat is 18 km long and 11 km wide with a land mass of about 102 km^2 Its highest mountain (Chance's Peak) rises more than 900 m above sea level (Fergus 1983). Natural vegetation is confined to very small areas of the interior mountains, where rainforest (mostly secondary), and elfin woodland still remain on the higher slopes. Secondary dry scrub has developed on the glacis slopes and lowlands where there is no recent cultivation. "Acacia savannah" predominates in coastal areas (Lang 1967).

Montserrat has a dry season from January to May and a wet season from June to December. Annual rainfall in coastal areas is less than 100 cm. The annual mean temperature is 26.1 °C in the lowlands, ranging from a minimum in January (24.2 °C) to a maximum in September (27.8 °C) (Lang 1967).

Our study site was within the Fox's Bay Bird Sanctuary, in a small (6 ha) mangrove swamp located about 2.8 km northwest of the capital city of Plymouth, on the southwestern coast of Montserrat. White mangrove (*Laguncularia racemosa*) was the dominant vegetation type at the study site and within the center of the swamp. Small clumps of black mangrove (*Avicennia germinans*) grew along the swamp's inland border.

METHODS

Five weekly visits were made to the colony from 24 June to 22 July 1984. Each visit began shortly after sunrise and lasted three to four hours, depending on weather conditions. We were able to work longer on overcast days (when cloud-cover reduced both the intensity of the sun's rays and the threat of heat exhaustion in young egrets), but we departed immediately at the onset of rain showers or intense sunlight.

Cattle Egrets begin their reproductive cycle at the onset of the wet season (Brown et al. 1982). During our study, 307 Cattle Egret pairs were nesting. We found many incomplete clutches and freshly constructed nests on 24 June. This fact, together with the recent arrival of the heavy rains that marked the beginning of the wet season in late May 1984 in Montserrat (A. Wheeler pers. comm.) suggest that the egret's breeding season had just begun.

The boundaries of the colony were measured to the nearest meter with a fiberglass measuring tape. We measured nest heights (vertical stratification) from the ground or water's surface, distances from trunks, branch extremities (distal end), and nearest neighbors (horizontal habitat partitioning) to the nearest meter for 290 of the 307 nests. Seventeen nests were inaccessible. Nest dimensions (maximum diameter and vertical thickness) were measured to the nearest centimeter. Clutch size was determined using only nests (n = 153) that contained an equal number of eggs on at least two visits. No nests containing young were included in clutch size analysis because we did not determine egg or nestling mortality. Eggs were measured with dial calipers accurate to 0.01 mm.

The mass of eggs was determined with a 50-g spring scale accurate to 0.5 g. Fresh eggs (unsoiled and dull, not yet showing the characteristic shine produced by the feather friction of the incubating adult) and "pipping" eggs (star pip) were recorded separately. Egg weight loss was determined by subtracting the weight of star-pipped eggs from freshly laid eggs. Although we are certain of the "pipping" egg weights, fresh egg weights may be slightly underestimated because adults of this species are known to begin incubation with the laying of the first egg. Therefore, in a nest of three "fresh" eggs, incubation may have begun 1-2 days previously. We did not separate eggs by laying order. Egg volume and fresh egg weight were calculated from the sample egg dimensions using formulas evaluated by Hoyt (1979). A species-specific egg weight constant (K_w, where K_w is fresh egg weight divided by egg length times the square of the egg breadth or W/LB^2) was calculated (Hoyt 1979). No attempt was made to analyze hatching or fledging success, mortality rates, or reproductive success because of the infrequency of our visits and the brevity of our study.

Nest placement data were analyzed using box plots (McGill et al. 1978, Velleman and Hoaglin 1981), a nonparametrics procedure that graphically summarizes descriptive statistics (extremes, upper and lower quartiles, and medians) and statistically assesses comparative data using Gausian-based asymptotic approximation of the standard deviation of the median (Kendall and Stuart 1967). Despite the sometimes skewed distributions, nest placement data were also compared (Table 1) using a parametric statistical test (Student's t-test) because of large sample sizes (>100 observations). Significance was assumed at the 5% level in all statistical tests.

RESULTS

Colony Site

The colony site covered 0.6 ha (about one tenth of the entire swamp) and was located in white mangrove vegetation. Average tree height for the entire colony was 3.8 ± 0.78 m (s.d.) N = 36, range = 2.1-5.7 m). Average tree height at the colony's center and periphery were, respectively, a similar 3.9 ± 0.72 m, (range = 2.1-4.3 m) and 4.1 ± 0.99 (range = 2.1-5.7 m). In general, tree height was fairly uniform throughout the colony, the exception being a small group of little-used white mangrove nest trees (two of which reached almost 6 m in height) on the colony's periphery.

Nest Size and Placement

Average nest diameter of 290 Cattle Egret nests was 17.9 ± 2.96 cm (range = 7.6-25.4 cm), which is much smaller than average diameters reported in the literature (Table 1). A cup or hollow was seldom observed. Most nests resembled platforms more than definitive nests. Nest (or plat-

Table 1. Geographical variation in nest size of the Cattle Egret.

NEST									
Diameter (cm)				Depth (cm)					
x̄	range	sd	cv	x̄	range	sd	cv	Location	Source
36.3	29-44							South Africa (Paarl)	Siegfried (1971)
35.8		7.9	22	20.1		7.7	38	United States (New Jersey)	Burger (1978)
34.5	23-46			17.8	13-23			South Africa (King Williams Town)	Skead (1966)
32.5	20-45			18.5	12-25			West Palearctic	Cramp & Simmons (1977)
31.9	18-61	7.3						North America (Texas)	Telfair (1983)
31.0	20-46							Central America (Costa Rica)	Leber (1980)
30.0				12.0				Soviet Union (Lenkoran)	Dementiev & Gladkov (1969)
17.9	8-25	2.9	17	12.9	5-20	3.3	26	West Indies (Montserrat)	this study

form) thickness averaged 12.9 ± 3.30 cm (range = 5.1-20.3 cm).

Clusters of nests were found at the center of the colony (core nests) and along the colony's periphery (peripheral nests). Core nest sites were used before peripheral nest sites. Because of the physiognomy of the mangrove vegetation, dead snags, and waterways, there was no intermediate zone in which egrets could nest. Whereas most nests were placed in white mangroves standing in water, some nests towards the interior border (landward) of the swamp were placed in white mangroves on dry ground. Water levels rose gradually to 0.9 m toward the center of the colony.

None of the 135 core nests was placed at heights exceeding 3.73 m. However, 41 of 155 peripheral nests (27%) were placed at heights greater than 3.73 m, some as high as 4.98 m (Fig. 1, Table 2). Despite a wider distribution of peripheral nests at varying heights, more egret pairs throughout the colony nested at a height of 1.5 m than at any other height (21% of the core nesters and 16% of the peripheral nesters). Whereas core nesters tended to place their nests at heights of about 1.5 m (x̄ = 1.8 m), many peripheral nesters placed their nests higher (x̄ = 2.4 m). Less than half of the core nesters (44%) placed their nests above 1.5 m. However, almost two-thirds of the peripheral pairs (72%) placed their nests at greater heights, some as high as 4.98 m (Fig. 1, Table 2). Mean nest height was significantly different between core and peripheral nests (Fig. 1, Table 2).

No core nests were found farther than 1.2 m from the trunk, whereas 13% of the peripheral nests were placed at greater distances, out as far as 2.10 m from the main trunk (Fig. 1, Table 2). Despite the wider distribution of peripheral nests at varying distances from the trunk, more egret pairs throughout the colony nested at the main trunk (34% of the core nesters and 29% of the peripheral nesters). Nests were usually placed in a fork at the main trunk. Throughout the colony, most nests were

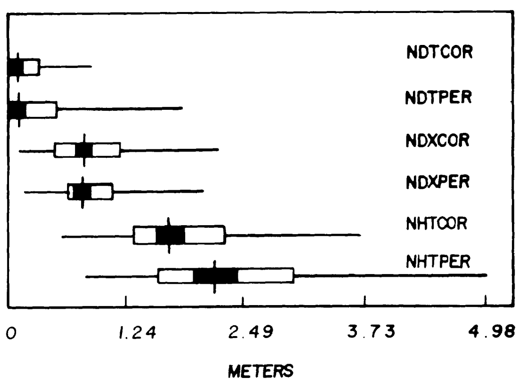

Figure 1. Box Plots showing a comparison of nest placement parameters at a Cattle Egret colony at Fox's Bay, Montserrat (1984), between core (COR) nests and peripheral (PER) nests: nest heights (NHTCOR, NHTPER), distance from main trunks (NDTCOR, NDTPER), and distance from distal ends of branches (NDXCOR, NDXPER). Horizontal lines show extremes, vertical lines are medians, open boxes designate lower and upper quartiles. Blackened areas between the quartiles that do not overlap (e.g., nest height) designate a significant difference (at the 95% level) between core and peripheral nest placement parameters.

Table 2. Comparisons of four nest placement parameters for core nests and peripheral nests in a Cattle Egret colony in white mangroves.

	Nest Height		Trunk Distance[1]		Branch Distance[2]		Nearest Neighbor[3]	
	C[4]	P[5]	C	P	C	P	C	P
$\bar{x}$	1.80	2.37	0.44	0.58	0.89	0.77	52.40	56.00
sd	0.68	0.99	0.40	0.57	0.48	0.48	17.15	24.08
cv	38	42	91	98	54	62	33	42
Range	0.7-3.73	0.8-4.98	0-1.20	0-2.10	0.1-2.40	0.2-2.30	23.4-90.00	0-96.5
t[6]	8.06		2.05		1.42		0.95	
p	<0.001		>0.05		>0.05		>0.05	
n	135	155	135	155	135	155	135	155

[1]Nest distance (m) from trunk
[2]Nest distance (m) from distal end of branch
[3]Inter-nest distances (cm)
[4]Core nests
[5]Peripheral nests
[6]Student's t-test

placed within 0.6 m of the main trunk (77% of the core nests and 67% of the peripheral nests). Mean nest distance from the trunk was not significantly different between core and peripheral nests (Fig. 1, Table 2).

Distributions of nest distances from branch extremities for core and peripheral nests are similar for both groups (Fig. 1, Table 2). Throughout the colony, 49% of the Cattle Egret pairs (142 of 290) placed their nests within about 1 m of the distal end of the supporting branch. Fifty percent of the core nests were placed at distances of 0.9 m to 1.2 m from branch extremities, and 49% of the peripheral nests were placed from 0.6 m to 0.9 m from the distal end of the branch. Mean nest distance from branch extremity was not significantly different between core and peripheral nests (Fig. 1, Table 2).

A comparison of mean nest distance from the trunk for all 290 nests throughout the colony with mean nest distance from the branch extremity for the same 290 nests showed that Cattle Egret pairs placed their nests significantly closer to the trunk than to the distal end of the branch: mean distance to trunk = 0.5 ± 0.49 m; mean distance to branch extremity was 1.8 ± 1.48 m; T = 6.81, P <0.001.

No nearest neighbor nest distance was greater than 90 cm for core nesters, whereas some peripheral nesters (8%) placed their nests at distances up to 96.5 cm from other nesters (Fig. 1, Table 2). Most egret pairs throughout the colony maintained a distance of from 0.4 m to 0.6 m from their closest neighbors (64% of the core nests and 60% of the peripheral nests). Inter-nest distances among nearest neighbors was not significantly different between core and peripheral nests (Fig. 1, Table 2).

Egg Characteristics

Mean clutch size in 153 nests at the Fox's Bay Cattle Egret colony was 2.2 ± 0.71 eggs (range: 1-5 eggs). Egg weights and dimensions recorded at the Fox's Bay Cattle Egret colony are summarized in Table 3. We estimated egg volume, fresh egg weight, and egg weight loss during incubation of 330 Cattle Egret eggs using observed egg weights and mean egg length and breadth: egg volume = 24,117.04 mm^3; fresh egg weight = 23.9 g; the species-specific weight constant K_w = 0.506; and egg weight loss during incubation = 2.9 g (12%).

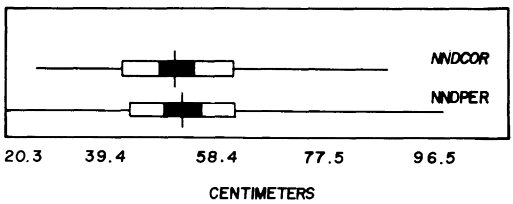

Figure 2. Box Plots showing a comparison of inter-nest (nearest neighbor) distances at a Cattle Egret colony at Fox's Bay, Montserrat (1984), between core (NNDCOR) nests and peripheral (NNDPER) nests. Explaination of boxplot summary statistics is the same as in Figure 1.

Table 3. Egg weights and dimensions of Cattle Egret eggs from a mangrove swamp nesting colony near Fox's Bay, Montserrat.

	Statistics				
	n	x̄	sd	cv	Range
Egg weight (all) (g)	330	23.96	2.49	10	18.10-30.50
Fresh egg weight (g)	27	24.37	3.06	13	20.20-30.50
Pipping egg weight (g)	18	21.48	2.24	10	18.10-25.50
Egg length (mm)	330	45.56	2.03	4	40.73-51.37
Egg breadth (mm)	330	32.22	1.28	4	29.27-35.18

Fox's Bay Mangroves

The stands of white and black mangrove forest and associated wetlands vegetation at Fox's Bay have never been extensive (D. Gibbs pers. comm.). Nonetheless, historically, the swamp has covered more than 15 ha (D. Gibbs pers. comm.) and local residents have observed a steady die-off of mangrove trees and subsequent decrease of the swamp's total area for the last decade, with an even more accelerated tree mortality and reduction in the swamp's total area within the last five years (1980-1984). Two main causes have been suggested for this phenomenon. Some residents feel that the ever-growing population of Cattle Egrets is causing the deaths of mangrove trees. Others blame the destructive cloudburst and severe flooding that occurred on 3 September 1981 for the accelerated die-offs, claiming that as a consequence of the flooding, riverine drainage patterns were greatly altered and run-off waters now bypass the swamp. Associated with this is the fear that construction of new roads near the swamp's interior border subsequent to the 1981 flood also added to the re-channeling of run-off waters away from the swamp.

Mangrove forests are dynamic ecosystems. Factors such as sedimentation rates, soil subsidence, freshwater run-off, tidal forces, and changes in sea level influence mangrove growth and survival (Jimenez et al. 1985). We made a preliminary assessment of the present condition of the Fox's Bay wetlands area and its mangrove vegetation, noting possible factors that may be influencing the swamp's disappearance. We found what appears to be a multiplicity of factors that may be acting synergistically in hastening the death of the mangrove ecosystem. We did not detect the normal inundation and flushing of the swampland or surrounding low-lying areas that usually accompanies heavy showers, though occasional heavy rains fell during our 2.5 month stay on Montserrat. These observations suggest that run-off waters were not reaching the swamp. The soil in the swamp's interior was parched and compacted. Soil compaction and continued degradation of vegetation along the swamp's interior border was augmented by the continual and uncontrolled grazing of sheep and cattle (pers. obs.). Water in the swamp's interior was shallow, appeared stagnant, and exhibited elevated temperatures (pers. obs.), also suggesting that the periodic flushing by tidal action and drainage from interior watersheds so vital to the existence of the mangrove-adapted vegetation (Jimenez et al. 1985) was not occurring. In view of the apparent alteration in drainage patterns, a water sample was sent to be tested for salinity and sediment content. However, the results—regarding salinity and sediment content—were inconclusive.

Habitat Destruction

Cattle Egrets are apparently using all available nesting materials in and around the swamp, both dead and living. Much of the nesting area vegetation showed signs of physical damage caused by nesting Cattle Egrets. Small branches, and especially green leaves and twiglets, were broken off and used as nest materials. Branches supporting nests were visibly stressed and some had broken under the weight of too many nests. Other data gathered at the egret nesting colony, such as small nest size and occasional egg-laying virtually on bare branches, as well as information obtained from local residents, suggest that nest materials are scarce. Also, once the nesting vegetation dies, egrets abandon it in search of live vegetation (D. Gibbs pers. comm., pers. obs.). Cattle Egrets are known to fly many kilometers in pursuit of nesting materials. However, the land for many kilometers around the mangrove swamp is developed or under intense agriculture. Although we conducted extensive field studies within interior forests, Cattle Egrets were never observed flying long distances to reach forest borders in search of branches.

DISCUSSION

Nest Placement

Colonial-nesting ardeids have been shown to differentially partition nest site resources on a spatial and temporal basis in mixed-species heronries (Lowe-McConnell 1967, Dusi and Dusi 1968, 1970, Jenni 1969, Weber 1975, Burger 1978, McCrimmon 1978, Hafner 1980, Telfair 1980, and many others). Variant nest placement (variable nest height and specific site in vegetation) and unsynchronized breeding among species is thought to increase reproductive success by reducing interspecific competition in multiple-species colonies (Burger 1978, McCrimmon 1978). The Cattle Egret often breeds in mixed-species heronries, thereby interacting with a variety of other ardeid species. Such interspecific interaction could potentially affect its selection of habitats and nest sites as well as its reproductive behavior. We hypothesized that under keen interspecific competition for nest space, each species would be forced into a narrower niche (i.e., a more limited vertical stratification and horizontal partitioning of habitat) than if it nested alone. Nest heights and horizontal distance measures would be more variable and show wider ranges in single-species colonies than in mixed-species heronries. In support of our hypothesis, Svardson (1949) found that where intraspecific competition for nest sites caused crowding, the tendency was for species to occupy a broader range of habitats, including sub-optimal sites. Conversely, where interspecific competition prevailed, each species tended to nest in a more restricted area corresponding to its optimum habitat.

Leber (1980) stated that "In order to define the fundamental niche of a species one must study each species in the absence of the others, where each may exhibit its full potential utilization of resources without interference or exploitation." Therefore, to test our hypothesis, we reviewed the literature to compile information on nest site characteristics of Cattle Egrets nesting in mixed-species heronries to compare with our results at the Fox's Bay single species (i.e., Cattle Egret) colony.

Nest height data for Cattle Egrets nesting in mixed- and single-species colonies were compared with this study (Table 4). Vegetation types ranged from bushes and mangroves, to broadleaf trees. However, with the exception of only one study (Hafner 1980), where nesting vegetation averaged about 15 m in height, all other vegetation types averaged a comparable 3-5 m in height. All Cattle Fgrets in both mixed- and single-species colonies placed their nests at a mean height of about 1.9 m, with the exception of Cattle Egrets in Hafner's (1980) colony in which mean nest height was 7.4 m. The range of nest heights (using maximum nest height difference) at 6 mixed-species heronries varied by a mean difference of only 1.5 m. However, at two Cattle Egret colonies (this study and Rencurel, 1972), the range of mean nest height differences was a much broader 4.3 m and 4.5 m, respectively. There was no apparent correlation (R^2 = 0.40, $P > 0.05$ between mean nest height and latitude among the ten studies we compared. On the other hand, by using the range of nest heights we did show that there is a strong tendency for nest height to be more uniform for the Cattle Egret in mixed-species heronries than in colonies where it nested alone. In comparing the ranges of nest heights, the 4.3 m range found in this study and the 4.5 m range reported for Rencurel's (1972) Cattle Egret colony are more than double any of the ranges reported for multiple-species heronries.

As with a narrower range of nest heights, the standard deviation of vertical nest placement should be much smaller for mixed-species heronries. With the exception of Hafner (1980), the data presented in Table 4 are supportive, being very much smaller in all other studies. In fact, the standard deviation calculated for variation in nest height for this study is almost 17

Table 4. Nest Heights of the Cattle Egret at single- and mixed-species colonies of varying sizes.

Nest Height (m)					Height Diff.[1]	Colony	
N	x̄	sd	cv	Range	(m)	Size[2]	Source
93	2.00	?	?	0.80-3.20	2.40	40,930	Leber (1980)
1700[3]	2.74	?	?	1.83-3.66	1.83	3,572	Lowe-McConnell (1967)
5000[3]	0.84	?	?	0.46-1.22	0.76	3,291	Goering & Cherry (1972)
54	2.23	0.05	02	1.80-2.70	0.90	2,657	Maxwell & Kale (1977)
16	0.70	0.31	45	0.03-1.12	1.09	1,200	Burger (1978)
76	2.38	0.05	02	1.68-3.66	1.98	990	Jenni (1969)
25	7.39	2.57	35	2-13	11.00	850[4]	Hafner (1980)
290	2.09	0.83	40	0.70-5.00	4.3	614[5]	this study
76	2.26	0.38	17	?	?	504	McCrimmon (1978)
200[3]	3.75	?	?	1.50-6.00	4.5	200[5]	Rencurel (1972)

[1]Height of lowest nest subtracted from that of the highest nest
[2]Nest pairs
[3]Eestimated number of nests
[4]Mean number of breeding pairs each year during a 2-yr study
[5]Single-species (Cattle Egret) colony

times greater than those reported by Maxwell and Kale (1977) and Jenni (1969) (0.83 vs 0.05). As a further example of there being more spatial variation in nest height at single-species colonies, McCrimmon (1978) reported a mean vegetation (tree) height at a mixed-species heronry (504 breeding pairs) of 3.8 ±0.63 m, cv = 17. At the similarly-sized Cattle Egret colony (307 breeding pairs) in Montserrat, mean vegetation height was a similar 3.8 ± 0.78 m, cv 21. Thus, nesting egrets in both of these mixed-species and single-species colonies could potentially place their nests at similar heights and presumably with a similar vertical placement variability among individual nesters, if the physiognomy of the nest-support vegetation did not vary greatly between the two colonies. Whereas mean nest heights at both colonies were similar (2.09 m for this study and 2.26 m for the mixed-species heronry), the standard deviation calculated from the mean nest height at the Cattle Egret colony was greater than that reported for the mixed-species heronry (0.78 m vs 0.63 m). This larger standard deviation in vertical nest placement in the single-species colony substantiates our hypothesis.

Leber (1980) reported that Cattle Egrets nesting in mixed-species heronries usually placed their nests more than 1 m out from the main trunk on secondary branches less than 2 cm in diameter. However, McCrimmon (1978) offered the only comparable data on nest distance from the trunk for mixed-species heronries (his "distance to tree center"), with which to compare our data for a single-species (Cattle Egret) colony. At his mixed-species heronry, mean nest distance from the trunk was 1.1 ± 0.73 m, cv = 62, for Cattle Egrets. At our colony, mean nest distance from the trunk for all 290 nests was 0.51 ± 0.49 m, cv = 96. The standard deviations found in this study (0.49 m) and reported by McCrimmon (0.73 m, 1978) do not support our hypothesis that nest placement in reference to the trunk should be more variable in Cattle Egrets that are not competing with other species for nest sites; and yet the much greater coefficient of variation at our Fox's Bay colony (96 vs. 62 reported by McCrimmon) does support our predictions. However, as McCrimmon (1978) pointed out, the shrubby vegetation at his study site made accurate measurement of this variable quite difficult. Additional evidence that does not uphold our hypothesis regarding the nest placement pattern in reference to distance from the main trunk comes from Hafner's (1980) study of Cattle Egrets nesting in a mixed-species heronry in Camarugue, France, where the Cattle Egrets exhibited a nest placement pattern that was similar to what we observed at the Fox's Bay single-species colony.

It follows from our hypothesis that "nearest neighbor" inter-nest distances should be shorter, or at least less variable, in mixed-species heronries than in single-species colonies, because each species is being forced into more compact areas. However, the data available are not supportive. McCrimmon (1978) reported a transformed ($\sqrt{x}$) mean inter-nest distance for Cattle Egrets in a mixed-species heronry of 148 ± 0.65 cm, cv = 44. Likewise, for a large mixed-species heronry of 1,200 breeding pairs, in which individual species should intuitively be forced into closer contact, Burger (1978) reported a mean inter-nest distance of 92 ± 35.0 cm, cv = 38. Inter-nest distance at our Cattle Egret colony was only 54.4 ± 20.62 cm, cv = 38, or almost one-third and one-half, respectively, of those reported for the two large mixed-species heronries. However, this may be an artifact resulting from the limited suitable nesting vegetation at the Fox's Bay colony (see "Nest Size" below). Whereas the standard deviation in inter-nest distances is much larger in Burger's (1978) mixed-species heronries (as predicted), the opposite is true in McCrimmon's (1978) study (contrary to the predicted). It appears that inter-nest distances in the Cattle Egret are not greatly reduced by the pressures of interspecific competition for nest sites. In fact, these data support Burger's (1978) suggestion that nest height and inter-nest distance may be predicted from the intensity of aggressive interactions, nests being placed farther apart as interspecific aggression increases. However, this is a valid assumption only if ardeids nest interspersed, and especially in homogeneous vegetation, which is often not the case.

In summary, of four nest placement criteria, only nest height appears to be affected as a result of mixed-species nesters competing for nest sites at multiple-species heronries, being more variable in single-species colonies. More comparative data among studies are needed, however, to support these findings.

Nest Size

Nest size of 290 Cattle Egret pairs nesting at Fox's Bay was much smaller than that reported in the literature (Table 1). Mean nest diameter for six different Cattle Egret populations from widely separated geographical areas is 33.4 ± 2.59 cm, range = 30.0-36.3 cm. Mean nest depth is 17.1 ± 3.53 cm, range = 12.0-20.1 cm.

Clutch Size

Published data show that frequency distribution (rate of occurrence of different-sized clutches) and mean clutch size in the Cattle Egret are generally correlated with latitude (Table 5), possibly as a result of increased day length and super abundance of food at northern latitudes (Lack 1954). We compared our clutch size data with 20 published sources (Table 6) and found a positive correlation between clutch size and latitude ($R^2 = 0.6$, $P < 0.05$, $y = -13.41 + 13.15x$, where y = clutch size and x = latitude). Clutch size increased from a mean of 2.6 eggs per nest at 5 °N Lat. and 1.86 eggs per nest at 7 °N Lat., to 4.60 eggs per nest at 46 °N Lat. and 3.15 eggs per nest at 34 °S Lat. (Table 6). However, as Maxwell and Kale (1977) have pointed out, after finding significantly different-sized clutches in Florida heronries less than 500 km apart, other clutch size determinants are involved and include such factors as social stress from crowded

Table 5. Frequency distribution (in percentages) of clutch size of Cattle Egrets in mixed-species heronries and at a Cattle Egret nesting colony (this study).

No. of Nests	Number of Eggs per Nest 1	2	3	4	5	6	7	Latitude °N	Source
66	—	—	4.5	33.0	58.0	4.5	1 nest	46	Hafner (1980)
85	1.2	3.5	48.2	38.8	7.1	1 nest	—	29	Jenni (1969)
486	17.0	66.0	15.0	0.4	—	—	—	18	Delannoy (1976)
153	13.1	62.7	20.9	2.0	1.3	—	—	16	this study
40	5.0	42.5	37.5	10.0	1 nest	—	1 nest	10	Leber (1980)
335	7.0	67.0	25.0	—	—	—	—	7	Lowe-McConnell (1967)
								°S	
155	—	31.0	60.0	7.7	1.3	—	—	34	Blaker (1969)
310	2.6	14.5	62.3	16.1	3.9	0.6	—	34	Siegfried (1972)

Table 6. Latitudinal variation of mean and total clutch size in the Cattle Egret.

Clutch Size $\bar{x}$	(n)	Location	Latitude (°N)	Source
4.60	(66)	Camargue	46	Hafner (1980)
3.40	(20)	Atlantic City, New Jersey, USA	39	Burger (1978)
3.67	(12)	Chincoteague, Virginia, USA	37	Valentine (1958)
3.70	(87)	Noxubee County, Mississippi, USA	33	Summerour (1971)
3.33	(9)	South Carolina	32	Cutts (1958)
3.58	—[1]	Trinity, Neches, etc., Texas, USA	31	Telfair (1980)
2.42	(50)	Dothan, Alabama	31	Dusi and Dusi (1970)
3.50	(85)	Lake Alice, Florida, USA	29	Jenni (1969)
2.86	(36)	Lake County, Florida, USA	29	Weber (1975)
3.00	(31)	Vero Beach, Florida, USA	27	Maxwell and Kale (1977)
1.98	(486)	Jobos Bay, Puerto Rico	18	Delannoy (1976)
3.00	(18)	Senegal, Africa	16	Morel and Morel (1961)
2.15	(153)	Montserrat, West Indies	16	this study
2.70	(40)	Isla Pajaros, Costa Rica	10	Leber (1980)
2.17	(335)	Guyana, So. America	7	Lowe-McConnel (1967)
2.60	(89)	Ghana, Africa	5	Bowen et al. (1962)
			Equator °S	
1.86	(15)	Java, Indonesia	7	Hellebrekers and Hoogerwerf (1967)
2.20	(76)	Zimbabwe,	20	Brown et al. (1982)
2.48	(290)	Transvaal, Africa	25	Brown et al. (1982)
3.06	(—[1])	Cape Province, South Africa	34	Siegfried (1972)
3.15	(155)	Paarl, South Africa	34	Blaker (1969)

[1]— = not available

conditions, competition, weather conditions at critical times in the reproductive cycle, and even varying levels of toxic chemicals (and hormones) in nesters. Their data also suggest smaller clutches from marine heronries than from freshwater colonies, although this was not apparent in the studies we compared.

Egg Size and Weight

Clutch size may vary geographically due to inherent (e.g., age, physiological state, and body size of female), ecological (food constraints, competition, predation), and environmental (e.g., temperature, humidity, rainfall, and altitude) factors. However, geographic variation of egg size in the Cattle Egret reported in the literature is small (Table 7). We found very little correlation between egg size and latitude (R^2 = 0.23, P>0.1, y = 44.68+0.01x, where y = egg size and x = latitude). From 5 °N in the Neotropics to 46 °N Lat. in the Palearctic, average minimum egg length is 41.23 ± 1.02 mm, range = 41.0-43.9 mm. Average maximum egg length is 49.54 ± 1.82 mm, range = 45.7-53.0 mm. Average minimum egg breadth is 31.55 ± 1.12 mm, range = 30.0-32.8 mm. Average maximum egg breadth is 35.56 ± 0.65 mm, range = 34.5-36.5 mm. Egg dimensions of the Montserrat Cattle Egret population are very similar to those reported in the literature (compare Tables 2 and 7).

Because our egg volume formula did not contain any volume coefficient constants, which had to be derived using our observed data, and because our mean egg dimension measures closely resemble those reported for the Cattle Egret in the literature, we believe that our estimation of egg volume for *Bubulcus ibis* from egg length and breadth data using the formula tested by Hoyt (1979) is accurate. Our estimate of egg volume is substantiated by the results of Loftin and Bowman (1978, Table 1) who calculated an egg volume for the Cattle Egret of 24.07 ml using their "egg volumeter".

Our estimated fresh egg weight may be somewhat lighter than the actual weight of freshly laid Cattle Egret eggs. Our calculation was dependent upon the species-specific weight constant K_w that was obtained using not only exacting measures of length

Table 7. Geographic variation in egg size of the Cattle Egret.

Egg length			Egg breadth				
x̄	min.	max.	x̄	min.	max.	Location	Source
47.4	43.9	50.0	33.8	32.8	34.8	Soviet Union	Dementiev & Gladkov (1969)
46.5	42.0	52.0	33.7	31.5	38.2	Southern Ghana	Bowen et al. (1962)
46.0			34.0			United States	Harrison (1984)
46.0			33.8			West and Equatorial Africa	Bannerman (1953)
45.7	41.2	49.8	34.2	32.5	36.0	Great Britain	Witherby et al. (1939)
45.6	40.7	51.4	32.2	29.3	35.2	West Indies (Montserrat)	this study
45.3	41.2	49.3	34.4	32.7	36.0	South Africa	Chapin (1932)
45.2	41.3	49.6	32.8	30.5	35.7	Central America (Costa Rica)	Leber (1980)
45.2	41.3	49.0	33.0	30.8	35.1	United States (Alabama)	Dusi (1966)
45.0	41.0	49.0	34.3	32.5	36.0	East & North-East Africa	Mackworth-Praed & Grant (1952)
45.0			34.0			Southern third of Africa	Mackworth-Praed & Grant (1962)
45.0	41.0	53.0	34.0	32.0	36.0	West Palearctic	Cramp & Simmons (1977)
44.4	41.2	46.6	33.0	32.3	33.9	Indonesia (Java)	Hellerbrekers & Hoogerwerf (1967)
44.1			36.5			India	Ali & Ripley (1968)
44.0	41.0	51.0	34.0	30.0	35.0	South Africa	Brown et al. (1982)
43.4			33.5			India	Whistler (1935)
43.4	40.0	49.0	33.4	30.0	34.5	United States (Florida)	Weber (1975)
43.1	40.4	45.7	34.1	31.7	36.5	areas lumped	Hancock & Elliott (1978)

and breadth, but also observed fresh egg weight. Adult Cattle Egrets sometimes begin incubation with the laying of the first egg. This could make our calculation somewhat low because, in addition to fresh clutches (1 egg in the nest), we also measured partial (2 eggs) and completed (3 eggs) clutches. Thus incubation may have begun 1-2 days previously in nests with partial and completed clutches, causing the eggs to lose some of their original weight. However, our estimation of the species-specific weight constant K_w (= 0.506) is similar to the 0.501 calculated by Loftin and Bowman (1978) for the Cattle Egret and those given by Hoyt (1979) for species with similarly sized and shaped eggs.

Rahn and Ar (1974) found that the "ideal" egg loses about 18% of its initial weight during incubation, mainly due to water loss (see also Lundy 1969, Lomholt 1976) Even though our calculated fresh egg weight is almost identical to that of our observed fresh egg weight (23.9 g and 24.4 g, respectively) and Weber (1975) reported egg weight for "light blue eggs" (meaning early stage of incubation?) as 24.0 g, his and our measurements may underestimate true fresh egg weight. Moreover, Vleck et al. (1980, p. 407) give initial egg mass for *Bubulcus ibis* as 28 g (sample size and geographical origin of the eggs not included), thus substantiating this possibility. Our estimated egg weight loss of 11.8% during incubation using fresh egg weight minus "pipping egg" weight is almost half that reported by Rahn and Ar (1974) for the "ideal" egg. If we subtract observed "pipping egg" weight from Vleck et al.'s (1980) 28.0 g value for initial egg weight, the result is a loss of 6.5 g during incubation, or 23%, which is somewhat closer to the predicted weight loss for the "ideal" egg, although questionably higher.

Habitat Destruction

Colonial-nesting herons are known to adversely affect surrounding vegetation. Jenni (1969) reported that the weight of nesting and roosting birds broke limbs. Nest-building birds eventually broke off every available twig in the colony and then began breaking off green twigs. He added that when the size of the suitable nesting habitat is small, the herons may effectively destroy the habitat. Whereas Telfair (1980) suggested that Cattle Egrets are beneficial to mangrove ecosystems because they transfer nutrients and energy from terrestrial to aquatic systems, Burandt et al. (1977) warned that herons affect vegetation not only through physical abuse, but by deposition of wastes on vegetative parts. Indirect effects may occur resulting from accumulated excreta in aquatic ecosystems (Dusi et al. 1971, McDonald 1971). Gilham (1960) found that indigenous heath and scrub vegetation within inland heronries was destroyed as a result of soil reactions to an increased fertility resulting from the addition of bird guano, which was found to be rich in phosphorus, nitrogen, and potassium. In addition to increasing soil fertility, guano modified soil pH, making it more alkaline, thereby causing an unfavorable osmotic balance set up in the soil by the accumulation of salts (see also Weseloh and Brown 1971, and Dusi 1978, 1983).

Throughout the Cattle Egret colony at Fox's Bay, we found markedly smaller nests than previously reported in the literature. This suggests that suitable nesting materials were virtually exhausted. One egg was found balanced in a fork at the main trunk of an inclined white mangrove with literally two or three twigs holding it in place. In comparison with normally dense white mangrove vegetation that we had experienced on other islands, we found the stands at Fox's Bay to be quite "open" and easy to penetrate. The usual entanglements of dead branches and vegetative debris were uncommon.

Telfair (1980) stated that "Cattle Egrets may cause changes which shorten the "life-span" of nest site vegetation, necessitating frequent establishments of new heronries." This may have already occurred on Montserrat. The scarcity of suitable nesting materials suggests that the swamp vegetation is no longer adequate to support the Fox's Bay egret population, which has been estimated at 1,800 individuals and has covered more than 2 ha in the past (D. King pers. comm.). We found only 307 nests or 614 breeding Cattle Egrets in June and July of 1984. Either a small percentage of the population was breeding, or many egrets had emigrated. Whereas Fox's Bay was believed to be the only nesting site of the Cattle Egret on the island for many years, a few egrets have been found recently nesting in neem trees (*Melia azedarach* L.) at a nearby golf course (D. Gibbs pers. comm., pers. obs.). We also observed Cattle Egrets near Trant's Bay some 8 km away on the windward side of the island. While it is possible that individuals from the Fox's Bay population make daily foraging flights to this area, young Cattle Egrets, prospecting for new heronries, are known to wander 5,000 km (Browder 1973) and could found new colonies on the windward side of Montserrat.

In addition to the pressures placed upon the Fox's Bay mangrove ecosystem by the Cattle Egret, the swamp continues to suffer from the impact of natural storms and human activities. Heavy rains, landslides, urban development, and other human activities near the swamp have affected proper drainage (pers. obs.). Impoundments (e.g., roads) altered drainage patterns, upland watershed deforestation increased siltation, reduced flooding promoted the oxidation of reduced compounds in the soil, resulting in a lowering of the pH, and stagnant waters with elevated temperatures produce a synergistic effect with hypersalinity to kill mangrove vegetation (Jimenez, et al. 1985). Charcoal burners and grazing cattle have selectively eliminated much of the natural vegetation, leaving behind only plants that are adapted (i.e., with spines, thorns, and toxic chemicals) to withstand such predation pressures. As mentioned previously, there are signs of salinity changes in the normally brackish water at Fox's Bay, siltation, and soil compaction (pers. obs.), all of which will greatly affect the mangroves and associated vegetation. Local residents agree that the size of the swamp has been diminishing each year, partly due to wood cutting and grazing, but mostly due to an increased natural mortality of the vegetation.

Conclusions and Recommendations

The Cattle Egret population at Fox's Bay will probably keep adjusting to the continued reduction of suitable nesting habitat, as all the available signs suggest, by founding new settlements elsewhere on the island, perhaps inland. Although the Cattle Egret was shown to damage, and in some cases destroy mangrove vegetation, we believe that it should not be considered a major cause in the apparent death of the mangrove ecosystem, nor should steps be taken to discourage the egret's presence within the Fox's Bay Bird Sanctuary.

There is a need to continually monitor the status of the mangrove ecosystem at Fox's Bay. In the past, the entire Cattle Egret population on Montserrat was thought to breed solely in the small mangrove swamp at Fox's Bay. The recently discovered nests outside the swamp suggest that the population is expanding, probably owing to the dispersal of fledgling egrets and emigration of adult egrets from the now over-crowded and possibly sub-optimal nesting site at Fox's Bay. Future studies on Montserrat, both at the original (founder) colony and elsewhere on the island (including probable inland colonies), could estimate growth rates for these small island populations, comparing coastal and inland populations with those of continental populations. Also, the similarities and differences between the reproductive ecologies of the early founder populations could be compared with those of larger or, at least, allopatric populations (coastal versus inland) on Montserrat.

Subsequent studies could assess the ecological status of the Fox's Bay mangrove ecosystem and could evaluate the progress of management steps, should they be undertaken in the near future. It is imperative that wood cutters and grazing animals be excluded from the area to allow regeneration of the remaining natural vegetation. Periodic monitoring of the mangrove swamp (testing for water salinity, siltation rates, pH, and degree of soil compaction) should be carried out. In-depth surveys of watersheds and impoundments above the swamp should be conducted to evaluate the rate of deforestation, soil erosion, and existing drainage patterns. Urban planners and local residents must be made aware of the dynamic state, complex needs, and most importantly, the fragility of the Fox' Bay mangrove ecosystem in order to eliminate existing threats to the wetlands habitat and the bird sanctuary. Future development should be planned keeping the basic needs of the mangrove ecosystem in mind.

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