DYNAMICS OF RANGE EXPANSION OF CATTLE EGRETS IN FLORIDA

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AFRICAN CATTLE EGRETS (*Bubulcus ibis ibis*) were originally confined to the Old World. Following an increase and expansion of range in Africa since 1900 (Skead, 1952), they colonized northeastern South America about 1930 (Haverschmidt, 1950, 1953; Dugand, 1954). In 1948 they invaded North America (Sprunt, 1953) and are now well established and abundant in Florida around Lake Okeechobee. In the past twenty years Indian Cattle Egrets (*B. i. coromandus*) have also spread from the Moluccas to New Guinea and Australia (Peterson, 1954). This has offered a unique opportunity to study a species during a period of rapid range expansion. Much is still unknown about this process, partly because the birds have not previously been studied during the initial phases of their establishment in a new region.

During the spring and summer of 1954, I was fortunate enough to witness the first appearance and nesting of Cattle Egrets in North Florida, a region where they did not previously occur and which is 180 miles from the next-nearest nesting colony. My observations help to fill some of the gaps in our knowledge of the process of range expansion and lead to some interesting ecological, ethological, and zoogeographical speculations.

David K. Caldwell, Thomas W. Hicks, Edwin H. McConkey, Edward L. Mockford, and Minter J. Westfall assisted me in the field on numerous occasions. Fred D. Bartleson generously made his own records available to me. Archie Carr and the late W. C. Allee read the manuscript and offered many valuable suggestions.

The observations reported herein were made at Lake Alice, one half mile southwest of Gainesville, Alachua County, Florida. This lake is the site of a large heron and ibis colony. A low shrubby swamp consisting of red maple (*Acer rubrum*), willow (*Salix longipes*), buttonbush (*Cephalanthus occidentalis*), and elderberry (*Sambucus simpsoni*) covers much of the lake's 90 acres; the remainder consists of open water, dense mats of water pennywort (*Hydrocotyle* sp.), and small patches of flag (*Typha, Sagittaria, Pontederia*) marsh. There is a fringing swamp of tupelo gum (*Nyssa biflora*).

The following species of birds nest in the colony, arriving in early March and leaving gradually in the late summer and autumn. A few remain all winter. The figures indicate the number present (maximum counts of the evening flights) in 1954 prior to the nesting

season; the total is approximately doubled when the young are on the wing.

Water Turkey (*Anhinga anhinga*)	100
Great Blue Heron (*Ardea herodias*)	4
Greater Egret (*Casmerodius albus*)	44
Snowy Egret (*Leucophoyx thula*)	505
Tricolored Heron (*Hydranassa tricolor*)	52
Little Blue Heron (*Florida caerulea*)	276
Cattle Egret (*Bubulcus ibis*)	6
Green Heron (*Butorides virescens*)	5
Black-crowned Night Heron (*Nycticorax nycticorax*)	12
Yellow-crowned Night Heron (*Nyctanassa violacea*)	15
White Ibis (*Eudocimus albus*)	2200
Eastern Glossy Ibis (*Plegadis falcinellus*)	56

Most of these birds, along with Wood Storks (*Mycteria americana*) and Sandhill Cranes (*Grus canadensis*), feed about three miles south of the colony on Payne's Prairie, a 13,000-acre wet prairie and marsh used for cattle pasture. Such prairies are characteristic of much of southern and southeastern Alachua County and adjacent parts of Marion and Putnam counties and are vegetationally and faunistically similar to, but isolated by many miles from, the prairies and marshes of the upper St. Johns River, the Kissimmee Valley, and Lake Okeechobee, the last being the only other area in North America where Cattle Egrets are known to nest.

Observations by Karraker (1953) and Benjamin B. Leavitt (unpublished) have proven beyond reasonable doubt the absence of Cattle Egrets in this area prior to 1953.

1953.—I first began regular field work in Alachua County in February, 1953. I am certain that no Cattle Egrets were present during most of that year, for the following reasons: I visited the Lake Alice colony almost weekly during the spring and early summer; I was always alert for Cattle Egrets and could not have missed them if they had been using the colony. During the summer and autumn I looked at thousands of egrets on Payne's Prairie, now the Cattle Egrets' feeding area, and saw none there. Having a special interest in the symbiosis between Snowy Egrets and cattle, I carefully observed every egret I saw associating with cattle and found no Cattle Egrets.

The first Cattle Egret seen in North Florida was found by Fred Bartleson on 20 November in a roadside ditch just north of Payne's Prairie.

1954.—I first noticed that the herons and ibises had returned to the Lake Alice colony on the evening of 11 March. On 25 March, I made the first census of the evening flight and saw three Cattle

Egrets; at least one was an adult beginning to assume nuptial plumage. On subsequent weekly visits I counted up to a maximum of six Cattle Egrets. On the evening of 29 April, six were seen, two of them in full nuptial plumage, three in partial nuptial plumage, and one in winter plumage. Earlier observations indicated the presence at that time of one additional bird in winter plumage. This makes a total pre-nesting population of seven, a figure supported by subsequent observations.

Since certain of the Cattle Egrets in full nuptial plumage centered most of their attention on a single clump of bushes, I suspected they might be nesting. On 2 May, I began searching for nests and soon located one by watching the adult birds and following them when they went to feed their nestlings. This nest was in a red maple about four feet above the water. The three young birds which it contained were well covered with down; I estimated that they were between two and three weeks old. This indicates that laying took place between 20 and 30 March. In the same clump of bushes with the Cattle Egrets' nest were nests of Snowy Egrets, Little Blue Herons, and Tricolored Herons. I examined the nest again on 5 May, but the young had not changed noticeably.

On 22 May, the nest was empty. On that date I saw two nearly fledged juvenile Cattle Egrets perched on a bush near the nest site. I am not certain that they came from the same nest. From the behavior of the adult birds, I suspect that there was a second nest nearby.

During subsequent weeks I did not look for additional nests, assuming that the nesting season was over. The difficulty of finding and identifying nests when the adults are not feeding nestlings also helped prevent my finding any more. However I continued seeing the Cattle Egrets every week during the evening flights to the colony and noticed that most of the adults remained in full nuptial plumage well into July. During this period I counted a maximum of seven Cattle Egrets, including at least one young of the year.

On 25 July I discovered two more nests by watching the adults feed the young birds. One was in a buttonbush three feet above the water and contained two nearly fledged young. The other was in a nearby buttonbush two and a half feet above the water and contained two young birds slightly younger than those in the neighboring nest. These were probably second nestings; laying had evidently taken place about the end of May. On 28 July the young from the former nest were perched in the bushes above the nest; the young were still on the latter nest. Both broods were still being fed by the

parents. On 29 July the young were gone from the former nest; one fully fledged immature bird was seen at the colony. On 4 August two immature birds, one of which was perhaps unfledged, were there.

On the morning of 28 July, I watched the birds depart from the colony. I saw twelve Cattle Egrets. Four were in nuptial plumage and were the parents of the nestlings in the two nests. Three adults were in non-nuptial plumage. One bird was a fully-fledged juvenile, probably the one observed earlier in the evening flights and probably from the earlier nest. The other four were the four nestlings. Unless there were additional immature birds present from the first nest (or nests), these twelve birds were probably the total population at the close of the nesting season.

I continued to observe Cattle Egrets in the evening flights later in the summer. At least one adult in full nuptial plumage was present as late as 26 August; on that morning I watched it for over an hour, and it gave no indication of having a nest or dependent young. At least two adults in non-nuptial plumage were also seen that day.

Although these data are too meager to use in drawing conclusions regarding nesting success, it is probably not significantly different from that of the other small herons using the colony, nor different from that of Cattle Egrets in Spain (Riddell, 1944: 505), where they have always occurred in abundance.

1955.—The Cattle Egrets arrived at the colony on 11 April, when I counted five in the evening flight.

On 29 April, I counted seven Cattle Egrets. Three were in nuptial plumage; the other four, presumably year-old birds, were in non-nuptial plumage. I found two nests, and from the behavior of the birds I am certain that one more nest was present, making a total of three nests. Since the four birds in non-nuptial plumage undoubtedly were not breeding, it can safely be assumed that three additional breeding adults were present. This makes a total of ten Cattle Egrets at the colony.

I left Florida in the early summer of 1955, so have no data on the fate of these nests, or on second broods.

Range expansion is dependent on the ability of a species to disperse to unoccupied areas, which may require crossing distributional barriers, and on its ability to establish itself in new areas. Each of these factors may be discussed separately.

Dispersal.—Two questions regarding dispersal must be answered: Where did the birds come from? And why did they move to the Lake Alice region, across 180 miles of territory where the species is unknown?

There can be little doubt that the Cattle Egrets at Lake Alice came from the flourishing colonies around Lake Okeechobee, one of which contained over three hundred nests in the spring of 1954 (Sprunt, *in litt.*).

The adults of most species of birds, including herons, tend to occupy the same home range year after year, even if they are migratory, and use it only during the breeding season. Therefore I do not believe that random wandering can satisfactorily account for the establishment of new nesting colonies. Skead (1952: 210) holds a different opinion. In South Africa, wandering flocks of Cattle Egrets, the origins of which are obscure, may, he believes, found new colonies. There is no evidence of such wandering *flocks* in the Americas. Two alternative explanations of the dispersal will be considered: (1) Wandering immature Cattle Egrets could have settled in the area, or (2) adult Cattle Egrets could have mingled with flocks of other species of herons from Lake Alice and accompanied them to the breeding colony.

In most species of birds it is the young individuals without established home ranges which tend to wander and settle in unoccupied areas. Young herons hatched in the southern states regularly wander north during the late summer. A number of Cattle Egrets appeared in northern regions (Massachusetts, New Jersey, Virginia, Maryland, Illinois, Newfoundland) in the summers of 1952 and 1953 (Peterson, 1954). This would seem easily to account for the presence of the Cattle Egrets which nested at Lake Alice. But this explanation is untenable, as the evidence will show.

First, the exodus to the north takes place in late summer. The birds at Lake Alice arrived in the spring. I am certain, for reasons previously stated, that there were no Cattle Egrets in the Lake Alice and Payne's Prairie region in the summer and early autumn of 1953. Second, wandering immature herons return south in the autumn; they do not remain in the northern areas to nest. Third, the Cattle Egrets nested at Lake Alice their first year there. Cattle Egrets do not breed until the second season following hatching (Riddell, 1944: 507). Therefore at least five of the birds at Lake Alice were at least two years old and could not have arrived the previous summer as young of the year. We must therefore conclude that wandering immature birds were not the source of the Lake Alice colony.

The herons and ibises from Lake Alice winter in South Florida, where Cattle Egrets are already well established and fairly abundant. Since the interspecific flocking reaction is strong in the small herons,

the Cattle Egrets, once becoming associated with a flock of Snowy Egrets or other small herons from Lake Alice on their feeding and roosting grounds, would very likely remain with them during their northward migration to the Lake Alice colony.

All of my observations support these speculations. The Cattle Egrets arrived at Lake Alice in the spring at the same time as the other herons and ibises. Both at Lake Alice and in the Lake Okeechobee region, I have always found Cattle Egrets associating with flocks of the other small herons during the morning and evening flights. Around Lake Okeechobee I have seen both Cattle Egrets and Snowy Egrets feeding with the same herd of cattle.

The most logical conclusion is that the Cattle Egrets became mixed with the local herons on their wintering grounds and accompanied them to Lake Alice. In a similar manner they could have spread from South America to Florida, as many North American herons winter as far south as the Caribbean coast of South America, where Cattle Egrets are now quite common. They also could have spread from the Moluccas to Australia in the same way. However no herons migrate across the Atlantic, so their arrival in the New World from Africa was probably fortuitous, migrating birds having been driven off course by adverse weather. This is a common enough phenomenon, but one which results in the establishment of new colonies only under the most favorable conditions.

Establishment.—For successful establishment, the region must meet the ecological requirements of the species, and the initial colonizers must be able to maintain their numbers.

Cattle Egrets are apparently obligate commensals of large grazing mammals; I have seen hundreds of them around Lake Okeechobee but have never seen them feeding away from cattle. The recent growth of the cattle industry has made available to Cattle Egrets a vast new territory, because no large grazing mammals are indigenous to the New World tropics. In Florida, Snowy Egrets have recently developed a facultative feeding relationship with grazing cattle (Rice, 1954); observations which I plan to publish later indicate that they are ineffectual competitors of Cattle Egrets. Little Egrets, *Egretta garzetta* (Roberts, 1940: 21; Roosevelt, 1910: 467), and Lesser Egrets, *Mesophoyx intermedia* (Caldwell and Caldwell, 1931: 298), engage in a similar facultative symbiosis with large hoofed mammals within the Cattle Egrets' Old World range.

In colonial birds there exist numerical thresholds, below which the breeding cycle is not completed (Darling, 1938: 108). Fulmars (*Fulmarus glacialis*) can establish new breeding colonies only if a

certain minimum number of birds is present (Fisher and Waterston, 1941: 250). Many species of herons are highly gregarious, always nesting in large colonies. Cattle Egret colonies in South Africa contain from ten to two thousand nests, although it was not stated (Skead, 1952: 207) whether other species shared the colonies. I do not believe that Cattle Egrets would breed in colonies of fewer than ten pairs of birds.

There was an initial population of only seven Cattle Egrets at Lake Alice. If the above assumption is correct, they would not have nested if it had not been for the presence of the other species of herons. The latter apparently supplied the necessary stimulus to initiate the reproductive cycle, a stimulus ordinarily furnished by other members of the same species. Great Black-backed Gulls (*Larus marinus*) usually nest in colonies, but where other species of gulls are present, occasional pairs will nest in colonies of the latter (Darling, 1938: 57). This interspecific social facilitation could also explain the unusual success in South America of a very few Cattle Egrets arriving fortuitously from Africa.

Observations on Cattle Egrets suggest that mutual *inter*specific reactions to social stimuli have enabled this species to disperse to unoccupied areas with much greater facility than would have been possible otherwise. Furthermore, they have enabled the species to establish new breeding colonies with much smaller initial populations, thus overcoming the disadvantages of undercrowding which result from innate sociality, without giving up the ecological advantages of colonial nesting. This could conceivably give the species a slight, but perhaps critical, advantage over competing species when both are expanding into unoccupied range. Concomitant with this is a wide and often discontinuous geographical distribution with all its evolutionary potentialities.

SUMMARY

African Cattle Egrets (*Bubulcus ibis ibis*) became established in North Florida for the first time in the spring of 1954. At Lake Alice, Alachua County, an initial population of seven birds hatched three or four broods of young in a large heron and ibis colony. At least twelve Cattle Egrets were present at the close of the nesting season. In the spring of 1955 there were ten Cattle Egrets, including three breeding pairs, at the colony.

The initial seven Cattle Egrets doubtless came from Lake Okeechobee, 180 miles to the south. Observations suggest that they became associated with flocks of wintering herons from Lake Alice and ac-

companied them there. Emigration from South America to Florida, and from the Moluccas to Australia, possibly occurred in the same way. Summer wandering of juveniles is apparently an unimportant factor in this rapid "explosive" type of range expansion.

Range expansion was made possible by the cattle industry creating a suitable niche for the species.

It seems probable that so few Cattle Egrets could not have established a nesting colony at Lake Alice if it had not been for the presence of the other herons, which furnished sufficient stimulus to initiate the reproductive cycle.

The habit of associating with other species of herons would thus seem to be of survival value in facilitating dispersal and establishment.

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