A STUDY OF THE ECOLOGY OF FOUR SPECIES OF HERONS DURING THE BREEDING SEASON AT LAKE ALICE ALACHUA COUNTY, FLORIDA[1]

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INTRODUCTION

In spite of the large literature on various aspects of the biology of the cosmopolitan family Ardeidae, we know little about their breeding ecology. Our knowledge is especially lacking when it comes to events taking place inside the heronry, and at least one author (Valverde, 1955-56) suggests that the heronry shall remain forever a mystery. In recent years many reports documenting the remarkable range expansion of the Cattle Egret *(Bubulcus ibis)* have appeared, yet little information is available concerning its reproduction.

The purpose of this paper is to compare the breeding ecology of 4 common species of Ardeids in the Gainesville, Florida, area. This is done by comparing the breeding biology, feeding, and food habits of the Snowy Egret *(Leucophoyx thula)*, Cattle Egret, Little Blue Heron *(Florida caerulea)*, and the Louisiana Heron *(Hydranassa tricolor)* in 1958, 1959, and 1960. All 4 species bred at Lake Alice on the University of Florida campus. Except for the work of Meanley (1955) on the Little Blue Heron, there had been little information available on the breeding biology of these birds. The study was also planned to provide information on the birds' interspecific relationships, and on their relationships with their environment, with special emphasis on the heronry. Besides helping interpret the significance of the heronry it was thought that a comparative approach would provide data helpful in understanding the population explosion of the Cattle Egret.

After this study was begun, Meyerriecks (1960a) made a significant contribution to our knowledge of North American herons by providing a detailed account of the breeding behavior of the Green Heron *(Butorides virescens)* as compared with the breeding behavior of the Great Blue *(Ardea herodias)* and Great White Herons *(Ardea occidentalis)*, Reddish Egret *(Dichromanassa rufescens)*, and the Snowy Egret. Meyerriecks (in Palmer, 1962) made excellent

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summaries of existing knowledge on all aspects of the reproduction of the North American herons. In these latter summaries he also included much new information on the breeding behavior, especially courtship and pairing behavior, for many species, and on all phases of the breeding biology of the Green Heron. In 1965 Teal published on the nesting success of several ciconiiformes, including the Snowy Egret and Louisiana Heron. Unfortunately he was able to visit the heronry only once per week, and the relatively high losses of eggs, nests and young must therefore be interpreted with caution.

Considerable work has been done in Europe on the breeding biology of several heron species. The most important early work on the Gray Heron *(Ardea cinerea)* was Verwey's study of breeding behavior (1930). Lowe (1954) summarized the work done on the Gray Heron. More recently Owen (1960, and earlier papers) has made important contributions to our knowledge of the Gray Heron and to heron reproductive biology in general. Steinfatt (1939), Owen and Phillips (1956), and several others have worked on various aspects of the breeding biology of the Purple Heron *(Ardea purpurea)*. Valverde (1955-56) published an excellent account of the ecology of the Little Egret *(Egretta garzetta)* and other herons at Camargue, France. Additional studies are cited in later sections of this paper.

The systematics of the Ardeidae have received much attention in recent years (see Dickerman and Parkes, 1968, for a recent partial bibliography). In this paper I have followed the American Ornithologists' Union Checklist 1957. In this paper I use the term heronry to refer to the breeding place of gregarious herons and egrets. The term rookery, though often applied to the nesting place of other gregarious birds, should be restricted to the breeding place of Rooks *(Corvus frugilegus)*. For extra-continental species I have used the names as they appeared in the papers cited.

DESCRIPTION OF STUDY AREA

Most of the observations reported here were made near Gainesville, Alachua County, Florida, primarily at Lake Alice and Payne's Prairie, but additional observations were made in many other Florida localities. The climate of Gainesville is almost semitropical. The long summers are warm and wet and the relative humidity is high. Winters are short and mild. Rainfall and relative humidity are less than in the summers. Temperature approaches freezing occasionally during the winter months, but ice is rare on Lake Alice and Payne's Prairie.

Gainesville, just southeast of the center of Alachua County, Florida is located in the Central Highlands (Cooke, 1945) near the northern end of the Florida Peninsula and is about midway between the Atlantic Ocean and the Gulf of Mexico. The terrain is mostly gently rolling hills with numerous ponds and sinks and with several large wet prairies and lakes to the south. The area is underlain by limestone and parts of the uplands show early karst topography. The height above sea level varies from 15 to 61 m; the large wet prairies in the southern part of the county all lie at about 15 m. Practically all the soils are fine sand originally derived from Coastal Plain sediments (Taylor *et al.*, 1954). There are 3 major types of vegetation: hardwood hammocks, pinelands and wetlands. Mesic hammocks bordering the prairies and lakes are characterized by magnolia *(Magnolia grandiflora)*, water-oak *(Quercus nigra)*, laurel-oak *(Quercus laurifolia)*, and cabbage palm *(Sabal palmetto)*, and the more open upland hammocks by live-oak *(Quercus virginiana)*, hickory *(Carya glabra)*, and sometimes longleaf *(Pinus palustris)* or loblolly pine *(Pinus taeda)*. There is practically no virgin mesic hammock in the area today; most of it has been cut over, and much of it is now maintained as pasture. Northeast of Gainesville are extensive pine flatwoods dominated by longleaf pine and saw-palmetto *(Serenoa repens)*. Laessle (1942) and Taylor *et al.* (1954) describe the vegetation of north central Florida in detail.

The extensive wetlands are vital to the maintenance of the native heron population in the Gainesville area. The largest and most important of these wetlands is Payne's Prairie or Alachua Lake. In recent years this 13,000 acre prairie has been the principal feeding ground for herons around Gainesville. Parts of this nearly level prairie are permanently flooded, but extensive areas are periodically inundated by changes in water level. The conspicuous vegetation of the deeper parts of the prairie includes water-hyacinth *(Eichhornia crassipes)*, pickeral weed *(Pontederia lanceolata)*, and arrowhead (*Sagittaria* spp.), while the shallower and less often flooded parts of the prairie support dog-fennel (*Eupatorium* spp.), maiden cane *(Panicum hemitomum)*, and a wide variety of other grasses. The vegetation and physiography of Payne's Prairie has been described in detail by Birkenholz (1963).

There are several other extensive wet prairies in the area. Levy Lake, Ledwith Lake, Tuscawilla Lake, Kanapaha Prairie, and Hogtown Prairie are the larger and more important of these areas. They are roughly similar to Payne's Prairie and are covered with similar vegetation. In addition to these prairies there are extensive marshes and wetlands surrounding Orange Lake, slightly farther south. Throughout the region are many small prairies, ponds, and sinks with marshy shore lines similar to Payne's Prairie. Practically all such areas are used by the herons for feeding at least occasionally.

Social herons have nested in at least 3 separate mixed colonies in the Gainesville area. A floating island, Bird Island, in Orange Lake, has supported a heronry for many years (Baynard, 1912). Herons formerly bred in emergent trees and bushes in Bivin's Arm just south of Gainesville (Dickinson, 1946). Since 1948 there has been a large mixed heronry at Lake Alice on the University of Florida campus. In 1948 the herons failed to breed at Bivin's Arm, 1.5 miles southeast of Lake Alice, and had not reestab-

lished themselves there at the time of this study. It appears that the birds that deserted Bivin's Arm were the ones that occupied Lake Alice. These 3 heronries have several features in common: the vegetation is similar, they are surrounded by and in the most part are over water at least several feet deep; there are American alligator populations *(Alligator mississipiensis)* in all 3 lakes, there is little if any mammalian predation, and human disturbance has been minimal. The less social Green Heron and Least Bittern *(Ixobrychus exilis)* also nest at these places as well as other localities near Gainesville. Great Blue Herons also nested in colonies near Gainesville.

Most of the observations presented in this report are based on data gathered at Lake Alice. Lake Alice was for many years a small pond of about 10 acres, although its extent fluctuated considerably. In 1948 an earthen flood control dam was built just west of the "lake," and an area of about 90 acres was inundated. In this newly flooded area were a low lying buttonbush *(Cepalanthus occidentalis)* marsh and the margins of an extensive hammock of live oak, loblolly pine, and sweet-gum *(Liquidamber styraciflua)*. Except for the buttonbush, this woody growth was all killed by the rising water. Since that time, the hammock trees have been replaced by the buttonbush and by wax myrtle *(Myrica cerifera)*, willow (*Salix* spp.), red maple *(Acer rubrum)*, and elder *(Sambucus simpsonii.)* What probably attracted the herons to Lake Alice was the abundance of bushes and trees.

The only remnants of the original hammock in 1960 were a few huge oak stumps. Beginning in 1958 and continuing through 1960 there was a gradual decline in the vigor of the trees and bushes, and many of them died. Most of the buttonbush rooted in less than a meter of water was in poor condition and put out only a few new twigs each year. The most luxuriant woody growth in the lake during those years was on a shallow sand bar in the west end of the lake, in other shallow areas near the middle of the south shore, and on the floating islands. There are several floating islands in the southeast bay of Lake Alice. Nearly all of the nesting during the 3 years of this study was on these islands and the west bar.

The quantitative data on the breeding ecology of the herons was collected in 1960 on the floating islands. The islands were anchored by tree roots and were surrounded by water at least 2 m deep. The island rafts were composed of living and dead roots, which acted as the principal binding agent, and which together with other decayed and decaying organic matter made up the bulk of the substrate. The living plants, especially their roots and tubers, played an important role in maintaining the island. Water pennywort (*Hydrocotyle* spp.) grew over most of the area and was the only ground cover in the heavily wooded portions. A begonia *(Begonia semperflorens)* grew where there was partial shade, and broadleafed cattail *(Typha latifolia)* and water willow *(Decondon verticillatus)* grew in exposed places. In some places water pennywort grew out over the water for several meters around the edge, but water hyacinth grew over deeper water. Lush growths of water hyacinth marked the positions of holes in the island mat and of channels which transected the islands. Red maple was the dominant tree on the islands. Buttonbush was as abundant but did not attain the size of the red maple; it occurred over all the islands, but was least abundant around their edges. Wax myrtle, though not abundant, was scattered over the islands. Willow grew mostly around the edges of the island; its large, irregular trunks extended out over the water. Elder grew around the edges and in other sites exposed to sunlight.

The ardeids that nested at Lake Alice during this study included Green Heron, Little Blue Heron, Cattle Egret, Snowy Egret, Louisiana Heron, Black-crowned Night Heron *(Nycticorax nycticorax)* and the Least Bittern. The Glossy Ibis *(Plegadis falcinellus)* also nested at Lake Alice in 1958, 1959, and 1960. The Common Egret *(Casmerodius albus)* had not nested there since 1958. The White Ibis *(Eudocimus albus)* did not remain at Lake Alice to breed in 1960 although they roosted there early in the spring. White Ibises had nested at Lake Alice every year from 1948 through 1959. Anhingas *(Anhinga anhinga)* also nested in association with the heronry. Other ardeids known to occur at Lake Alice, but not known to have nested there, included Great White and Great Blue Herons, Yellow-crowned Night Heron *(Nyctanassa violacea)*, and Wood Ibis *(Mycteria americana)*.

METHODS

Observations of adults, nestlings, and fledglings were made from outside the heronry during 1958, 1959, and 1960. In 1960 detailed observations were also made inside the heronry. As each nest was found, the limb beneath it was tagged with a number. These nests were visited daily and the condition of the nest, number of eggs, or number of young was recorded. A chrome-plated tin attached to a pole was used to see into overhead nests. All eggs laid in nests low enough to reach were marked with waterproof ink and the fate of each individual egg was followed. Two blinds were placed in the heronry.

During the 1960 season a total of 495 nests were tagged. There was no immediate way of identifying the owners of these nests, but because they were all visited daily, those that were completed were eventually identified. However, many of these 495 nests were not completed and others were destroyed before the identity of the adults could be determined. The ownership of some nests was not determined until the young hatched. By the end of the season, daily observations had been made on a total of 280 marked and identified nests. This number included 102 Snowy Egret nests, 85 Cattle Egret nests, 58 Little Blue Heron nests, and 35 Louisiana Heron nests. Observations of most of these nests extended from early nest building through rearing of the young.

Duration of daily observations varied from a brief daily check of each marked nest in the middle of the heronry to longer observations of nests that could be watched with binoculars or spotting scope from outside the heronry proper.

Study of nestling food habits was based on the analysis of material regurgitated by the nestlings. When disturbed or excited, by the investigator for example, young herons often regurgitated. The pellets they regurgitated represented the most recent meal of the birds and not the undigestible remains of several meals. Herons also produce pellets composed solely of undigestible remnants similar to those produced by raptors and though they have been studied (Hibbert-Ware, 1940, and others), they can give very misleading ideas about the diet of the birds as shown by Owen and Phillips (1956), and they are of rather limited value (Hartley, 1948). By systematically collecting pellets of regurgitated food not yet acted on by digestion it was possible to acquire a series of heron meals without collecting the birds. Because a large series of pellets is potentially available, the investigator can, as was done in this study, reject pellets which show even moderate digestion. Pellets could be taken repeatedly from the same individuals, and this might be especially advantageous if few broods could be found. The possible effects this collecting had on the survival of nestling herons at Lake Alice is discussed later.

Pellets of identifiable food were preserved immediately in 10% formalin. From one to several days later the pellets were washed and transferred to 30% isopropanol. Later the food items were identified and counted. After drying the food items on paper towels, their volume was determined by measuring the volume of water they displaced.

Numerical data are usually presented as mean data. The mean, in most cases, is followed by the standard error, and is usually accompanied by a parenthetical statement of the size of the sample and the range of the observations. Where redundant, this parenthetical information is omitted. The relatively robust "t" test is used to compare means (Simpson, Roe and Lewontin, 1960). Analysis of variance and χ^2 tests are also used. The level of significance is 0.05, unless otherwise stated.

BREEDING ECOLOGY

Some differences between the ecology of the Snowy Egret, Cattle Egret, Little Blue Heron, and Louisiana Heron during the breeding season are the direct result of interspecific relationships within the heronry during the breeding season. Others are the result of differences in the total biology. There is one quantitative study of the Little Blue Heron (Meanley, 1955) which provides comparable data and one study on the Snowy Egret and Louisiana Heron (Teal, 1965). Available data for all North American species was summarized by Meyerriecks (in Palmer, 1962).

WINTER STATUS AND SPRING ARRIVAL

Herons and egrets are conspicuous wintering birds in south Florida, but they are noticeably less abundant along the northern Florida coasts and along the Central Highlands. Gainesville is marginal as a wintering area for most of the ardeids, but it is not far distant from optimum wintering habitat. Their numbers around Gainesville during the winter fluctuate drastically and appear to be related to changes in weather, especially temperature.

The Cattle Egret did not follow this pattern of irregular winter use, but used Lake Alice as a regular winter roost. Throughout the winter of 1959-1960 approximately 100, and in 1960-1961 approximately 250 Cattle Egrets roosted at Lake Alice. The primary feeding area of the Cattle Egrets during these winters was in rolling uplands 4 to 10 miles northwest of Lake Alice. They roosted in emergent buttonbushes in the middle of the swamp and not on the floating islands. These winter feeding and roosting areas were not the same as those used by Cattle Egrets during the nesting seasons of 1958-1961. Craufurd (1966) reports that from late November through early April, during the nonbreeding season, Cattle Egrets feed exclusively in gardens near Rokupr, Sierra Leone, where there are no cattle.

Starting in February, or as early as late January in some years, there was a gradual increase in the number of herons roosting at Lake Alice until a maximum was reached shortly after nesting began. In 1960 the number of ardeids at Lake Alice increased from 197 on February 23 to 322 on March 10. On March 19, 619 ardeids were roosting on the lake. Their number increased rapidly to 1770 on April 5, when some of the herons had started nesting.

During the 1960 breeding season, the populations of ardeids at Lake Alice were estimated at: Green Heron, 8 pairs; Little Blue Heron, 225 pairs; Cattle Egret, 300 pairs; Snowy Egret, 275 pairs; Louisiana Heron, 150 pairs; Black-crowned Night Heron, 2 pairs; and Least Bittern, 12 pairs. There were nearly 2,000 adult ardeids using the heronry during the nesting season.

ONSET OF BREEDING

Beginning in mid-March a few individuals returned to the Lake Alice heronry as early as 2 hr before sunset. In the morning a few stayed as long as 2 or 3 hr past the departure of most of the others. These individuals perched in the bushes and trees part of the time but spent much of their time moving about in the heronry, hopping from limb to limb and making short flights from one part of the heronry to another. They soon centered their activities around a specific bush or tree, and their short flights brought them back to this place. Here they directed threat displays at every heron that approached closely, regardless of species. Here they eventually performed the courtship displays. The males did not feed in these areas. After pair formation one of the pair usually remained in the territory while the other fed.

A complex sexual display, the Stretch Display, is apparently common to all herons. However there are significant differences in the way the display is performed by the different species. Meyerriecks (in Palmer, 1962) gives excellent descriptions of the Stretch Displays. At Lake Alice a male of any species who performed a series of Stretch Displays was soon surrounded by a group of his kind. When approached too closely by one of these individuals the male interrupted the displays to drive the encroaching individual away. A female ready for pair formation repeatedly approached the male and retreated from him without showing hostile behavior when he threatened her. Eventually the male's hostility lessened and the pair bond became established.

Within a few days the pair distinguished between individuals flying through their territory and those invading it. They tended to ignore the transients. Throughout this time there was a gradual decrease in size of the defendend area. This decrease is described in detail for the Green Heron by Meyerriecks (1960a).

NEST SITE

In 1958 the different species of herons at Lake Alice selected slightly different types of nest sites. As a result the nests were vertically stratified. Although Snowy Egret nests were between 1.0 and 1.5 m above the heronry floor, a few were as high as 3 m (all heights were estimated from the shore in 1958). Snowy Egrets nested around the edges of the heronry and around clearings in the middle of the heronry, in more exposed sites than the other species. Cattle Egrets started nesting in the middle of the heronry in dense vegetation. Their nests were usually from 1.2 to 2.4 m above the heronry floor. Later in the season, as the size of the heronry increased, Cattle Egrets started nesting around the edges and around other openings as well as in the middle of the area. They also started selecting higher sites. Cattle Egret sites were similar to the earlier Snowy Egrets, mostly around 3 m and occasionally higher. Little Blue Heron nests were in better sheltered, sturdier locations than were Snowy Egret nests. Louisiana Herons nested at heights of 0.5 to 1.5 m, lower than any of the other species. In contrast to the Snowy Egret, the Louisiana Heron nests were in well sheltered places.

In 1959 the nests were again stratified, but not so conspicuously as in 1958. Stratification became less conspicuous late in the season. Some Cattle Egrets nested higher than did any of the other species. Louisiana Herons again nested lower than the others. However, there was much overlap, and many individuals of all 4 species nested between 1.2 and 1.8 m above the heronry floor. To clarify this pattern, detailed observations of nest sites were made in 1960.

Snowy Egrets, Cattle Egrets, Little Blue Herons and Louisiana Herons built their nests within the territories established during courtship. The male typically performed his displays on a sturdy site offering considerable support, and the nest was usually built in the same place. The nest site was the center of most pair behavior.

Old nest platforms offered especially sturdy places to court, preen, copulate, and eventually nest. The earliest nesting herons, Louisiana Herons and Snowy Egrets, occupied most of the old nests. In 1960 old nests were occupied before Cattle Egrets and Little Blue Herons started nesting. However, Cattle Egrets, and less often the other herons, utilized nests built earlier in the season by other herons and later abandoned. Those Cattle Egrets which started nesting in late July sometimes used nests recently abandoned by young Snowy Egrets or Little Blue Herons. Although old nests were not available to Little Blue Herons at Lake Alice, Meanley (1955) found that Little Blue Herons in Arkansas did not use old nests when available. At Lake Alice only a few nests persisted from one season to the next; however, a very few were built in such favorable locations that they persisted for many years. Some nests had been rebuilt at least five times. Heron nests are sometimes more permanent than they were at Lake Alice. In the spring of 1955 on western Long Island, New York, Meyerriecks (in Palmer, 1962) found 59 of the 63 Green Heron nests he had marked the previous fall. Lowe (1954) describes Gray Heron nests as near-permanent and mentions nests known to have persisted for more than 11 years.

At Lake Alice in 1960 the most common nest sites of Little Blue Herons were horizontal limbs with the nest structure wedged against the main trunk. Other sites included: forks of large horizontal limbs, with the nest placed either over the fork or between the two branches just beyond the fork; places where two branches crossed; or almost any place where the first few twigs could be lodged. Although Snowy Egrets built in similar places, they tended to nest more frequently in open exposed areas and often placed their nests farther from main trunks, in more precarious situations. Some herons broke twigs off living trees, and when the terminal shoot, especially of wax myrtle was thus pruned, growth of limbs immediately below that point was stimulated. This growth produced a basket-like structure which made sturdy nest sites. Snowy Egrets sometimes nested in these sites. Louisiana Herons that did not obtain old nests nested in low, thick vegetation. Cattle Egrets were the last to start breeding at Lake Alice and generally acquired territories and nest sites higher in trees and bushes than did the other species.

Heron territories at Lake Alice had definite vertical as well as lateral limits. Both dimensions decreased following pair formation until the territory consisted of a very small area around the nest.

The nesting substrate of Snowy Egrets in Florida is described as cypress and mangrove swamps and buttonbush ponds by Howell (1932), and willow islands by Bent (1926). In Texas they nest in prickly pear, huisache and reeds (Bent, 1926). In Nevada they nest in hardstem bulrush (Giles and Marshall, 1954). In North Carolina they nest in red cedar

TABLE 1. The species of trees and bushes used by four species of herons as nest sites at Lake Alice, 1960.

Species (Number of Nests)	Percent of Nests in Each Type of Tree				
	Maple	Buttonbush	Elder	Wax Myrtle	Willow
Snowy Egret (88)	43	26	18	6	7
Cattle Egret (73)	33	29	19	12	7
Little Blue Heron (43)	49	36	11	—	4
Louisiana Heron (28)	11	29	39	18	4

and wax myrtle (Funderburg, 1960a), and in Missouri they nest in pines (Peterson, 1965). They nest in a great many other sites as well, apparently using whatever substrate is available from bulrushes to trees. Nests are placed on lower limbs from 2.4 to 3.7 m above the water (Howell, 1932), in willows of 2.4 to 4.6 m (Bent, 1926); but nests on Vingt-une Island, Texas, were very close to the ground up to heights of about 1.6 m (Bent, *loc. cit.*). At Snake Key, Levy County, Florida, the lowest nests are in mangroves about 2.4 to 3.7 m above the ground. Nest height in mangrove colonies is highly variable because of great variation in mangrove height.

In 1960 at Lake Alice, 96 Snowy Egret nests were built at an average height of 1.74 ± 0.04 m above the heronry floor or the lake surface (range 0.91-3.35 m). Data on nest heights for 1960 includes only those nests which were actually measured. Snowy Egrets built more nests in red maple than in any other tree or bush. The relative importance of the various nest trees and bushes is summarized for all 4 heron species in Table 1.

Cattle Egrets nest in a variety of sites throughout their extensive range, but most commonly at heights of less than 6 m. I have observed that they nest in mangroves in coastal heronries in Florida, and in willows and maiden cane at Lake Okeechobee. Funderburg (1960b) records their nests in a live oak and red cedar heronry with yaupon understory in coastal North Carolina, and in Missouri they nest in pines (Peterson, 1965). They nest in reed beds in East Africa (Mackworth-Praed and Grant, 1957) and from 15 to 24 m in eucalyptus trees in South Africa (Skead, 1956). Whistler (1949) says that in India they often nest at "considerable heights." In Japan they nest 3 to 6 m from the ground in the low branches of trees, shrubs, or bamboos (Austin & Kuroda, 1953). Whitherby *et al.* (1947) reports that they also nest in big cork-oaks on dry ground, on rocky islets, and in big trees in towns in Egypt. In Guyana (Lowe-McConnell, 1967) early Cattle Egret nests were mostly between 2 and 3 m, but later nesting individuals nested higher.

The average height of 76 Cattle Egret nests in 1960 at Lake Alice was 2.38 ± 0.05 m (76 nests, range 1.68-3.66). Most of their nests were placed either in red maple or in buttonbush (Table 1).

According to Howell (1932), Little Blue Herons build their nests in willow, wax myrtle, and, in northern Florida, in titi. Buttonbush and swamp privet are used in Arkansas (Meanley, 1955). Box elder, water maple, overcup oak, and elm are sites in Tennessee (Ganier, 1960). Nests are built in catalpa in Oklahoma (Tomer, 1955), and in pines in Missouri (Peterson, 1965). In North Carolina they nest in live oak, red cedar, and wax myrtle (Funderburg, 1960a, 1960b). Most of these sites are over water or on islands, but the Oklahoma catalpa tree and Missouri pine heronries were on dry land. Bent (1926) writes that on the willow islands of the upper St. Johns River in Florida, the Little Blue Herons nest in bushes on the outer edges of the islands, from 0.6 to 1.2 m above the ground. Howell (1932) notes that the nests are from 1.2 to 2.4 m above the water. In the woods described by Ganier, most nests were between 4.9 and 7.6 m. In Arkansas, Little Blue Herons build their nests closer to the shore than do the other species, and build them at an average height of 2.4 m (range 0.9-4.6 m) with other nests placed up to 7.6 m (Meanley, 1955). In the catalpa woods they nested $2.7 - 5.5$ m above the ground.

The average height of Little Blue Heron nests at Lake Alice in 1960 was 2.19 ± 0.06 m (49 nests, range 1.37-3.20). However, Little Blue Herons had two distinct peaks of nesting activity in 1960. In the early peak, clutches completed before April 28, the average nest height was 2.04 m. In the later period, with most clutches completed between June 10 and June 30, the average nest height was 2.59 m. The late nests were significantly higher ($t = 5.68$). As can be seen in Table 1 this species showed stronger nest site perferences than the others.

In Florida, Louisiana Herons nest in willows, mangroves, buttonwoods, and rushes (Bent, 1926, Howell, 1932). In North Carolina they nest in red cedar and wax myrtle (Funderburg, 1960a). In Texas, Bent (1926) records their nesting in these, and also in cane, mesquite, huisache, and occasionally in prickly pear. The nest height in one Texas heronry is given as 0.3 to 0.6 m, in another as 3.0 to 4.6 m (Bent, 1926). Howell (1932) gives the nest height in Florida as 0.6 to 6.0 m. Bent (1926) reports that on the upper St. Johns River, Florida, they nest in the middle of heronries at 0.6 to 3.7 m and

at 1.8 to 3.7 m throughout the Cuthbert Lake heronry.

The average height of Louisiana Heron nests in 1960 at Lake Alice was 1.74 ± 0.05 (30 nests, range 1.07-2.29). Louisiana Herons were the only species to build most often in elder (Table 1).

There are at least 5 reports of nest stratification involving these species. In Arkansas Little Blue Herons selected the sites closest to land, American Egrets ranged in an intermediate section, and Snowy Egrets nested in the outermost bushes near the open water. The Snowy Egret nests were also lower than nests of the other 2 species (Meanley, 1955). On a small island in a reservoir in southern Ghana, the Cattle Egret nested in the lower branches, the Long-tailed Chag *(Phalocrocorax africanus)* nested in middle and upper branches, and the African Darter *(Anhinga rufa)* nested around the periphery (Bowen *et al.*, 1962). On Little Marin Island in San Francisco Bay, Snowy Egrets nested lower than did the Common Egret (Ralph and Ralph, 1958).

In 2 mixed heronries where many species bred, the different species selected different sites (in Spain, Valverde, 1958, and in Guyana, Lowe-McConnell, 1967).

NEST CONSTRUCTION

In these 4 species nest construction before pair formation varied from none to essentially complete nests (Meyerriecks, in Palmer, 1962). At Lake Alice in 1960, most nest construction was done by the female with twigs and branches gathered by the male following pair formation. Nest construction was seldom complete when the first egg was laid, but was usually completed early in the egg-laying period. Although some individuals of all 4 species added to the nest throughout the period of egg-laying and incubation, this behavior usually waned rapidly after egg-laying started.

The twig-passing display is similar in these 4 species. The returning male elevated the crest, drew the neck into a shallow "S" curve, and elevated the aigrettes. The female responded with similar feather and neck movements and then took the twig in her bill. As construction progressed the intensity of this display diminished. The general behavior that followed twig passing was also similar for the four species. Both sleeked their plumage, the female turned to the nest with the twig, and if the nest was just being started she often laid the twig on top of the others. If the nest was nearly complete, considerable effort was sometimes used to push the twig into the nest, sometimes getting it partially lodged, pulling it out, and starting over again, until it was well anchored. Frequently the twig was dropped.

Snowy Egrets spent an everage of 4.4 ± 0.25 days building their nests before the first egg was laid (21 nests, range 3-8). Snowy Egret nests were relatively incomplete when the first egg was laid but were usually completed early in the egg-laying period.

Male Snowy Egrets returned directly to the heronry floor from the nest and walked around until they located an acceptable twig. Snowy Egrets occasionally picked up and rejected several twigs and sometimes attempted to pick up tree roots or branches of large limbs. Early in the season, the males frequently walked to the nest tree and climbed up to the nest, but later in the season when the vegetation became dense, the males often flew back to the nest with the twig. Although some Snowy Egret nests were constructed entirely of mud-coated dead sticks, others contained fresh twigs, some still with leaves. They apparently found the fresh twigs beneath nests of other herons where they had fallen during nest construction. Because Snowy Egrets usually found dropped twigs on later twig-hunting trips, and often returned directly to the ground to recover them, twigs were rarely found on the ground beneath their nests in 1960.

Cattle Egrets spent an evarage of 6.6 ± 0.37 days building their nests before laying the first egg (26 nests, range 3-11). Cattle Egret nests were more complete when the first egg was laid than were nests of the other species. There was considerable individual variation in the rate at which they added to their nests. Many Cattle Egrets added substantially to their nests every day up to egg laying. A few completed their nests several days before laying the first egg. Because their nests were more complete, Cattle Egrets seldom lost their first egg through the nest floor.

At Lake Alice in 1960, Cattle Egrets collected most, if not all, of their nesting material from standing trees and bushes. The Cattle Egrets, after delivering the twig, flew directly from their nests to the upper parts of trees and bushes and were rarely seen on the heronry floor. However, in South Africa, where they nest at the unusual height of from 15 m to 24 m, they gather material from the ground as well as from the trees (Skead, 1956). Meyerriecks (in Palmer, 1962) found a few gathering twigs below the Lake Alice heronry in 1959. At Lake Alice in 1960, dead, brittle twigs within the heronry were broken off by the earliest nesting Cattle Egrets and Little Blue Herons. Cattle Egrets nesting later could find only live, tough twigs, and spent much time looking for twigs they could reach. After locating twigs these males were often unsuccessful in breaking them off. By mid-season the supply of twigs in the heronry was greatly reduced and Cattle Egrets gathered twigs from bushes and trees around the lakeshore and from distant parts of the marsh. Late in the 1960 season Cattle Egrets brought twigs back from a small swamp more than a half mile south of Lake Alice. However, they continued to gather a few twigs about the heronry as the vegetation grew.

Little Blue Herons spent an average of 4.8 ± 0.41 days building their nests before laying the first egg (12 nests, range 3-8). Little Blue Herons lost the first egg through the floor of incomplete nests more often than did the other three species.

At Lake Alice in 1960 nearly all Little Blue Heron nest material was broken from trees and bushes. They collected twigs from the uppermost reaches of

TABLE 2. Dates of egg laying and clutch completion at Lake Alice in 1960.

	Dates of first and last eggs	Percent of clutches completed per 2 week interval							
		4/1–4/14	4/15–4/28	4/29–5/12	5/13–5/26	5/27–6/9	6/10–6/23	6/24–7/7	7/8–7/21
Snowy Egret (102 clutches)	3/30–6/16	38	49	4	5	3	1	—	—
Cattle Egret (85 clutches)	4/11–7/15	—	19	45	5	9	4	11	8
Little Blue Heron (58 clutches)	3/28–7/4	47	21[1]	—[1]	3[1]	9	9	12	—
Louisiana Heron (35 clutches)	3/29–5/20	63	31	3	3	—	—	—	—

[1]No clutches completed between 4/26 and 5/21.

trees down to the lowest limbs and branches, and sometimes from the heronry floor. However, at Lake Alice in 1959 (Meyerriecks in Palmer, 1962) and in Arkansas in 1954 (Meanley, 1955), Little Blue Herons collected most of their nest material from beneath the heronry. Little Blue Herons frequently dropped twigs while working them into their nests. At the peak of building in 1960, the ground beneath Little Blue Heron nests was often littered with twigs, a condition never found beneath Snowy Egret nests. Little Blue Herons were apparently much less persistent than Snowy Egrets in recovering dropped twigs.

Data on the duration of nest building prior to laying the first egg was obtained on only two Louisiana Heron nests. The periods were 4 and 5 days. This sample is too small to justify comparisons with the data for the other species. Louisiana Herons seldom lost the first egg through the nest floor. This fact would tend to indicate that they usually spend more than 4 or 5 days contructing their nests. However, because Louisiana Herons selected sturdier nest sites they should have been able to construct sturdier nests than did Snowy Egrets and Little Blue Herons in the same period of time. (See earlier section on nest site.)

EGG LAYING

Dates of first and last eggs and percent of clutches completed during 2-week periods at Lake Alice in 1960 are summarized in Table 2. Louisiana Herons completed most of their clutches during the first 2 weeks of April. This was also the peak period for Little Blue Herons, but none of the other herons concentrated their laying in such a narrow stretch of time as did the Louisiana Herons. The peak of clutch completion was in later April for Snowy Egrets and early May for Cattle Egrets. In Guyana (Lowe-McConnell, 1967), where herons began nesting with the onset of the rainy seasons, Cattle Egrets were the first to nest. Snowy Egrets, Little Blue Herons, and Louisiana Herons all began nesting after the Cattle Egrets did.

There was a conspicuous hiatus in Little Blue Heron nesting. Although they completed no clutches between April 26 and May 21, they completed 33 percent of all their clutches between May 21 and July 4.

Females of all four species laid at intervals of one or two days. I observed no interval greater than two days. The average interval for the Snowy Egret was 1.9 ± 0.04 days between eggs (114 intervals, range 1-2 days). Dawson (1915), on the basis of hatching pattern, concluded that the eggs are laid on alternate days. In Snowy Egret nests the 2nd egg was laid an average of 1.8 days after the 1st egg. Other intervals were 2.0 days between the 2nd and 3rd eggs, 1.9 days between the 3rd and 4th, and 1.8 days between the 4th and 5th eggs. Typically there was only one, one-day interval per nest.

The interval between egg laying was 2 days for the Cattle Egret (89 intervals, all 2 days).

Little Blue Herons laid at a rate of every 1.7 ± 0.07 days (48 intervals, range 1-2 days). Intervals between the first and second eggs, as well as all subsequent intervals, averaged 1.7 days. In one nest with 5 eggs the intervals between the 1st and 2nd and between the 4th and 5th eggs were both one day. In no other nest was there more than one, one-day interval, and in some all eggs were laid at 2-day intervals. Meanley (1955) says the eggs are deposited on an average of one nearly every other day.

The average inteval between laying for the Louisiana Heron was 1.7 ± 0.10 days (40 intervals, range 1-2 days). The 1st and 2nd eggs were laid on consecutive days about half the time and on alternate days about half the time (average 1.6 days). The frequency of 2-day intervals increased with each successive egg. The average interval was 1.7 days between the 2nd and 3rd eggs and 1.8 days between the 3rd and 4th.

CLUTCH SIZE

Snowy Egret clutches at Lake Alice (Table 3) averged 3.9 ± 0.07 eggs (102 clutches). The number of eggs in the nest when the female stopped laying was considered the full clutch. Howell (1932) reports the clutch as three or four, but Bent (1926) says the clutch is ordinarily four or five, sometimes three and rarely six. Clutches reported by Teal (1965) averaged 3.2. Early clutches at Lake Alice, those completed between April 4 and April 28,

TABLE 3. Frequency distribution of clutch size of Snowy Egrets, Lake Alice, 1960.

	Clutch Size			
	2	3	4	5
All nests	3	15	69	15
April 4 to April 28	0	7	67	15
April 29 to June 16	3	8	2	0

TABLE 4. Frenquency distribution of clutch size of Cattle Egrets, Lake Alice, 1960.

	Clutch Size					
	1	2	3	4	5	6
All nests	1	3	41	33	6	1
April 15 to May 12	0	0	28	22	4	0
May 13 to July 15	1	3	13	11	2	1

averaged 4.1 ± 0.05 eggs (89 clutches). Clutches completed between April 29 and June 16 averaged 2.9 ± 0.17 (13 clutches.) The difference between early and late clutches is significant ($t = 7.79$) at the 0.001 level. The average number of eggs laid in all nests that eventually contained complete clutches was 4.1 ± 0.06 (100 nests, range 2-8), but an average of 0.2 eggs were lost before the clutches were completed.

At Lake Alice, Cattle Egret clutches averaged 3.5 ± 0.07 eggs (85 clutches). Clutches completed between mid-April and mid-May averaged 3.6 ± 0.07 eggs (64 clutches), and those completed between mid-May and mid-July averaged 3.4 ± 0.18 eggs (31 clutches, Table 4). The late clutches were not significantly smaller ($t = 0.84$). In Maryland 12 nests averaged 3.67 eggs per clutch (range 2-5, Valentine, 1958), and in South Carolina nine nests averaged 3.33 eggs (range 3-5, Cutts, 1958). In southern Ghana 89 Cattle Egret clutches averaged 2.6 eggs (range 1-5, Bowen *et al.*, 1962). In Senegal 20 clutches averaged 2.9 (range 1-5, Morel, 1961), and 18 other nests averaged 3.0. Morel gives a frequency table for the first 20 clutches and the average is significantly less than the Lake Alice average ($t = 3.66$). It is given as 3 to 5 in Japan (Austin and Kuroda, 1953), 1 to 3 in East Africa (Mackworth-Praed and Grant, 1957), 2 or 3 in South Africa (Skead, 1956), 4 or 5 in India (Whistler, 1949), and 4 or 5, 6 occasionally is given as a generalization by Witherby *et al.*, (1947). Georgraphic variation in clutch size is discussed later in this paper.

Little Blue Heron clutches averaged 3.7 ± 0.10 eggs (58 nests, Table 5). An average of at least $3.8 \pm .09$ eggs (56 nests, range 2-6) was laid in nests that eventually held complete clutches. According to Bent (1926) the Little Blue Heron usually

TABLE 5. Frequency distribution of clutch size of Little Blue Herons, Lake Alice, 1960.

	Clutch Size			
	3	4	5	6
All nests	3	18	31	6
April 1 to April 28	0	3	30	6
April 29 to July 4	3	15	1	0

TABLE 6. Frequency distribution of clutch size of Louisiana Herons, Lake Alice, 1960.

	Clutch Size			
	3	4	5	6
All nests	4	22	9	1

lays 4 or 5 eggs, sometimes 3 and occasionally 6. According to Howell (1932) they usually lay 4 or 5 eggs. Meanley (1955) gives an average of 4.04 eggs for 50 nests in Arkansas (range 3-5), significantly more than at Lake Alice ($t = 2.96$). Clutches completed between April 3 and April 26 at Lake Alice averaged 4.1 ± 0.08 eggs (39 clutches). Clutches completed between May 21 and July 4 averaged 2.9 ± 0.10 eggs (19 clutches). The late clutches are significantly smaller ($t = 9.07$) at the 0.001 level. The significance of the smaller later clutches will be considered in the discussion. Because most of the early broods were still being cared for by the parents, only the last 6 nests could have been started by Little Blue Herons which had already raised broods.

Louisiana Heron clutches averaged 4.1 ± 0.11 eggs (35 nests, Table 6). An average of at least 4.3 ± 0.18 eggs were laid (35 nests, range 3-9), but some eggs were lost before incubation started. Howell (1932) gives the clutch as 3 to 5, but Bent (1926) says they usually lay 4 or 5 eggs, sometimes 3, occasionally 6, or very rarely 7. The average of the clutches reported by Teal is 3.1. There was an indication that late clutches at Lake Alice tended to be smaller, but few late nests were found. Egg laying was finished by April 27 in 33 of the 35 nests found in 1960. The two late clutches was finished May 2 and May 20.

Louisiana Heron clutches were significantly larger than Cattle Egret and Little Blue Heron clutches at Lake Alice in 1960 ($t = 4.32$, and 3.00), and Snowy Egret clutches were significantly larger than Cattle Egret clutches ($t = 3.93$). However, none of the other possible differences were significant.

Quantitative data on clutch size is known for a few other herons. Miller reported that the average of 347 clutches of the Great Blue Heron in the Philadelphia region averages 4.37 eggs (quoted by Meyerriecks, in Palmer, 1962). Gray Heron clutches averaged 3.9 in Germany (data by Knabe in Lowe, 1954). Gray Heron clutch size in three heronries in England

averaged 3.8, 3.9, and 4.1 eggs (Owen, 1960). In these 3 heronries Owen found no significant differences in clutch size between heronries, years, or first versus repeat clutches. Steinfatt (1939) gives clutch size of the Purple Heron at 3 to 5, usually 4. Common Egret clutches on Avery Island, Louisiana averaged 3.2 (based on actual counts of second census of Simmons, 1959). First clutches of Green Herons on Long Island averaged 3.87 eggs while 2nd nestings all had 3 eggs (76 and 32 nests, respectively, Meyerriecks, in Palmer, 1962). Completed Black-crowned Night Heron clutches averaged 4.1 on Long Island (Meyerriecks, in Palmer, 1962) and Gross (1923) reported 3.14 eggs per clutch in Massachusetts, but did not indicate whether the clutches were complete.

Although no intentional egg-removal experiments were done, predators removed eggs from many nests. In 3 nests where the predators began removing the eggs during the egg-laying period the females continued laying. At one Snowy Egret nest in which all eggs were laid at 2-day intervals, the first 5 eggs were removed by predators but the female continued to lay and completed a clutch of three eggs. At another Snowy Egret nest the first 3 eggs were removed, and 4 more eggs were laid and incubated. At a Louisiana Heron nest the first 5 eggs were removed and the female continued laying until she completed a clutch of 4. These data suggest that the Snowy Egret and Louisiana Heron are indeterminate layers, but in all 3 cases the females were able to complete clutches by laying about twice the normal number of eggs. The data do not indicate the maximum number of eggs they might be capable of producing.

INCUBATION

Incubation period as used here means the number of days from the laying of the last egg to the hatching of that egg (Nice, 1953). The eggs were marked each day after laying, so the last egg was positively identified.

The Snowy Egret incubation period averaged 22.4 ± 0.12 days (39 nests, see also Table 7). The incubation period of 18 days reported by McIlhenny (in Bent, 1926), is the figure given by Sprunt and Chamberlain (1949). Eighteen days was approximately the duration from the laying of the last egg to the hatching of the first young at Lake Alice.

The Cattle Egret incubation period averaged 22.9 ± 0.04 days (30 nests). According to Witherby *et al.*, (1947), the incubation period is 21 to 24 days. Skead (1956) gives, with reservation, the incubation period as 26 days, which would be about the time from the laying of the first egg to the hatching of the last young in the clutches of two or three eggs which he observed. This species had the least variable incubation period of the four species studied.

The incubation period of the Little Blue Heron averaged 22.8 ± 0.17 days (19 nests). Meanley (1955) says that incubation is 22 to 24 days, usually 22 or 23 days, and Sprunt and Chamberlain (1949) give the incubation period as 21 to 23 days.

TABLE 7. Frequency distribution of incubation period for the 4 species of herons, Lake Alice, 1960.

	Incubation Periods in Days				
	21	22	23	24	25
Snowy Egret	3	21	12	3	0
Cattle Egret	0	2	28	0	0
Little Blue Heron	0	8	8	1	2
Louisiana Heron	0	0	3	6	1

The incubation period of the Louisiana Heron averaged 23.8 ± 0.19 days (10 nests). The widely published incubation period of 21 days is credited to Audubon by Bent (1926).

In addition to the definition of incubation period above, Nice (1954) subsequently added the criterion that all eggs must hatch. Clearly this stipulation would be mandatory for determining incubation period in any nests in which the eggs were not individually marked after each was laid. However, when they are marked the original definition is meaningful. If the incubation period is calculated on the basis of Nice's 1954 definition the results are essentially the same: Snowy Egret, 22.6 days (24 nests), Cattle Egret, 23.0 (20 nests), Little Blue Heron, 22.7 (15 nests), and Louisiana Heron, 23.7 (9 nests).

Both sexes incubated in all 4 species. In late spring and summer, the adults often stood over the eggs and shaded them. Cattle Egrets shaded their eggs more than the other species, probably because at Lake Alice they nested later and in higher sites with less natural shade. The nests of all 4 species were open networks of twigs which offered little protection against cold or wind from below. The Louisiana Heron is the first to nest and has the longer incubation period, however, there appears to be no clear correlation between weather or clutch size and length of incubation period.

Based solely on the pattern of hatching, effective incubation started with the laying of the first egg in about half the Cattle Egret clutches (based on back dating the average incubation period, from the date of hatching), and the day after the laying of the first egg in the rest of their nests. Only rarely (in 2 of 50 nests) was effective incubation delayed until the 2nd egg was laid. In the Snowy Egret and Little Blue Heron nests effective incubation began the day after the 1st egg was laid in about half the nests and the day the 2nd egg was laid in the others; only rarely was it delayed till the day the 3rd egg was laid. In the Louisiana Heron the beginning of effective incubation was more irregular. It typically began the day after the 2nd egg was laid or the day the 3rd egg was laid. Less frequently it began earlier.

HATCHING AND THE YOUNG

After each young hatched, the adults removed the empty eggshells, but some shells were crushed. This behavior is known for several herons (Meyerriecks, in Palmer, 1962). About the time the first egg pipped, the adults also removed any cracked, empty eggshells, though they may have incubated the empty shells for the full incubation period.

On the first day of hatching, Snowy Egret nests averaged 1.5 ± 0.07 chicks (80 nests, range 1-3). The second day they averaged 2.4 ± 0.09 chicks, and on the third day they averaged 2.9 ± 0.11 chicks. An average of nearly one chick hatched per nest between the first and second day. In 3 nests which Dawson (1915) found in California, the young hatched on alternate days, a sequence observed in less than 2% of the Snowy Egret nests at Lake Alice.

The 1st day of hatching Cattle Egret nests averaged 1.1 ± 0.04 young (49 nests, range 1-2), and the 2nd day they averaged 1.6 ± 0.09. They averaged 2.1 on the 3rd day, 2.6 on the 4th, and 3.0 on the 5th. The 2nd chick hatched one day after the first chick about half the time and 2 days after the first chick the rest of the time. After the 2nd chick all chicks hatched on alternate days.

The first day of hatching Little Blue Heron nests averaged 1.6 ± 0.11 chicks (37 nests, range 1-3). The 2nd day they averaged 2.5 ± 0.17 and the 3rd day they averaged 2.9.

The first day of hatching Louisiana Heron nests averaged 2.2 ± 0.17 chicks (25 nests, range 1-3). The next day they averaged 2.7 ± .18 chicks, the 3rd day they averaged 3.1, and the 4th day they averaged 3.1.

In all 4 species the adults spent considerable time sitting on the eggs prior to the beginning of effective incubation. Either they do not keep the eggs warm during these sittings, or the long periods when the eggs are not warmed delays their hatching.

The average total number of Snowy Egrets hatching per nest was 3.3 ± 0.10 (91 nests, range 1-5). Hatching extended over 3.2 ± 0.13 days (75 nests, range 1-6). An average of 3.2 ± 0.09 young Cattle Egrets hatched per nest (73 nests, range 1-5). The hatching time was 4.7 ± 0.29 days per nest (41 nests, range 1-8 days). An average of 3.2 ± 0.14 Little Blue Herons hatched per nest (51 nests, range 1-5). Hatching required 3.2 ± 0.26 days (31 nests, range 1-7). An average of 3.7 ± 0.14 young Louisiana Herons hatched per nest (29 nests, range 2-5). Their clutches hatched in 3.4 ± 0.23 days (24 nests, range 2-5).

The young were weak and relatively inactive for the first few days; and they were able to raise their heads only briefly. Within a few days they held their heads up for long periods and called frequently. Although brooding sometimes continued, the adults appeared to become increasingly restless. Some individuals stood up, looked at the young and moved around a great deal. In most of the later nests brooding of the young chicks and eggs during midday consisted primarily of shading them. Because they nested late, Cattle Egrets were conspicuous in this regard. They stood over the nest with the body at a right angle to the sun's rays, and often drooped the wing nearest the sun and shaded the young.

At first the chicks picked food off the floor of the nest where it was regurgitated by the adults. After a few days, they passed quickly through a stage of taking food from the parents' bills and began grabbing and pulling on the parent's bill. This presumably acts as a stimulant to regurguitation and has been recorded for many species. In broods that hatched over a period of several days the oldest young was intercepting food while its youngest sibling was still too weak to hold its head up more than briefly. The peck order that Skead (1956) noted in Cattle Egrets was probably based on this kind of dominance of larger, older chicks over smaller, younger ones.

TABLE 8. Mortality of eggs and nestlings of four herons, Lake Alice, 1960.

	% Mortality of Eggs or Young			
	Snowy Egret (91 nests)	Cattle Egret (73 nests)	Little Blue Heron (52 nests)	Louisiana Heron (28 nests)
Laying to day before hatching	6.2	4.0	4.0	3.9
Day before through hatching	14.7	6.9	10.4	10.5
Laying through hatching	19.9	10.6	13.9	14.0
Hatching through two weeks	28.1	8.2	27.6	25.4
Over-all mortality from laying through two weeks	42.5	17.9	37.7	35.8

MORTALITY OF EGGS AND YOUNG

Mortality of eggs and young is condensed for all 4 species in Table 8. Mortality figures do not include losses of entire nests prior to hatching. A few mortality figures are available in the literature and additional ones can be calculated from data given. Snowy Egret mortality in Georgia was 33% for eggs and 62% for nestlings (Teal, 1965). Cattle Egret mortality in Ghana was 38% for eggs and 54% for nestlings (Bowen *et al.*, 1962). These figures give a 71% over-all mortality for eggs and young. Figures for the Little Blue Heron in Arkansas (Meanley, 1955) are more comparable to the Lake Alice data; the mortality of hatchlings in one set of 10 nests was 18.8% during the first 2 weeks. In another 30 nests, the loss of both eggs and young was 25.8% Louisiana Heron mortality was 19% for eggs and 57% for nestlings in Georgia (Teal, 1965). Mortality of nestling Great White Herons was about 40% (Meyerriecks, in Palmer, 1962). Nestling mortality of Gray Herons in England varied from 2 to 46% for 3 heronries over several years, but these figures exclude predator losses (Owen, 1960). Purple heron

clutches of 3 to 5, usually 4, produced 2 or 3 and in many cases only one fledgling (Steinfatt, 1939).

In the 4 species studied, the number of nestlings decreased following hatching. The decreases in brood size during the first two weeks are statistically significant for the Snowy Egret, Little Blue Heron and Louisiana Heron, but not for the Cattle Egret.

The average number of Snowy Egret hatchlings that survived until 2 days after the last young hatched was 3.0 ± 0.10 (86 broods, range 1-5). Seven days after hatching the brood was 2.7 ± 0.10 chicks, significantly different from the number at 2 days ($t = 1.98$). Only 2.2 ± 0.10 young survived for 14 days. The chicks of all 4 species sometimes left the nest earlier than 2 weeks after the last young hatched, but at that time the oldest chick began to spend so much time away from the nest that later counts became increasingly difficult and unreliable. Regular observations of older broods were terminated at most nests. The over-all loss of Snowy Egrets exceeded an average of one chick per nest (from 3.3 at hatching to 2.2 at two weeks). Practically all this loss was due to starvation. The last chick to hatch was considerably behind the earlier ones in development and size. The last chick was apparently incapable of competing successfully with four nest mates and was often incapable of competing with even three. As each day passed the older nest mates developed and grew while the youngest waned until eventually it died of starvation. Occasionally the two youngest chicks both starved.

Snowy Egret nests that contained 4 chicks 2 days after hatching averaged only 2.5 chicks 2 weeks after hatching. Broods that contained 3 chicks after hatching were reduced to 2.3 by the end of their second week. Even broods of 2 were similarly though much less drastically reduced to 1.8 chicks. Thus, 1.5 young were lost from broods of 4, 0.7 from broods of 3 and 0.2 from broods of 2. It appears that in 1960 some adults were able to feed and raise a maximum of 3 young per nest while others could raise only 2, and a few could not even manage that many. Of the 31 nests in which 4 or more young hatched, only 2 nests still held 4 young 2 weeks later. The young that starved were sometimes trampled into the nest by their siblings, but more often were ejected from the nest.

Cattle Egrets were extremely attentive and lost few eggs and nestlings. The number of nestlings alive two days after the last one hatched was 3.1 ± 0.10 (70 broods, range 1-5). The brood was reduced to 3.0 ± 0.10 at the end of the first week, and to 2.9 ± 0.11 at the end of the second week. The loss between hatching and 2 weeks of nest life was slight (average of 0.3) and the difference is significant only at the 0.10 level ($t = 1.78$).

Little Blue Heron broods averaged 3.0 ± 0.13 young 2 days after the last egg hatched (47 nests, range 1-5). They were reduced to 2.8 ± 0.13 at one week and to 2.4 ± 0.12 at 2 weeks. The difference between the numbers at one week and 2 weeks is significant ($t = 2.17$). An average of nearly one young per nest (0.8 ± 0.09) was lost during the 2 weeks following hatching. Practically all this loss was due to starvation of the youngest hatchlings. Of 30 Little Blue Heron nests that lost young, 23 nests lost only one, 6 nests lost 2, and one lost 4.

The average number of Louisiana Heron hatchlings that survived until 2 days after the last one hatched was 3.4 ± 0.20 (30 nests, range 1-5). They were reduced to 3.1 ± 0.15 by the 7th day after hatching. Two weeks after hatching 2.8 ± 0.14 young survived. The number of young decreased significantly between the 2nd day after hatching and 2 weeks ($t = 2.59$). An average of nearly one chick (0.94 ± 0.14) was lost per nest during the first 2 weeks of nest life. Most of this loss was due to starvation of the youngest chick. Typically only one young starved per nest (17 of 19 nests in which young starved) but occasionally 2 starved (2 of 19 nests). In about one out of every 3 nests all the young survived.

Although starvation was responsible for most nest nestling loss at Lake Alice, nestlings also met a variety of violent accidents. In 2 heronries located high in tree tops (Skead, 1956; Lowe, 1954) young that fell to the ground were not fed by the adults and died of starvation. At Lake Alice as in many other heronries where trees and bushes are short and scrubby the young which fell to the ground were usually, but not always, able to get back to their nests. Young herons are extremely agile and use their heads and necks as prehensile aids in climbing. If they could not climb their own tree at Lake Alice, they sometimes were able to climb a nearby tree and travel back to their nest through the canopy. At Lake Alice those young that were unable to get back into the trees, or that wandered about on the ground before returning to the trees sometimes fell prey to American alligators. On 5 separate occasions in 1960 I saw alligators catch and eat young Cattle Egrets. Wandering about in strange trees was not safe either because adults of all species would drive intruders from their territories. A little Blue Heron chick about 3 weeks old was repeatedly attacked by adult Cattle Egrets and Little Blue Herons while it blundered through their nesting territories. It reached the nest refuge with a bloody back and wing and disappeared during the following night.

The day after a heavy wind I found 2 large juvenile Snowy Egrets hanging dead. One was upside down with the foot caught in a narrow fork, and the other was caught by a wing. The day after an extremely heavy rainfall (3.55 inches on June 18, 1960) I found 2 nearly dead young Little Blue Herons on the floor of the heronry. Their feathers were wet and packed with mud and their wing feathers had been pounded into the mud by the rain. The next day they had not returned to the nest tree and could not be found. A fledgling Louisiana Heron fell and landed on its back, wedged in a narrow fork of a branch where it was found dead. Bent (1926) also found dead Louisiana Heron young entangled in the vegetation.

Even before the first egg was laid, various mortality factors began to operate. Wind often blew down nests that were just started. In some cases it appeared that adults tried to build nests in impossible sites. Other herons would remove twigs from temporarily unprotected nests and if the nest was just being started it usually fell to the ground. Even sturdy nests seldom survived the removal of more than a few twigs. These delays in nest completion may have resulted in the first eggs being laid before the nest was complete enough to hold them.

Sometimes the birds never succeeded in their efforts to build a nest. One nest that was never completed was started on April 20, 1960; it was there the 21st, but completely gone the next day. On April 26 a nest was started at the same place; the next day it was a large nest but a day later only a few twigs remained. April 30 there was no evidence of the nest. On May 3 it was started, but on May 5 it was gone. On May 7 it was started again, and on May 9 it was gone. In 19 days this nest was started 4 times. This nesting effort was the work of Little Blue Herons, but whether more than one pair was involved is not known. There was no activity at the site for the next month and a half, but in late June a pair of Cattle Egrets built a nest at the same site. They laid and hatched 5 eggs with no unusual delays.

Predators sometimes found a nest and removed the eggs as regularly as they were laid. A Snowy Egret nest that never did produce young was started on April 5, 1960. The first egg was found on the 11th and on the 13th there were 2 eggs. On the 14th only the first egg remained; the 15th another egg was added, but the next day there were none. On April 17th the 4th egg was laid, but the next day the nest was again empty. On April 19, one egg was added but it was removed by the next day. Then the clutch was completed; eggs were laid on the 21st, 23rd, and 25th. A total of 8 eggs were laid in this nest. Incubation proceeded for 9 days. On June 5 egg number two disappeared. On the 7th, number one was gone, and on the 8th the last egg, number three was gone. On June 9 the nest was reduced to a few twigs scattered beneath the tree. Most of these eggshells were recoverd. The eggs had been opened and eaten by birds, apparently Boat-tailed Grackles *(Cassidix mexicanus)*.

Purple Gallinules *(Porphyrula martinica)* also took eggs from nests at Lake Alice. On three separate occasions I saw Purple Gallinules fly directly to temporarily vacated heron nests, pick up an egg and fly away. The fate of one egg was undetermined, but the other two were taken to downy young Purple Gallinules which ate them. A few eggs that had been crushed, the outer shell a cluster of tiny fragments held together by the membrane, were found at widely scattered locations. They had apparently been taken and eaten by snakes. The only arboreal snakes seen in the heronry were rat snakes *(Elaphe obsoleta)*.

Fish Crows *(Corvus ossifragus)* were common on the university campus adjoining Lake Alice . They often perched in tall pines around the lake, and nearly every day of the 1960 breeding season they were seen flying over the heronary. In 1960, Fish Crows were never seen in the heronry proper and there was no mortality either of eggs or young that could be attributed to these birds. There was no evidence of any mammalian predation. In fact there was no evidence of mammals in the heronry other than small rodents (droppings found) and marsh rabbits (*Sylvilagus palustris*, numerous sight records).

Raccoons *(Procyon lotor)* and other potential mammalian predators are doubtless incompatible with the American alligator, which is abundant at Lake Alice.

At Lake Alice a great many nests were blown down, destroyed, robbed or deserted during construction, egg laying and early incubation. Probably less than half of the nest started ever reached the point of containing a full clutch. Once the clutch was complete and incubation under way, the eggs were relatively safe. However, when a predator found a nest and took one of the eggs, it typically took the entire clutch over the next several days.

FOODS AND FEEDING BEHAVIOR

The ardeids show great diversity in their feeding behavior. Meyerriecks (1959, 1960a and 1962) has demonstrated many differences in the feeding behavior of North American herons and egrets and has shown how these differences reduce competition. Valverde (1955-56) found differences in the feeding behavior of herons in southern France and related them to differences in leg length. As these authors have shown, the maximum dept for feeding by wading is restricted by size, but in herons behavioral differences are often of greater importance than are size differences. Valverde (1958) also reported that the different herons in the large Coto Doñana heronry in Spain ate different foods. In Guyana (Lowe-McConnell, 1967), the different heron species showed differences in their feeding behaviors. Around Gainesville, the Snowy Egret, Little Blue Heron, and Louisiana Heron, which are nearly the same size, all feed in wetlands. Potential differences in depth of practical wading are slight and important differences between them would more likely be behavioral. The Cattle Egret feeds on higher, drier ground than these three and only occasionally feeds in the same areas.

Food is more abundant in the Gainesville region during the time of year the adults are feeding young than at any other time. However, as already discussed, an average of nearly one young per nest starves in nests of three of the species studied. Snowy Egrets, Little Blue Herons and Louisiana Herons did not provide sufficient food for their broods, especially for the larger broods. It seems reasonable to assume that with high nestling food requirements the birds probably feed near their maximal efficiency, regardless of whether this limit is imposed by time, anatomy, physiology, or behavior. If this is true, the birds probably catch the kind of

food they can catch the most of, and search for it in those places where it is most available to them.

ADULT FEEDING BEHAVIOR

Practically all feeding behavior of these 4 herons around Gainesville during the breeding season falls into three general, though not necessarily distinct, categories: (1) Stand and Wait; (2) Wade or Walk Slowly; and (3) Active Pursuit. Stand and Wait, and Wade or Walk Slowly (Meyerriecks, 1960a) are specific types of feeding behavior and are typical of herons. Although these two types are often modified, the more unusual and dramatic means of gathering food are mostly forms of Active Pursuit. These basic types need only be reviewed briefly here.

In Stand and Wait feeding, the heron situates itself, poses its body in readiness and waits. It remains immobile and makes a strike if food approaches; if not, it eventually moves to a new place. The body may be held low and horizontal, the ankles flexed, and the neck slightly withdrawn in a soft S-curve; at other times the body is held upright, the feet and legs straight and the neck extended.

In Wade or Walk Slowly type of feeding, the heron moves slowly and deliberately, sometimes "freezing" or making a short dash just before striking at prey. The body is held horizontal, the neck slightly withdrawn, and the bill pointed forward; or the body is held upright, the neck straight, but at an acute angle to the ground, and the bill pointed forward often toward the ground in front of the heron. The body, neck and head are usually held rigid as the heron moves, but the neck sometimes bobs slightly with each step. Just before making a strike the head may be withdrawn slightly; sometimes it is also undulated sideways. Individuals hunting by the Stand and Wait technique often Wade or Walk Slowly while moving from one stand to another.

Active Pursuit includes Meinertzhagen's (1949) type, Disturb and Chase. The most frequent form of Active Pursuit in the Gainesville region was simply walking or running in shallow water, chasing fish and making strikes here and there. A technique employed around Gainesville by 3 of these species, but not observed in the Louisiana Heron, was to walk through fields, catching insects, frogs, or other prey that flushed at the heron's approach. The body was not held rigid as in Wade or Walk Slowly. The bird did not "sneak up" on anything, but walked along catching those animals it disturbed. Herons, including these 4 species, use many other types of Active Pursuit, and these form the basis of many notes on unusual heron feeding behavior. Such behavior comprised a small but conspicuous part of the feeding repertoire of these four species around Lake Alice during the breeding season. One of the more frequent of these unusual types, which has been reported in the Gainesville area (Dickinson, 1947), is reaching down and taking food from the water while on the wing. Hovering (Meyerriecks 1960a) has been recorded for many heron species.

Snowy Egrets, widely recognized for their active feeding habits, employed Active Pursuit more often than did the other species which nested at Lake Alice. They frequently dashed about through very shallow water, twisting, turning, stopping and taking off in new directions, striking here and there at the fish. Snowy Egrets also employed Stand and Wait, and Wade or Walk Slowly. However, they often interrupted such behavior to chase after fish. The occasional association of Lake Alice Snowy Egrets with cattle has been reported previously (Rice, 1954). Although the Snowy Egrets of this heronry were more social in their feeding than were Little Blue Herons and Louisiana Herons, and many individuals fed together in small areas, solitary individuals often fed by themselves.

Cattle Egrets fed in grasslands and open meadows, and although they occasionally frequented wet places, they usually fed away from water. They walked along near the head or side of a grazing cow and caught prey flushed by it. However, they sometimes made short excursions away from their beater, and at those times they caught food they disturbed themselves. Individual Cattle Egrets occasionally fed by themselves, independent of cattle or other large ungulates, but this method of feeding was much less common during the breeding season than during the winter. The highly social Cattle Egrets usually fed in groups. The size of the feeding groups tended to be smaller around Gainesville during the breeding season than during other seasons.

Although not as social as Snowy Egrets, Little Blue Herons often fed in the same general area. They probably employed the Wade or Walk Slowly technique of feeding more than the other 3 species, although they also used the Stand and Wait technique. Little Blue Herons frequently froze while wading, slowly lowered the head and neck, and then struck. They typically fed around the edges of ponds and on the prairies, but many left the water to feed in open grasslands and pastures during midsummer.

Louisiana Herons were normally solitary feeders during the nesting season; feeding individuals were widely scattered across prairies, along streams and ditches and around ponds away from the prairies. Lowe-McConnell (1967) noted that they are solitary feeders in Guyana. During the breeding season they usually fed by stealth, using both the Stand and Wait, and Wade or Walk Slowly techniques. They regularly fed in deeper water than did the other 2 aquatic feeding species and often waded in water up to the belly. In the Gainesville area, Louisiana Herons occasionally fed by some form of Active Pursuit. The two most frequently observed patterns were running through shallow water herding fish by waving their wings, and reaching down into the water to grab food in the bill while hovering or flying low across open water.

Little Blue Herons and Louisiana Herons occasionally joined Snowy Egrets and other herons around a roadside culvert, along a small meadow canal, or on a pond. In most cases these concentra-

tions were brought about by unusual, abundant supplies of food, and often they were related to the sudden filling or rapid drying of areas.

FOOD OF NESTLINGS

An ecologically significant time to study the food habits of the herons is when the heronry is full of flightless young. It is then that the adults must gather substantially more food per day than at any other time of the year.

Snowy Egrets only a few days old were not disturbed as easily as were older nestlings and usually did not regurgitate, but such nestlings sometimes ate the food which older and more excitable siblings regurgitated. Each older nestling, when disturbed and if recently fed, typically produced 2 well-compacted pellets.

The contents of 50 pellets recovered from Snowy Egret nestlings were: fish 87.9% by volume, invertebrates 7.0%, and amphibians 4.8%. Table 9 lists the food items, the total number found in 50 pellets and the percent of the total volume of each item. Of 46 amphibians eaten, 35 were small tadpoles and they comprised only 2.9% of the total diet.

Grasshoppers and crickets (Locustidae, Tettigoniidae, and Gryllidae combined, 4.8%) were as important in the over-all diet as were the amphibians. (Relative importance refers to the percent of the total volume contributed by that particular item.) Although most pellets contained a few insects, 2 of the 50 pellets were composed entirely of insects and amphibians, and unlike the 48 other pellets contained no fish. Dragonfly nymphs or adults (Anisoptera) composed only 1.0% of the diet but were found in 11 pellets.

Two prey species were much more important than any of the others and together composed nearly 57% of the diet. The mosquitofish *(Gambusia affinis)* was the most frequent as well as the most important, and the flagfish *(Jordanella floridae)* was second in importance. The 4 next important species, though much less important, were also fish.

The pellets averaged 29.0 individual items. They included an average of 0.9 amphibians, 7.6 invertebrates, and 20.5 fish. The five most important food species, mosquitofish, flagfish, redfin pickerel *(Esox americanus)*, golden topminnow *(Fundulus chrysotus)*, and banded sunfish *(Enneacanthus obesus)* comprised 77.2% of the total diet. Mosquitofish were included 456 times in the 50 pellets and the least killifish *(Heterandria formosa)* was the second most frequently taken species.

According to Baynard (1912), 50 pellets regurgitated by young Snowy Egrets at Bird Island, Orange Lake, contained 120 small suckers, 762 grasshoppers, 91 cutworms, 2 small lizards, 29 small crayfish, and 7 small mocassins. Snowy Egrets from Orange Lake and Lake Alice fed in similar places and actually shared some feeding areas such as Payne's Prairie. It is difficult to explain the differences between Baynard's and my results unless availability of food was drastically different.

TABLE 9. Analysis of 50 pellets regurgitated by young Snowy Egrets.

	Number of Individuals	% of Total Volume
INVERTEBRATES		
Oligochaeta	1	0.02
Astacidae	6	0.70
Palaemonetes spp.	7	0.28
Zygoptera	7	0.06
Anisoptera (5 nymph)	18	1.00
Locustidae	188	2.78
Tettigoniidae	99	1.47
Gryllidae	32	0.47
Hydrophilidae	15	0.17
Corixidae	4	0.04
Arachnida	1	0.04
VERTEBRATES		
Unidentified tadpoles	19	1.21
Acris gryllus	10	1.06
Unidentified Hylid tadpoles	14	1.28
Unidentified Rana spp. tadpoles	2	0.43
Rana pipiens	1	0.85
Elassoma spp.	42	1.08
Enneacanthus gloriosus	2	1.49
Enneacanthus obesus	12	5.31
Esox americanus	15	8.29
Etheostoma barratti	21	1.06
Fundulus chrysotus	37	6.80
Gambusia affinis	456	36.14
Heterandria formosa	224	3.08
Jordanella floridae	195	20.83
Lepomis macrochirus	8	2.34
Leptolucania ommata	1	0.04
Lucania goodei	9	0.21
Micropterus salmoides	3	1.23

Few other quantitative reports are available, but they are consistent with the Lake Alice data. Trautman (1940) reported a gizzard shad *(Dorosoma cepedianum)*, a darter *(Poecilichthys exilis)*, a largemouth bass *(Micropterus salmoides)*, three crayfish *(Cambarus propinquus)*, and traces of 9 other crayfish from the stomach of an Ohio Snowy Egret. One of 2 Snowy Egret stomachs from Puerto Rico was nearly filled with bones of small gobies; the remainder consisted of fragments of grasshoppers and flies. The other stomach contained two dragonfly nymphs, a small crab, a lizard, and a small frog (Wetmore, 1916). One stomach from Logan, Utah (Knowlton and Harmston, 1943), contained 12 grasshoppers *(Camnula pellucida)*. Crayfish which are often included in generalizations on Snowy Egret foods are relatively unimportant to the Lake Alice Snowy Egrets and were included in only four pellets (0.7% of diet). Because crayfish are less rapidly digested than fish, their occurrence would doubtless be greater in stomach analyses than in pellet analysis. This would lead to an erroneous interpretation of the relative importance of crayfish in the diet of Snowy Egrets.

Young Cattle Egrets regurgitated more readily than did young of the other 3 species studied. If one young regurgitated, the other young in the same tree

TABLE 10. Analysis of 50 pellets regurgitated by young Cattle Egrets.

	Number of Individuals	% of Total Volume
INVERTEBRATES		
Zygoptera	1	0.01
Anisoptera	5	0.58
Locustidae	679	36.21
Tettigoniidae	279	6.85
Gryllidae	523	13.50
Coleoptera	10	0.17
Elateridae	1	0.01
Curculionidae	2	0.01
Diptera	3	0.12
Tabanidae	5	0.54
Lepidoptera	2	0.12
Arachnida	88	5.15
VERTEBRATES		
Scaphiopus holbrooki	1	1.25
Unidentified frogs	2	0.83
Unidentified Hylidae	2	0.42
Acris gryllus	69	13.29
Hyla spp.	2	0.42
Rana pipiens	23	15.78
Microhyla carolinensis	2	0.42
Thamnophis sauritus	1	2.08
Thamnophis sirtalis	1	1.66
Tantilla coronata	1	0.62

promptly followed suit and several pellets quickly rained down out of the tree. The pellets were tightly compacted and though held together by mucous, splattered over a considerable area if they hit a hard surface such as a limb.

The 50 pellets studied were composed of invertebrates 63.2% by volume, amphibians 32.3% and reptiles 4.4% (Table 10). Reptiles were represented by 3 snakes.

Short-horned grasshoppers (Locustidae) were found in 48 of the 50 pellets and were the most important prey of Lake Alice Cattle Egrets. The two pellets lacking locustids were each composed of single large leopard frogs. Crickets (Gryllidae), though the second most important invertebrate and the second most frequent item, contributed less volume to the diet than did leopard frogs. The third most important invertebrate, long-horned grasshoppers (Tettignoiidae), were less important than even the cricket frogs. Altogether the orthopteran insects contributed 56.6% of the diet by volume. Spiders (Arachnida) were taken with surprising regularity; 88 were included in this sample. A variety of other invertebrate groups each contributed less than 1% of the diet.

The sample included 101 frogs and toads. The leopard frog *(Rana pipiens)* was the most important amphibian although only 23 individuals were taken, while 69 individuals of the second ranked amphibian, the cricket frog *(Acris gryllus)* were taken. A large eastern spade-foot *(Scaphiopus holbrooki)*, and 8 small other amphibians totaled only 3.3% of the diet.

Cattle Egret pellets contained an average of 34.1 items: 0.1 snakes, 2.0 amphibians, and 32.0 invertebrates. The four most important groups—short-horned grasshoppers, leopard frogs, crickets, and cricket frogs—comprised 78.8% of the total diet.

Except for one report that their diet is varied, practically omnivorous (Mackworth-Praed and Grant, 1957), the Cattle Egret is recognized as a carnivore and primarily as a predator of grasshoppers. However, Bates (1933) says it is a common fish-eating river bird along the Niger. Grasshoppers are noted as being of first importance in India (Whistler, 1949), Belgian Congo (Chapin, 1932), Puerto Rico (Biaggi quoted by Schorger in Palmer, 1962), South Africa (Skead, 1956), Surinam (Haverschmidt, 1957), and Spain (Valverde, 1958).

The idea that Cattle Egrets associate with cattle for the purpose of obtaining ticks, or that they obtain ticks incidentally as a result of this association, has persisted. No ticks were found in this study, in 510 Cattle Egret stomachs from Egypt (Kadry, 1942, cited by North, 1945), 139 stomachs from Egypt (Kirkpatrick, 1925, cited by North, 1945), nor in 20 stomachs from Puerto Rico (Biaggi, quoted by Schorger in Palmer, 1962). Engorged, conspicuous ticks, even when abundant, are apparently not removed from cattle in Natal (Vincent, 1947). Skead (1956) does report having seen the egrets remove ticks from cattle in South Africa, but this behavior is not usual there and was not verified by stomach analysis. A bird shot in Arabia contained 26 female and 42 male ticks *(Hyalomma aegyptium)*, picked up from the ground where they had fallen from resting camels (Bates, 1937). Fitzsimmons (1923) reported having found 51 ticks, 1,200 newly hatched locusts, 400 grasshoppers, 8 beetles, and 3 caterpillars in the crop of a Cattle Egret. Fitzsimmons states that Cattle Egrets apparently take ticks from the ground, but later on states that they pick ticks off cattle but does not document the latter statement. Priest (1933) found very great numbers of ticks in the stomach of one Cattle Egret, but he believed they had been taken from the grass rather than from the cattle. There is no doubt that Cattle Egret do take something from the sides of mammals. Some observers state that the egrets take something other than ticks from the cattle (Meyerriecks, 1960b, Beven, 1946). Flies (Diptera) occur in the Cattle Egret pellets at Lake Alice and several other accounts record the presence of flies in the diet. Perhaps the flies are taken from the cattle. Ticks are taken on occasion, but when taken it is apparently from the ground or vegetation and not from cattle.

Besides a wide variety of insects, Cattle Egrets eat arachnids, centipedes, frogs, toads, clawed toads (*Xenopus* spp.), lizards, and mice (Whistler, 1949, Skead, 1956, and Witherby *et al.*, 1947). There are at least 3 reports of Cattle Egrets eating birds: a *Zosterops* sp. in South Africa (Skead, 1956), a Myrtle Warbler *(Dendroica coronata)* in Florida (Sprunt IV quoted by Schorger, in Palmer, 1962) and Blackpoll *(Dendroica striata)* and Myrtle Warblers (Cunningham, 1965).

Very young Little Blue Herons when they regugitated often dropped the pellet into the nest and later re-ate it. Older individuals usually spewed a rather neat pellet over the edge of the nest, or later still from their perch on a limb. Little Blue Heron pellets were conspicuously different because of the frequency of relatively large items. A redfin pickerel of 12 cm or more, or a bullfrog *(Rana catesbeiana)* with a snoutvent length of 6 to 8 cm, frequently composed the entire pellet.

The contents of the 50 Little Blue Heron pellets were: amphibians nearly 54% by volume, fish 32.5%, invertebrates 12%, and reptiles nearly 1% (see Table 11 for detailed analysis). Reptiles were represented by 2 snakes.

Of the variety of invertebrates taken by Little Blue Herons, only crayfish and spiders contributed substantially to the total food. Most of the spiders, dystiscsid beetles, and orthopterans listed in the table were from 10 pellets collected in mid-June. These pellets are discussed later.

Large ranid tadpoles (*Rana* sp.) and adult bullfrogs were the two most important food items. Although 27 large ranid tadpoles were taken, the four bullfrogs nearly equalled them in volume. Together they comprised 34.1% of the diet. Leopard frogs were about half as important as either of the first two. Green treefrogs *(Hyla cinerea)*, a pig frog *(Rana grylio)*, and six newts *(Notophthalamus viridescens)* composed nearly the balance of the amphibians. The supposedly noxious newt, found in pellets from three different nests, was of moderate but regular occurrence in the diet of young Little Blue Herons at Lake Alice.

The golden topminnow was the Little Blue Heron's most important prey and comprised nearly as much volume as the other 8 fish species combined. Although the least killifish was slightly less important than was the second-ranked banded topminnow *(Fundulus cingulatus)*, it occurred 10 times more often. The other fish were of minor importance and contributed from 1.0 to 2.6% of the food.

Little Blue Heron pellets averaged only 8 9 items: 3.0 invertebrates (including 1.5 spiders), 1.5 amphibians, less than 0.1 reptiles, and 4.3 fish. The most important were: ranid tadpoles, bullfrogs, golden topminnows, leopard frogs, crayfish, green treefrogs, banded topminnows and spiders, in that order. These eight forms comprised 75.1% of the diet. Three items stood out as being of prime and nearly equal importance: tadpoles, bullfrogs, and golden topminnows.

Late in the season, from mid-June through July, when many adult Little Blue Herrons were seen feeding in grasslands away from water, there was a major shift in the food brought the few remaining Little Blue Heron nestlings. Fish became much less important, whereas tree frogs, spiders and orthopterans became increasingly important. There was a definite trend away from aquatic and toward more terrestrial prey. Owen (1960) showed seasonal changes in the proportions of different foods brought to nestling Gray Herons in England. Changes in the proportion of prey reflected changes in their availability.

TABLE 11. Analysis of 50 pellets regurgitated by young Little Blue Herons.

	Number of Individuals	% of Total Volume
INVERTEBRATES		
Hirudinea	1	0.02
Astacidae	6	5.13
Palaemonetes spp.	3	0.10
Anisoptera (5 nymph)	15	0.91
Locustidae	11	0.53
Tettigoniidae	8	0.30
Gryllidae	10	0.08
Gryllotalpidae	1	0.12
Ephemeridae	2	0.12
Coleoptera (larvae)	4	0.34
Dystiscidae	12	0.55
Belostomatidae	4	0.10
Hydrophilidae	1	0.02
Tabanidae	1	0.02
Arachnida	73	3.96
VERTEBRATES		
Notophthalamus viridescens	6	1.18
Unidentified tadpoles	2	0.18
Acris gryllus	2	0.18
Hyla spp.	2	0.59
Hyla cinerea	6	4.73
Unidentified *Rana* spp. tadpoles	27	17.15
Rana spp.	7	2.60
Rana catesbeiana	4	16.95
Rana grylio	1	2.37
Rana pipiens	7	7.88
Seminatrix pygaea	1	0.69
Thamnophis sirtalis	1	0.08
Chaenobryttus gulosus	2	2.60
Enneacanthus obesus	2	0.99
Esox americanus	3	2.37
Fundulus chrysotus	50	14.78
Fundulus cingulatus	10	4.53
Gambusia affinis	28	1.58
Heterandria formosa	105	3.15
Jordanella floridae	8	0.99
Micropterus salmoides	7	1.38

Baynard (1912) analyzed 50 pellets from young Little Blue Herons at Orange Lake. They contained 1,900 grasshoppers, 37 small frogs, 149 cutworms, 8 lizards, and 142 small crayfish. E. A. Chapin (Howell, 1932), analyzed 46 Little Blue Heron stomachs, source of which was unspecified. They were composed of: crustaceans (principally crayfishes), 45% of the total food; small fishes (mainly minnows and killifishes with a few catfishes and sunfishes), 27%; insects, 16.5%; and frogs, small snakes and turtles, 8.5%.

Meanley (1955) collected 50 Little Blue Heron pellets in Arkansas and presented data on frequency of occurrence. A wide variety of insects, including many aquatic forms, were eaten. Leopard frogs were found in 14 of 50 pellets, and crayfish were found in 12 pellets. These large prey items must constitute an important part of the diet. Fish appear to have been less important and included only *Lepomis* sp.

(7 pellets), *Esox* sp. (2 pellets), and undetermined fish (6 pellets). However, both sunfish and pike may be large, and at Lake Alice single large redfin pickerel sometimes comprised an entire pellet.

Other published records also indicate that the Little Blue Heron diet varies widely. Fifteen stomachs from Puerto Rico contained: crustaceans (crabs and shrimp) 27.4%, lizards 29.4%, insects 39.7%, and a miscellaneous assortment of 2 frogs, 1 spider, and unidentified material 0.6%. The rest was incidental vegetable material (Wetmore, 1916). Van Tyne (1950) found a large number of spiders in two stomachs from the Canal Zone. McIlhenny (1936) observed that when water disappears from marshes and swamps, the Little Blue Herons subsist solely on insects obtained in grasslands.

Louisiana Herons regurgitated much less readily than did young of the other species. Other heron species also differ in how readily they regurgitate (Owen and Phillips, 1956). When disturbed, the older Louisiana Herons sometimes moved out of the nest and climbed up into the tree but still failed to regurgitate. Sometimes I could force them to regurgitate by shaking the tree, yelling, banging on the limb and otherwise annoying them, but usually this too failed. When they did regurgitate they often scattered individual fish about the ground beneath the tree. It was difficult to collect more than a few pellets from a brood throughout its nest life.

The 50 Louisiana Heron pellets collected at Lake Alice were composed of: fish, 95.4% by volume, various invertebrates, 4.2%, and amphibians, 0.2% (see Table 12). The occurrence of one cricket frog in 50 pellets indicates the relative unimportance of amphibians in the diet of young Louisiana Herons compared to the other three species.

The only invertebrates of importance were odonates. Of 58 invertebrates, 28 were dragonflies and 8 were damselflies (Zygoptera). Together they represented 3.2% of the total diet. Because of their long membranous wings these insects were conspicuous in the pellets. Their occurrence was sufficiently frequent to make unsafe the assumption that the birds took them rarely or by accident, as might be assumed for the 22 other invertebrate items (1.0% of the food).

The flagfish was by far the most important prey species, and was also the most frequently taken. Golden topminnows were extremely important in the diet, although only 81 of them were included as opposed to 205 individuals of third-in-importance mosquitofish. The banded topminnow was fourth in importance, and the least killifish was a relatively poor fifth in importance although a total of 143 individuals were taken. The following species were found in Louisiana Heron pellets, but not in pellets of the two other piscivorous herons: sailfin mollie *(Molliensa latipinna)*, pygmy sunfish (*Elassoma* sp.), crappie *(Pomoxis nigromaculatus)*, and starhead topminnows *(Fundulus notti)*.

Louisiana Heron pellets averaged 15.8 food items: amphibians less than 0.1, invertebrates 1.1, and fish 14.6 individuals. Flagfish, golden topminnow, mosquitofish, and least killifish comprised 81.0% of the diet.

TABLE 12. Analysis of 50 pellets regurgitated by young Louisiana Herons.

	Number of Individuals	% of Total Volume
ARTHROPODA		
Palaemonetes spp.	2	0.23
Zygoptera	8	0.25
Anisoptera (nymph)	28	2.92
Tettigoniidae	4	0.20
Gryllidae	9	0.17
Belostomatidae	2	0.20
Hydrophilidae	1	0.03
Dystiscidae	2	0.08
Diptera	1	0.03
Arachnida	1	0.08
VERTEBRATES		
Acris gryllus	1	0.17
Chaenobryttus gulosus	9	1.27
Elassoma spp.	30	0.79
Enneacanthus gloriosus	1	0.57
Enneacanthus obesus	1	0.42
Fundulus chrysotus	81	22.37
Fundulus cingulatus	19	7.93
Fundulus notti	8	1.13
Gambusia affinis	205	13.88
Heterandria formosa	143	4.53
Jordanella floridae	210	36.82
Leptolucania ommata	1	0.08
Lucania goodei	4	0.11
Micropterus salmoides	5	1.98
Molliensa latipinna	11	2.83
Pomoxis nigromaculatus	4	0.91

Killifish composed 68% of the total food in 48 Louisiana Heron stomachs analyzed by E. A. Chapin (Howell, 1932), and crustaceans (mainly prawns and a few crawfish) composed 20%. The balance included clam worms, spiders, and a variety of insects. A stomach from Puerto Rico (Wetmore, 1916) contained 1 goby (Gobiosoma) and 15 killifish. In 50 pellets from Orange Lake, Baynard (1912) found 2,876 grasshoppers, 8 small frogs, 17 cutworms, 6 lizards and 67 small crawfish. Although this latter data is dissimilar to the Lake Alice data, it might reflect a difference in food availability, or though much less probably, a change in preferences. Unfortunately there are fewer publisher records of the foods of the Louisiana Heron than of the other three herons discussed here.

DISCUSSION

Interspecific territory defense and selection of nest sites close to other species were special features of social nesting within this mixed heronry.

While establishing or defending territories at Lake Alice, males of all 4 species repelled herons of the other species when they approached too close. Herons which established territories later tended to establish them as close as possible to the holdings of the earlier arrivals. Later arrivals did not appear to select territories near birds of their own species in preference

to territories near other species. They took up territories near already established individuals, regardless of species. Because the size of the defended area of all four species decreased following pair formation until only a small area around the nest was defended, the heronry became more densely populated as the season progressed.

NEST SITE

A summary of the herons' nesting sites was presented in Table 1. The distribution of nests in the different species of bushes and trees was significantly different (by χ^2 test) among these 4 species ($p < 0.02$). The review of the literature earlier in this paper revealed a wide range in the nest sites used by these four species. The overlap is great, yet where they nest together, as they did at Lake Alice, differences in nesting sites appear. Of the four species compared in Table 1, the Snowy Egret, Cattle Egret, and Little Blue Heron all built most often in red maple and second most often in Buttonbush. Of the three, the Little Blue Heron showed the greatest preference for these two nest sites. However, the Louisiana Heron differed from these three and built most often in elder.

The heights of nests at Lake Alice in 1960 also differed for these 4 species ($p < 0.005$, "F" = 43.2). Paired "t" tests show that all the possible differences were significant ($p < 0.05$) except for the difference between Snowy Egret and Louisiana Heron. Although these two species nest at the same height, it has already been shown that they nested in different sites. Whether the selection of sturdier, better-sheltered nest sites by Louisiana Herons was the cause or the effect of their nesting in elders is not known.

The two sturdiest kinds of nest sites at Lake Alice were both artificial situations created by the herons. They were the old nest platforms and the basket-like growths of limbs caused by pruning terminal shoots in previous years. These were incorporated in the earliest established territories and appeared to be the preferred nest sites at Lake Alice. Obviously, by creating these favorable nest sites the herons tended to make the heronry more suitable for themselves in future years.

NEST BUILDING MATERIALS

Lake Alice provided these birds with nest building materials in addition to potential territories. All 4 species made nests of small sticks and twigs which they collected in or adjacent to the heronry. In 1960 there appeared to be some clear differences in the main sources of nesting material. Snowy Egrets picked most twigs from the ground. Louisiana Herons did likewise, but sometimes they broke twigs low in the bushes near the ground. Cattle Egrets and Little Blue Herons broke living and dead twigs off trees and bushes. Cattle Egrets tended to limit their twig gathering to the upper and outer reaches of the trees, where they took small twigs. Little Blue Herons collected twigs at all levels in the heronry, from the treetops to the ground, and sometimes from the ground. In 1959 Little Blue Herons at Lake Alice collected a much greater portion of their twigs from the heronry floor (Meyerriecks, in Palmer, 1962) than in 1960 and in Arkansas they characteristically collected from the heronry floor (Meanley, 1955). Cattle Egrets began taking nest material from trees around the edge of Lake Alice late in the 1959 nesting season and in 1960 started doing so in the middle of the nesting season. By the end of the 1960 season some Cattle Egrets were bringing twigs back from more than half a mile away. The utilization of a variety of sources for building twigs was adaptive. The birds appeared able to adjust their behavior so as to reduce, though by no means eliminate, competition among the four species for this material. Their nest gathering behavior also changed during the season as the availability of nest building material changed.

REGIONAL VARIATION IN CLUTCH SIZE

The average clutch size of many birds increases with increased distance from the equator (Lack, 1954). This trend has been suggested by the data available for several North American herons, but concrete data has been lacking (Meyerriecks, in Palmer, 1962). Little Blue Heron clutches averaged 4.04 in Arkansas (34° N., Meanley, 1955) and 3.7 at Lake Alice (29° N.). Cattle Egret clutches averaged 3.5 at Lake Alice (29° N.), 3.0 in Senegal (16° N., Morel & Morel, 1961), and 2.6 in Ghana (5° N., Bowen *et al.*, 1962). For these 2 species there appears to be a correlation between latitude and clutch size. Comparable data are not available for the other species. Teal (1965) presents data on clutch size for Snowy Egrets and Louisiana Herons from Sapelo Island, Georgia (32° N.). His clutch sizes averaged 3.2 and 3.1 respectively (compared with 3.5 and 4.1 for Lake Alice), but he visited the heronry only once per week and with the high levels of predation he reports, many eggs may have been lost from the nests before he recorded them.

The two most probable explanations for the apparent correlation between latitude and clutch size are: geographic differences in food abundance, and increased day length toward the north in summer months which allows more time for adults to find food (Lack, 1954). Any increase in total daylight would greatly increase the amount of time available for feeding because a certain mimimum amount of time is needed for the adults to fly back and forth between feeding and nesting areas, actually feed the young, and to care for themselves. Day-length in Arkansas is approximately one-half hour longer than at Lake Alice in late June. The Little Blue Herons in Arkansas had about 4% more daylight than did the Lake Alice birds and their clutches averaged 9% larger (calculations of day-length based on data in U.S.N. Observatory, 1960). At the time of year that Cattle Egrets were feeding their young at each place, the day-length at Lake Alice was 16% greater than at Senegal (Lake Alice clutches 16% greater) and 14% greater than at Ghana (Lake Alice clutches

35% greater). The Senegal clutches were 15% larger than the Ghana clutches, but day-length was 2.5% shorter. These data indicate day-length may be an important factor, but some other factor(s) must contribute to the differences in clutch size. Food availability might be more important as is suggested by the 90% fledgling success at Lake Alice, compared with a 46% fledgling success for Ghana. Although comparable data are not available for Senegal, losses were described as large.

The 1960 season was the 7th year that Cattle Egrets nested at Lake Alice (Rice, 1954) and the 8th year they are known to have nested in North America (Sprunt, 1955). Adaptation of clutch size thus appears to be rapid and is apparently under proximate control. Owen (1960) found no significant differences in clutch size of the Gray Heron in 3 heronries at essentially the same latitude in England. A study of geographic variation in clutch size in the Cattle Egret might help explain the factors controlling clutch size in birds in general as well as in Cattle Egrets.

Seasonal Variation in Clutch Size

At Lake Alice the 3 heron species with long nesting seasons had late clutches that were smaller than their early clutches. The difference is significant for both Snowy Egrets and Little Blue Heron clutches, but it is not significant for Cattle Egrets. If the peaks of breeding seasons of the Snowy Egrets and Little Blue Herons are assumed to be adapted to the seasons of greatest prey abundance for those species, then later broods were raised when food was less available and the decreased clutch size would be adaptive. The later nesting of Cattle Egrets and the stability in the size of their clutches throughout the season would indicate that their food did not become less available later in the summer. The fact that many Lake Alice Little Blue Herons and some Snowy Egrets changed their food habits and began hunting insects and amphibians in the uplands also indicates changes in the availability of food for these species through the summer.

The Significance of Asynchronous Hatching

For nidicolous species with synchronous hatching, Lack (1954 and 1966) has argued convincingly that average clutch size is evolutionarily adapted to agree with the average number of young that the adults can feed. The beginning of incubation among these 4 heron species, though it varied, invariably began before the last egg was laid. As a result hatching was asynchronous, that is the young hatched over a period of several days and there was considerable size disparity between siblings. The youngest chick in such broods, when the parents failed to provide sufficient food, was at such a disadvantage that it quickly starved. If food was especially short, the second youngest also starved. When this happened, brood size was promptly reduced. The surviving members of the brood appear to suffer comparatively little, I found no evidence of cannibalism. Lack's interpretation of asynchronous hatching is that it is an adaption that, while allowing for the production of a maximum number of young in years of food abundance, quickly adjust the number of nestlings downward to the number the parents can feed. Owen (1960) found considerable variation in the survival of nestling Gray Herons over a 5-year period in heronries in England. He concluded that when food is short the smallest chick dies, and when food is abundant all the chicks are raised.

The Cattle Egrets were able to raise nearly all their young at Lake Alice in 1960 and nestling mortality was only 8.2%. Cattle Egrets in Ghana in 1960 (Bowen *et al.*, 1962) had a nestling mortality of 54%. Presumably these birds were unable to find enough food for their young even though they laid much smaller clutches than the Lake Alice Cattle Egrets did (average clutch size of 2.6 as opposed to 3.5). Nestling mortality of the other three species at Lake Alice in 1960 was strikingly uniform, ranging from 25.4 to 28.1%. Snowy Egrets, Little Blue Herons, and Louisiana Herons were thus able to raise about 3 out of every 4 of their chicks.

Effects of Investigator on Birds

In any nesting study there is the possibility that the investigator's activities will adversely affect the birds, and this danger is great in colonial birds. In this study, nests within 10 ft of either side of a circular path through the study area were studied. I moved quickly from nest to nest along the path, and the adults returned promptly to their nests. Some mortality did result from my activities. Two eggs disappeared from a nest after I flushed the adult Cattle Egret. Although fledglings clung to the bushes and trees with amazing tenacity, occasional individuals fell to the ground. I kept records of these accidents and most of the young were back in their nest tree the next day, but 4 of the young that fell as they fled from my approach were not found on subsequent visits. Other possible effects are more difficult to evaluate but might be more important. Desertion of nests during construction or early egg laying might have been induced. The path remained the same throughout most of the season, and it is not likely that any nest was first disturbed later than the beginning stages of the nesting cycle. Although the birds continued to leave their nests at my approach, the area of disturbance became smaller after the first several visits into the heronry.

Nestlings more than a few days old regurgitated their last meal when disturbed and as noted earlier the youngest nestlings of these and other heron species often died of starvation. It is apparent that repeated loss of food might have increased the starvation rate. To help minimize this danger the heronry was never entered more than once each day after hatching began. It was often possible to count older young from a distance, and observations at some nests were terminated.

There was still a loss of food, and some nestlings did die. Yet, Cattle Egrets regurgitated more readily

and regularly than did the other 3 species and had a very low nestling mortality. Snowy Egrets and Little Blue Herons regurgitated with little provocation, but Louisiana Heron nestlings seldom regurgitated. The Louisiana Heron nestling mortality of 25% is not substantially different from Snowy Egret and Little Blue Heron mortalities of 28%. These figures are well within the range given for other nidicolous species by Lack (1954), and within the range Owen (1960) found in the Gray Heron.

The comparable nestling survival of the 3 aquatic feeding species, the much higher survival rate of Cattle Egret nestlings even with a greater food loss, and the fact that mortality did not appear to be excessive, all suggest, but by no means prove, that my effect on survival was not great.

FEEDING BEHAVIOR AND HABITAT

In the Gainesville area during the breeding season these four species fed in slightly different habitats, but there was a great deal of overlap. The 3 aquatic feedings species were usually limited to areas where the water was shallow (less than about 20 cm, usually much less) and to areas where emergent vegetation was not too rank. Cattle Egrets were similarly limited to areas where the vegetation was not too rank. The aquatic herons occasionally overcame this limitation by flying low over the water, or hovering and reaching down into the water to grasp prey in the bill. Sometimes too they fed from floating objects. In the summer around Gainesville, Snowy Egrets indulged in these unusual feeding patterns more often than the other two species, and the Louisiana Heron used them next most often. When they fed in these ways, the herons were not restricted by depth, but they probably employed such unusual techniques to enable them to take advantage of some bounty or, and I think this less likely, their normal feeding areas were temporarily unavailable.

The feeding behaviors of Snowy Egrets, Little Blue Herons, and Louisiana Herons are different (Meyerriecks, 1962) even though they employ many basic elements in common. My observations around Gainesville show that differences in feeding behavior coupled with differences in preferred feeding areas tended to reduce competition for food between these 3 species. Snowy Egrets fed in open areas and along the edges of openings, and they often actively pursued prey through shallow water. Little Blue Herons tended to feed in more heavily vegetated areas where stealth techniques were of prime importance. Louisiana Herons typically fed in deeper water and often waded to a depth of their leg or belly feathers. They also fed along the edges of canals and other banks where the water dropped off rapidly, and from floating or submerged vegetation in deeper water. In the Gainesville area during the breeding season Louisiana Herons fed primarily by stealth; however, they sometimes actively chased fish in shallow water. Regardless of whether these differences are basic differences between the species, they did reduce interspecific competition and were adaptive. Heron feeding behavior appears to be strongly influenced by proximate factors. For example, Louisiana Herons in Florida Bay (Meyerriecks, 1962) and during the breeding season at Cedar Key, employed Active Pursuit much more regularly than they did around Gainesville.

TABLE 13. Analysis of contents of 50 pellets regurgitated by the young of each of four species.

	% of Total Volume			
	Snowy Egret	Cattle Egret	Little Blue Heron	Louisiana Heron
Invertebrates	7.0	63.2	12.3	4.1
Fish	87.9	0.0	32.7	95.9
Amphibians	4.8	32.4	54.1	0.2
Reptiles	0.0	4.4	0.9	0.0
	Average Number of Items Per Pellet			
Invertebrates	7.56	31.96	3.04	1.11
Fish	20.50	—	4.30	14.64
Amphibians	0.92	2.02	1.48	0.02
Reptiles	—	0.06	0.04	—
All prey items	28.98	34.14	8.86	15.80

Cattle Egrets fed almost exclusively in the company of large grazing mammals around Gainesville during the breeding season as they did throughout their range. At this time they fed mostly around the edges of wet prairies and in neighboring pasture lands. Cattle Egrets walked beside the heads or flanks of grazing cattle and caught prey the cattle flushed. Although cattle frequently waded into the water, Cattle Egrets quickly abandoned those which moved into deep water. Snowy Egrets occasionally associated with cattle around Gainesville, and Snowy Egrets and Little Blue Herons occasionally fed away from water in high pastures. As already described, the frequency of such nonaquatic feeding increased during the midsummer of 1960. Louisiana Herons were not observed to feed in these areas.

FOOD HABITS

The food of the young of the 4 species at Lake Alice, as determined by the analysis of 50 regurgitated pellets from each species, is grouped into major categories and summarized in Table 13. Their parents brought these nestlings markedly different food. During the brood rearing season at Lake Alice these species not only took different proportions of the various classes of prey, as was shown earlier, but differences in the degree of diversification within each class of food are also conspicuous.

The mosquitofish was the Snowy Egret's most important as well as most numerous prey. Cattle Egret pellets averaged nearly two spiders and two nonaquatic frogs per pellet in addition to the numerous insects. The Lake Alice Cattle Egrets took no fish, tadpoles, aquatic invertebrates, nor pond-dwelling frogs during the nesting season.

Although Little Blue Herons ate nearly 3 times

as many fish as amphibians, amphibians made up the largest bulk of their diet. They did not eat the same kinds of frogs that Cattle Egrets ate (1.4 cricket frogs and 0.5 leopard frogs per pellet), but took instead pond-dwelling amphibians such as large ranid tadpoles and bullfrogs (0.5 and 0.1 per pellet). The Louisiana Heron's only important deviation from a straight fish diet was the inclusion of 30 dragonflies in the 50 pellets. All 4 species ate dragonflies, and the incidence of dragonflies increased with the incidence of fish. The flagfish was the most important and most numerous prey of Louisiana Herons.

It is apparent from a review of Tables 9-13 that even the 3 aquatic feeding species took different foods. Snowy Egrets ate mostly mosquitofish. Flagfish were a little more than half as important to them as mosquitofish were, and topminnows were relatively unimportant. The Louisiana Heron took primarily flagfish and topminnows were second most important. Louisiana Herons fed in deeper water than Snowy Egrets and their food habits around Gainesville were largely noncompetitive. The Little Blue Heron took mostly amphibians, although fish were also important. Its fish prey consisted primarily of topminnows. The Little Blue Heron fed in deeper water than did the Snowy Egret but ate practically no flagfish and thus did not appear to compete for fish with either Snowy Egrets or Louisiana Herons.

These differences greatly reduced competition for food among these four species around Gainesville during the nesting season and were adaptive. However, they do not necessarily hold for all places and all times. In the Gainesville area during the breeding season, it was possible, on relatively rare occasions, to find mixed feeding parties including the 3 aquatic feeders and other species as well, all apparently feeding on the same prey.

Pellet Volume and Number of Prey

The volume of the pellets regurgitated by young of these 4 herons varied. Little Blue Heron Pellets averaged 19.15 ml; Snowy Egret, 9.41 ml; Louisiana Heron, 6.06 ml; and Cattle Egret, 4.82 ml. In addition to real differences in pellet size at least 3 factors contributed to the differences. Little Blue Herons took some large prey, for example, the 4 bullfrogs eaten by them averaged 21.5 ml. Secondly, certain prey items, such as the dragonflies in Louisiana Heron pellets and the intact insects in Cattle Egret pellets, occupied an excessive amount of space for their volume. Thirdly, though less important, small fragments and disarticulated insect appendages were excluded from the pellet analysis and even though only undigested pellets were studied an occasional grasshopper appendage was discarded.

The average number of food items per pellet also varied (Table 13). The number of prey items and pellet volume were not correlated but number and size of prey items were. Average size of the invertebrates eaten by Snowy Egrets and Cattle Egrets (0.09 and 0.10 ml) was smaller than the average size of vertebrate prey eaten by them and by the other two. Little Blue Herons ate several fish species of large size, such as topminnows, warmouth, banded sunfish, and redfin pickerel, while Louisiana Herons and Snowy Egrets depended mostly on species of smaller size. Thus Little Blue Heron fish prey averaged 0.78 ml while Louisiana Heron and Snowy Egret fish prey averaged only 0.46 and 0.40 ml, respectively. However, even the average size of prey of the same species eaten by these three specis differed. For example, the average volumes of the golden topminnows taken were: Little Blue Heron, 1.50 ml; Louisiana Heron, 0.98 ml; and Snowy Egret, 0.86 ml. Even the average size of the tiny least killifish differed. Those taken by Little Blue Herons averaged 0.15 ml; Louisiana Heron, 0.11 ml; and Snowy Egret, 0.07 ml. Thus not only did these 3 species of herons select primarily different food but even when they took the same prey they took individuals of different sizes. The difference in size may also reflect their taking the prey from different habitats. Owen (1960) and Owen and Phillips (1956) found that Gray Herons in England and Purple Herons in Holland selected fish prey of certain preferred size classes from what was apparently available to them.

The Location of Heronries

Ideally, a breeding place for herons would: (1) be reasonably close to suitable feeding areas, (2) offer suitable space for territories, (3) have or be near an adequate supply of nesting materials, and (4) be relatively free from excessive predation and molestation. Freedom from excessive predation apparently means complete or nearly complete absence of mammalian predators. Places which offer appropriate territorial sites and nesting material near suitable feeding areas appear to be reasonably plentiful. However, the number of such places also free of predatory mammals is smaller. Floating islands, small mangrove islets, islands and spoil banks in lakes and bays provide sites for many heronries. Some heronries are found in trees growing in water several feet deep, while many others are located over dry land. In recent years heronries have been established in cypress trees in Florida phosphate settling ponds.

Many fresh water heronries in Florida are located where there are alligators and 2 heronries in the Gulf of Mexico near Cedar Key, Florida, are on islands which also support large populations of cottonmouths *(Agkistrodon piscivorus)*. American alligators at Lake Alice probably took mammals which wandered into the lake. Raccoon tracks, though seen on the shore, were never seen in the heronry. Alligators from 1 to 6 ft long, and occasionally much larger individuals, scavenged in the heronry. They ate dead nestlings, regurgitated fish, frogs, insects and anything else edible that fell to the heronry floor. Occasionally they also took live fledglings. At Lake Alice, watersnakes (*Natrix sipedon*, and possibly others) also scavenged in the heronry. These reptiles kept the Lake Alice heronry largely free of

the biological wastes that might have attracted such potential heron predators as raccoons, Fish Crows, and others.

A similar relationship existed near Cedar Key where cottonmouths scavenged over the heronry floor at night, picking up wastes from the heronry (Wharton, 1958). Perhaps the cottonmouths, as well as the alligators, were incompatible with raccoons. There were heronries and cottonmouths but no raccoons on two of the islands at Cedar Key, but on similar nearby islands, where there were no heronries and no cottonmouths there were large raccoon populations. Both alligators and snakes obtained food and in turn kept the heronry clean and less attractive to potential heron predators, and they probably killed and ate potential mammalian predators (at least the alligators). These relationships appear to be mutualistic; however the relationship must be facultative rather than obligatory because the species involved exist in many other places independent of one another. However, as Wharton (1958) has suggested, in certain special cases, as at Cedar Key, the cottonmouths and the herons may actually be interdependent.

The Lake Alice herons were an important factor in altering their own breeding habitat. Not only did they create favorable nest sites as discussed earlier, but they may also have damaged the area. The medium-sized colony of birds breeding at Lake Alice, was quite hard on the nesting vegetation. In inland heronries, but not coastal heronries where the herons nested primarily in mangroves, the bushes and trees that best satisfy the Herons' requirements may be growing in marginal situations as they were at Lake Alice. Not only did the weight of roosting birds break limbs, but twig gathering herons eventually broke off almost every available twig in the heronry. Earlier in this paper I reported the apparent exhaustion of twigs at Lake Alice in the 1960 season by Cattle Egrets. The total impact of these birds on the nesting substrate was great. When the extent of the suitable nesting habitat is small as it was at Lake Alice, the birds might effectively destroy the habitat. In larger areas, such as Bird Island in Orange Lake, the effect would be relatively less and the birds probably would not do much long-lasting damage. In describing the 1965 failure of a large mixed heronry in southeastern Alabama, Dusi and Dusi (1968) blamed a combination of drought with a concomittant decrease in food supply, increased predation, loss of social facilitation from other species, and interspecific strife from other roosting herons. Although the role of these factors is unproven, the correlation between the unseasonal drought and colony failure is impressive.

CATTLE EGRETS

Cattle Egrets at Lake Alice began and finished nesting later than did the other species. They selected territories close to already nesting herons regardless of species. They gathered most nest twigs from the treetops and left the heronry to gather twigs late in season. At Lake Alice the Cattle Egrets spent two days more in nest-building than did the other three species, and their nests were much sturdier when they started laying. The Cattle Egret laid fewer eggs per clutch than did the other species studied. Cattle Egrets at Lake Alice always laid on alternate days, while the other birds occasionally laid on consecutive days. They began incubation the day they laid their first egg or the day after, consequently asynchronous hatching was more pronounced in this species than in the others studied.

In spite of having the highest hatching success of the 4 species studied, the average number of Cattle Egrets hatching was still the lowest. However, in many Snowy Egrets, Little Blue Heron, and Louisiana Heron nests, the last to hatch was unable to catch up with his older siblings and quickly succumbed. Nestling mortality ranged from 25 to 28% for these species, but Cattle Egret nestling mortality was only 8% for the same period. Because of its low nestling mortality, Cattle Egrets averaged more young per nest at 2 weeks of age (2.9) than did the other 3 species (from 2.2 to 2.7). The other species but not the Cattle Egret thus appeared unable to provide sufficient food for all their young. If the significance of asynchronous hatching, discussed earlier, is interpreted correctly, then because the Cattle Egrets at Lake Alice raised nearly all their young, they must have been experiencing an abundance of food. The Cattle Egret population at Lake Alice had increased since 1954 when Cattle Egrets first nested there (Rice, 1956). The Cattle Egret erruption in North America and on other continents might be the result of their experiencing a similar food abundance. The worldwide explosion of Cattle Egrets appears to be based on their utilization of a previously vacant feeding niche which has been newly created by the development of the cattle industry. It is also possible that the Cattle Egrets' geographic spread has carried them beyond the range of their customary population controls. However, a lack of data precludes attempting to compare their densities in their original range with those in recently occupied areas.

CATTLE EGRET SYMBIOSIS

The close association of Cattle Egrets with large grazing mammals is a popular example of mutualism. In this relationship the Cattle Egret supposedly obtains food as a result of its association with the mammals, and the egret supposedly removes ticks and perhaps other ecto-parasites from the mammals. The egret is also suspected of acting as a sentry and warning its consort of approaching danger (Allee, *et al.*, 1949). There is amazingly little evidence to support the idea that Cattle Egrets remove ticks. Most food habits studies have yielded no ticks. In 3 cases where ticks have been recovered (Bates, 1937; Fitzsimmons, 1923 and Priest, 1933) the Cattle Egrets had apparently taken them from the ground rather than from the mammals. The removal of ticks from mammals by Cattle Egrets must be a very rare event.

In the Gainesville area during the nesting season, Cattle Egrets did most of their feeding in company with cattle and unquestionably caught prey disturbed by the cattle. They were not completely dependent on cattle in the Gainesville area during the winter, and even during the summer Cattle Egrets sometimes fed away from cattle. The relationship thus appeared to be somewhat less than obligatory, but the egrets were drawn to their associates. It is probable that Cattle Egrets were able to obtain more food during the breeding season when they fed with large mammals than when they fed alone. A large animal, like a cow, flushes insects over a wider area than does a smaller animal, such as a Cattle Egret. The primary benefit to the birds might well have been this greater flushing radius. This would explain why Cattle Egrets associate with such a wide variety of grazing animals. It is also compatible with the peculiar leapfrog feeding described by Meyerriecks (1960). In a flock of Cattle Egrets feeding independent of cattle the individuals at the rear of the group took wing, flew over the others and landed immediately in front of them. The birds proceeded like a continuous belt rolling across the field. The individuals flying and landing in front of the others greatly increased the flushing radius beyond that for an individual simply walking through the grass.

Around Gainesville the cattle did not appear to benefit in any appreciable and direct way from the association with Cattle Egrets. But the egrets did consume extremely large quantities of grasshoppers, especially during the nesting season when they were feeding their young. Perhaps in this way the large grazing mammals did profit by the relationship because the herbivorous insects on which the egrets fed were probably the grazing mammals' primary competitors. This would make the relationship truly mutualistic.

The association of Cattle Egrets with grazing mammals originally developed with nondomestic species. One can speculate that the original relationship was based, at least in part, on the egrets' removal of ticks, but there is no data to support this view and present food habits studies argue against the idea. The possibility that the egrets respond more quickly to approaching danger and warn their feeding associates of the danger remains an attractive but untested idea.

SUMMARY

Snowy Egrets, Cattle Egrets, Little Blue Herons and Louisiana Herons were the most abundant ardeids nesting in the mixed heronry at Lake Alice, Gainesville, Florida, during the 1958, 1959, and 1960 seasons. In 1960, daily records were obtained on 280 marked nests. These 4 species defended their territories against one another. Late territories were established as close to already existing territories as possible. The birds did not select territorial sites close to members of their own species in preference to sites close to other species. The 4 species differed in their peaks of nesting activity. Cattle Egrets started nesting later and their nesting season ended later than did the others.

Nests were stratified at Lake Alice. Differences in nest height and nest site preferences were both observed. In 1960 Snowy Egret and Louisiana Heron nests averaged 1.7 m, but were in different kinds of sites. Little Blue Herons nested significantly higher than these two, and Cattle Egrets nested significantly higher than Little Blue Herons. Late nests of the same species averaged higher than early nests. These differences reflected preferences of the birds, the decrease in availability of low nest sites as the season progressed and the kinds of sites available at Lake Alice.

Cattle Egrets spent approximately two more days in nest construction before laying than did the other species. Cattle Egrets always laid on alternate days, but the other species occasionally laid on consecutive days. Average incubation periods ranged from 22.4 to 23.8 days.

In spite of having the smallest average clutch, Cattle Egrets raised the largest broods because the adults were more attentive throughout the entire cycle. However, the biggest difference between Cattle Egrets and the three other species was in the survival of nestlings. The youngest sibling in practically all larger broods of the other 3 species starved to death, and sometimes the 2 youngest both starved. Cattle Egrets were able to provide enough food, and nearly all their young survived.

Clutch size of Little Blue Herons was smaller at Lake Alice than in Arkansas. Clutch size of Cattle Egrets at Lake Alice was larger than in Senegal and much larger than in Ghana. These differences follow the general trend for average clutch size of many bird species to increase with increased distance from the equator. Conflicting data from Georgia may not be comparable. Day-length may be related to clutch size, but perhaps food availability is more important. The rapid adaptation of clutch size argues for some proximate factor such as food.

Late clutches in the Snowy Egret and Little Blue Heron averaged significantly smaller than early clutches. The food brought to late broods by these 2 species also differed from what they brought early broods. It is concluded that the early peak in nesting was adapted to the time of maximum food availability for feeding the young. The reduced size of late clutches was adaptive because the parents were normally able to find less food at that time.

The starvation of the youngest chick or two quickly reduced the brood size to a number which the parents could feed and raise. All young survived when the parents were able to gather enough food. Asynchronous hatching was an adaption to bring brood size into line with food availability and to permit raising a maximum number of young in years of food abundance.

Analysis of 50 undigested pellets regurgitated by the young of each species and comparison of adult feeding habitats and behavior show that these species

utilized different food sources in the Gainesville area during the summers. Snowy Egrets and Louisiana Herons brought their young mostly fish (88 and 96% of total volumes respectively). Snowy Egrets took large numbers of the 2 small species, mosquitofish and least killifish, which they caught in shallow water. Louisiana Herons fished in considerably deeper water, where they took primarily flagfish and a few species of fish not taken by Snowy Egrets. Little Blue Herons ate mostly amphibians. They took many large ranid tadpoles and some large frogs. They also took fish, but they took different species than those taken by Snowy Egrets and Louisiana Herons. Cattle Egrets took mostly orthopterans (grasshoppers and crickets); however, amphibians (leopard and cricket frogs) were important in their diet.

American alligators at Lake Alice and cottonmouths on 2 coastal islands had mutualistic relationships with nesting herons. These reptiles promptly ate debris, such as regurgitated food and dead nestlings, that fell to the heronry floor. The heronry was thus kept less attractive to other scavengers which might have taken heron eggs and nestlings when the debris proved inadequate. The absence of raccoons from these heronries was striking.

The loss of few nestlings and the large size of late clutches strongly suggest that the Cattle Egrets at Lake Alice were experiencing an abundance of food throughout the 1960 nesting season. The adults have tapped an essentially vacant feeding niche and do not complete with other herons for food. Utilization of this artificial niche created by the cattle industry is probably a key factor in the recent and dramatic range expansion of the Cattle Egret.

There are no records of Cattle Egrets picking ticks from cattle in Florida, and they rarely take ticks anywhere. However, they do feed in association with cattle or other grazing mammals, and in Florida they do so most regularly during the summer season. Around Gainesville, the large mammals flushed grasshoppers, frogs, and other prey over a greater radius than did Cattle Egrets alone. The egrets could feed independent of the mammals, and did so regularly, especially during the winter. However, in the summer when vegetation was denser, they probably caught more food as a result of this association. The need to produce eggs and feed young obviously made this the period of peak food need. The Cattle Egrets aided the grazing mammals by removing large number of herbivorous insects from the pastures, but the mammals did not appear to be dependent on the egrets.

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