

EGG SIZE AND LAYING ORDER OF SNOWY EGRETS, GREAT EGRETS,
AND BLACK-CROWNED NIGHT-HERONS¹

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The nesting biology of the family Ardeidae (bitterns, herons, and egrets) has been intensively studied (e.g., Owen 1960, Milstein et al. 1970, Werschul 1979), but egg size in relation to laying order has not received attention. The last egg laid in gull and tern clutches is generally smaller than preceding eggs (e.g., Parsons 1970, Nisbet 1978). The relative size of the final egg in a clutch decreases with increased body size among bird species and this relationship may be correlated with an increased brood-reduction strategy (Slagsvold et al. 1984). Relative egg size could be an important component to brood reduction, because egg size can affect subsequent survival of young (Parsons 1970, Nisbet 1978, Lundberg and Väisänen 1979).

Asynchronous hatching can facilitate size differences among nestlings and assist in brood reduction (Lack 1954, Ricklefs 1965). In herons and egrets, asynchronous hatching results in senior broodmates who are superior to their younger siblings in both food handling and aggressive interactions (Fujioka 1985, Inoue 1985, Mock and Parker 1986).

Our objective was to describe egg size in relation to laying order for Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), and Black-crowned Night-Herons (*Nycticorax nycticorax*) in a southern Texas colony and Great Egrets in a southern Florida colony. Based on egg-size patterns in other colonial waterbirds and the occurrence of brood reduction in egrets and herons (see above), we predicted that the final egg laid in a clutch would be smaller than those laid earlier.

METHODS

Nesting Snowy Egrets, Great Egrets, and Black-crowned Night-Herons were studied on a dredge-material island in Lavaca Bay near Port Lavaca, Texas (28°36'N, 96°34'W; colony 609-121, Texas Colonial Waterbird Society 1982) from 14 April to 8 July 1988. The colony was visited every 2-3 days during the incubation period and every day during the hatching period; some

nests were visited daily during the incubation period. Nests were marked with flags, and eggs were individually marked with a felt-tipped permanent ink pen when first observed. Laying order was determined for 179 eggs in two- and three-egg clutches by hatching order ($n = 10$ eggs in two-egg clutches, 92 eggs in three-egg clutches) and order of appearance ($n = 22$ eggs in two-egg clutches, 55 eggs in three-egg clutches).

In Texas, the length and width of each egg ($n = 179$) were measured at least twice with a caliper to 0.01 mm and the values averaged. If the measurements differed by more than 0.2 mm, one or more additional measurements were taken and either one discarded ($n = 7$) or an average calculated ($n = 14$). Egg volume was determined in the field using the laboratory technique of subtracting the mass of an egg suspended in water from its mass in air (Evans 1969, Hoyt 1979). A battery-powered electronic balance accurate to 0.1 g was used to weigh eggs. Each egg's volume was determined twice on separate days. If the estimate of volume differed by more than 0.1 ml, a third measurement was taken and either one discarded ($n = 3$) or an average calculated ($n = 6$).

Nesting Great Egrets also were studied from 13 February to 2 May 1987 at a large mixed-species colony located in the central Everglades marshes near Andytown, Florida (26°11'N, 80°31'W). This colony was visited every 4-6 days during incubation and hatching periods. Eggs were numbered with indelible ink. Laying order was determined by order of appearance ($n = 28$) and hatching order ($n = 18$).

Length and width of Great Egret eggs in Florida were

TABLE 1. Frequency distribution in clutch size of Snowy Egret, Great Egret, and Black-crowned Night-Heron nests in Texas and Florida.

Species	Location	Number of eggs			
		2	3	4	5
Snowy Egret	TX	9	35	2	0
Great Egret	TX	11	33	2	1
Great Egret	FL	11	8	0	0
Black-crowned Night-Heron	TX	9	42	1	0

¹ Received 11 October 1989. Final acceptance 6 March 1990.

TABLE 2. Egg volume, length, and width in two- and three-egg clutches of Snowy Egrets, Great Egrets, and Black-crowned Night-Herons.

Clutch size	Species (location)	Laying order	n	Volume (ml)		Length (mm)		Width (mm)	
				\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
2 eggs	Snowy Egret (Texas)	A	6	22.0 A ¹	2.4	40.9 A	2.5	32.4 A	1.0
		B	6	21.5 A	1.1	40.8 A	2.8	31.9 A	1.5
	Great Egret (Texas)	A	5	46.6 A	3.7	55.5 A	2.4	40.4 A	1.3
		B	5	46.4 A	2.2	56.6 A	3.1	40.3 A	1.2
	Great Egret (Florida)	A	11	45.4 A	2.4	55.6 A	1.5	40.1 A	0.8
		B	11	43.6 B	3.6	54.9 A	2.6	39.5 A	1.1
	Black-crowned Night-Heron (Texas)	A	5	35.3 A	4.2	50.5 A	2.8	37.0 A	1.6
		B	5	33.4 B	3.5	50.3 A	1.4	36.1 B	1.5
3 eggs	Snowy Egret (Texas)	A	12	22.0 A	1.1	42.8 A	1.3	31.8 A	0.9
		B	12	21.5 AB	1.4	42.1 AB	1.5	31.7 A	0.9
		C	12	20.9 B	1.1	41.7 B	1.7	31.3 A	0.9
	Great Egret (Texas)	A	20	45.6 A	3.9	55.3 A	2.1	40.2 A	1.3
		B	20	46.2 A	4.1	55.7 A	1.8	40.3 A	1.4
		C	20	43.5 B	4.2	55.7 A	2.1	39.2 B	1.4
	Great Egret (Florida)	A	8	45.0 AB	4.1	55.2 A	3.2	40.0 AB	1.2
		B	8	47.2 A	2.5	55.9 A	3.2	40.8 A	0.9
		C	8	43.1 B	2.7	53.9 A	1.9	39.6 B	1.0
	Black-crowned Night-Heron (Texas)	A	17	37.2 A	2.8	52.6 A	2.5	37.3 A	1.2
		B	17	36.9 A	2.9	52.4 A	2.0	37.2 A	1.4
		C	17	35.0 B	3.0	51.8 A	2.0	36.4 B	1.5

¹ Means between or among laying orders by clutch size and species not sharing the same letter are significantly different from one another (two-way ANOVA; nest \times laying order; $P < 0.05$).

measured with a caliper to 0.5 mm. Egg volume was estimated by the equation (Hoyt 1979), volume = 0.509 \times length (cm) \times width² (cm²). The constant 0.509 was obtained from Texas Great Egret eggs (T. W. Custer, unpubl. observ.) and is similar to that found earlier for Florida Great Egret eggs (0.508, Loftin and Bowman 1978).

Relative size of the final egg laid was calculated as percent deviation from mean volume of all eggs in the clutch (Slagsvold et al. 1984). Analysis of variance (ANOVA) techniques were used to compare means. Means were separated using Bonferroni mean separation tests (Neter and Wasserman 1974).

RESULTS

Eggs generally hatched in the same order that they were laid. For nests where one or more eggs were of known laying order, hatching order was the same in Texas in 29 of 30 cases (Snowy Egrets: eight of eight nests; Great Egrets: 12 of 13 nests; Black-crowned Night-Herons: nine of nine nests). In one Great Egret nest the A egg (first egg laid) hatched second in a three-egg clutch. In Florida, hatching order was identical to laying order in all eggs of 14 Great Egret nests.

The modal clutch size was three eggs for all three species in Texas and two eggs for Great Egrets in Florida; only a few clutches had four or more eggs (Table 1). Thus, the analysis is concentrated on three-egg clutches and secondarily on two-egg clutches.

Most of the size variation in the egret and heron eggs arose from interclutch rather than intraclutch differences. For three-egg clutches, interclutch differences

accounted for 68.7%, 79.2%, and 78.6% of the total variation (R^2) in egg volume of Snowy Egrets, Texas Great Egrets, and Black-crowned Night-Herons, respectively (one-way ANOVA by nest, $P < 0.01$); laying order only accounted for 11.3%, 7.9%, and 11.1%, respectively (one-way ANOVA by laying order, Snowy Egret: $P = 0.138$; Great Egret: $P = 0.096$; Black-crowned Night-Heron: $P = 0.60$). For Florida Great Egrets, the interclutch differences for three-egg clutches accounted for 40.3% of the variation ($P = 0.223$) and laying order only accounted for 23.8% ($P = 0.057$).

Egg volume, length, and width were not significantly different between A and B eggs in two-egg clutches of Snowy Egrets and Texas Great Egrets (Table 2). In contrast, the B egg in two-egg Black-crowned Night-Heron and Florida Great Egret clutches had significantly smaller volume than the A egg; width also was significantly smaller in the B than A egg of Black-crowned Night-Herons.

The C egg in three-egg clutches of Texas Great Egrets and Black-crowned Night-Herons was significantly smaller in volume and width than the A and B eggs; the A and B eggs, however, were not different from one another (Table 2). The C egg for Florida Great Egrets was significantly smaller in volume and width than the B egg; however, there were no other significant differences among laying order. The C egg for Snowy Egrets was significantly smaller in volume than the A egg, but there were no differences in width among laying order ($P = 0.057$). Egg length was not significantly different among laying order for Texas Great Egrets ($P = 0.454$), Florida Great Egrets ($P = 0.813$), and Black-crowned

Night-Herons ($P = 0.300$); for the Snowy Egret, however, the C egg was significantly shorter than the A egg. Mean percent deviation in volume of the final egg in two- and three-egg clutches was -1.2% and -2.6% for Snowy Egrets, -0.2% and -3.5% for Texas Great Egrets, -2.0% and -4.4% for Florida Great Egrets, and -2.6% and -3.8% for Black-crowned Night-Herons.

Some individual C eggs were the largest or second largest in three-egg clutches. One C egg was the largest egg in the clutch for each species and location. For Snowy Egrets, Texas Great Egrets, and Florida Great Egrets, three C, four C, and three C eggs, respectively, were the second largest eggs in the clutches.

DISCUSSION

This study and an earlier one support the use of hatching order to predict laying order in egrets and herons. In this study, hatching order and laying order were identical in 43 of 44 egret and heron clutches; the A and B egg hatched in reverse order in one three-egg clutch. Hatching order and laying order were also identical in nine of 10 Little Egret (*Egretta garzetta*) clutches (total 47 eggs); an A and B egg also hatched in reverse order in one clutch (Inoue 1985).

Our results demonstrate that the last egg laid in egret and heron clutches is generally smaller than other eggs in the clutch, a pattern observed in other colonial waterbirds (e.g., Parsons 1970, Nisbet 1978). In this study the C egg in three-egg clutches of Snowy Egrets, Great Egrets, and Black-crowned Night-Herons was smaller in volume than either or both the A or B egg. The B egg in two-egg clutches of Black-crowned Night-Herons and Florida Great Egrets, but not Snowy Egrets and Texas Great Egrets, was also smaller than the A egg.

Our data support the hypothesis that small final eggs are associated with brood reduction and that within species there is a negative correlation between relative size of the final egg laid and clutch size (Slagsvold et al. 1984). It is argued that if the clutch is increased by one egg, it is important that this egg is small so that the brood reduction will operate effectively (Slagsvold et al. 1984). Brood reduction through asynchronous hatching of eggs has been documented in egrets and herons (Owen 1960, Werschkul 1979, Fujioka 1985, Inoue 1985, Mock and Parker 1986). In our study, the last egg laid in egret and heron clutches was smaller than earlier eggs. In addition, for all three species in our study, the percent deviation in volume of the last egg laid from the mean volume of all eggs in the clutch was greater in three- than two-egg clutches.

The importance of egg size in egrets and herons is unknown, but based on other studies of colonial waterbirds deserves further attention. Chick survival is positively correlated with egg size in gulls and terns (Parsons 1970, Nisbet 1978, Lundberg and Väisänen 1979), and although female age and time of laying influence egg size (Coulson 1963, Coulson et al. 1969), egg exchange experiments demonstrate a relationship between egg size and survival independent of parental care (Parsons 1975, Nisbet 1978). Females may be nutrient limited and produce a small final egg early rather than delay laying further to produce a larger egg (Birkhead and Nettleship 1982). On the other hand,

because egg size is negatively correlated to the length of incubation, small final eggs may be an adaptation to reduce the degree of hatching asynchrony (Parsons 1972).

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LITERATURE CITED

- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63:300-306.
- COULSON, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age compositions of populations. *Proc. Zool. Soc. Lond.* 140:211-227.
- COULSON, J. C., G. R. POTTS, AND J. HOROBIN. 1969. Variation in eggs of the Shag (*Phalacrocorax aristotelis*). *Auk* 86:232-245.
- EVANS, R. M. 1969. Specific gravity of White Pelican eggs. *Auk* 86:560-561.
- FUJIOKA, M. 1985. Sibling competition and siblicide in asynchronously-hatching broods of the Cattle Egret *Bubulcus ibis*. *Anim. Behav.* 33:1228-1242.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73-77.
- INOUE, Y. 1985. The process of asynchronous hatching and sibling competition in the Little Egret *Egretta garzetta*. *Colonial Waterbirds* 8:1-12.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LOFTIN, R. W., AND R. D. BOWMAN. 1978. A device for measuring egg volume. *Auk* 95:190-192.
- LUNDBERG, C. A., AND R. A. VÄISÄNEN. 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). *Condor* 81:146-156.
- MILSTEIN, P. LE S., I. PRESTT, AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. *Ardea* 58: 171-257.
- MOCK, D. W., AND G. A. PARKER. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40:459-470.
- NETER, J., AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Homewood, IL.
- NISBET, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 120:207-215.
- OWEN, D. F. 1960. The nesting success of the heron

- Ardea cinerea* in relation to the availability of food. Proc. Zool. Soc. Lond. 133:597-617.
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228:1221-1222.
- PARSONS, J. 1972. Egg size, laying date and incubation period in the Herring Gull. Ibis 114:536-541.
- PARSONS, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117:517-520.
- RICKLEFS, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67:505-510.
- SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, O. LOR-ENSTEN, AND M. HUSBY. 1984. On the adaptive value of intraclutch egg-size variation in birds. Auk 101:685-697.
- TEXAS COLONIAL WATERBIRD SOCIETY. 1982. An atlas and census of Texas waterbird colonies 1973-1980. Caesar Kleberg Wildlife Research Institute, Texas A&I Univ., Kingsville, TX.
- WERSCHKUL, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. Auk 96:116-130.

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