

# NESTLING MORTALITY AND THE ADAPTIVE SIGNIFICANCE OF EARLY LOCOMOTION IN THE LITTLE BLUE HERON

DAVID F. WERSCHKUL<sup>1</sup>

*Department of Biological Sciences, Mississippi State University,  
Mississippi State, Mississippi 39762 USA*

**ABSTRACT.**—I studied the reproductive biology and ecology of the Little Blue Heron (*Florida caerulea*) from 1975 to 1977 in Mississippi and Alabama. Incubation began after the second egg was laid, producing an asynchronous hatching of later eggs. The primary cause of nestling mortality was starvation of late-hatching chicks because of their failure to compete successfully with older siblings for food. Late-hatching chicks grew as fast as early-hatching chicks when older siblings died. Nestlings from broods manipulated so that young were even-aged grew as fast as older chicks from uneven-aged broods. This suggests that the ability of adults to distribute food equally among nestlings, not the amount of food delivered, limited the growth of late-hatching chicks.

The developmental pattern of nestlings was dominated by the rapid growth of the feet and by the development of ambulatory skills by the age of 13 days. When the young were older than 19 days, both adults foraged away from the nesting area, returning to feed young during the day and brood at night. By this time the nestlings had developed thermoregulation, ambulatory abilities, and an escape response. Nestlings were essentially free of parental care after 21 days of age except for feeding, which continued until fledging at approximately 50 days of age. The rapid development of motor skills effectively shortens the nestling period from 56 to 19 days. I attribute the rapid development to an increased rate of food delivery (by releasing both adults to forage away from the nesting area), to increased food consumption (a consequence of sibling competition during feeding), and to decreased predation (by early maturation of the escape response). The pattern of nestling development is viewed as a preadaptation to large body size, as it allows a longer nestling period (= increased time for growth) than would be expected if young were dependent on adults for protection from predators until fledging. *Received 27 September 1977, accepted 11 October 1978.*

PATTERNS of avian development have received considerable attention (see Ricklefs 1968, 1973, 1977 for reviews) and some generalities can be made. Because of relatively high nestling mortality rates and efficient use of food resources, selective pressures have generally operated to shorten the nestling period by increasing growth rates to a physiological maximum (Ricklefs 1969). However, for large species reproductive strategies are complicated because of the long nestling periods and low growth rates correlated with increasing body size (Dunn 1975). Clearly there can be multiple solutions for increasing fitness under the conflicting demands of minimizing the duration of the nestling period and increasing body size. Decreased clutch size, low fledging weight, precocial development, and other morphological and behavioral characteristics are in part adaptations to shorten the nestling period.

In general, studies on avian reproductive strategies have treated the brood as a unit and have been concerned with the question of how selection has acted to maximize the return on parental investment. Because of this, the adaptive significance of nestling development has frequently been interpreted in terms of nest productivity rather than in terms of individual survival. Trivers' (1972, 1974) proposal that selection frequently results in parent-offspring conflict and sibling strife has helped stimulate a more refined theory of reproductive strategies (e.g. Brockelman, 1975,

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<sup>1</sup> Present address: Mississippi-Alabama Sea Grant Consortium, Gulf Coast Research Laboratory, Ocean Springs, Mississippi 39564 USA.

Graul et al. 1977). Still, only recently have these concepts been applied to data on nestling development (O'Connor 1977a, 1977b, 1978; Werschkul and Jackson in press).

In this paper I report on reproductive success, nestling behavioral and physical development, and parent-young interactions in the Little Blue Heron (*Florida caerulea*). I address these questions: (1) What are the causes and rates of nestling mortality? (2) Are the chances of survival equal for all young within a brood with respect to position in the hatching sequence? (3) In what way is the pattern of behavioral and physical development adaptive to the nestling environment? (4) Finally, are adaptations of the young to sibling competition limiting nest productivity?

#### METHODS

Observations were made from 1975 to 1977 on the reproductive biology and ecology of the Little Blue Heron in two mixed-species heronries in Mississippi and Alabama (for details on the heronry structure and species composition see Werschkul 1977a, 1977b). I made all observations in areas where Little Blue Herons nested without other species of wading birds. I tried to minimize the adverse effects of my presence on the nesting birds by dividing the heronry into sections and making observations in different sections within the heronry for the different aspects of the study, e.g. the areas where observations on nesting success were made were distinct from areas where nestling growth measurements were made. When data collecting required observations from the heronry for periods longer than 30 min, I restricted my activities to 0700–1000 on days with moderate temperatures and without heavy rains or high winds.

I visited nests every 2–7 days and measured nesting success as the number of viable eggs and/or young. I viewed the contents of each nest by using a mirror attached to a pole (Parker 1972). Nest visits continued until the young were 4 weeks old, when their ability to fly short distances prohibited accurate counts of the number of young. At 14 days young could climb out of the nest when I approached; if I was unsure of the exact number of young, I would record the nest as active but with an unknown number of young. I collected data on the relationship between position in the hatching sequence and nestling mortality from observations on nests used for growth measurements. Observations on the causes of chick mortality were made during nesting success measurements and from blinds.

I marked nestlings from 46 nests by marking their legs with permanent ink at hatching and later tagging them with USFWS bands and color bands. These nestlings were visited every 2–7 days and the following measurements made: body weight (to the nearest g on a triple beam balance), bill length (the upper mandible from the tip to base as marked by the feathers on the forehead), wing length (from the carpal-ulna junction to the distal end of the phalanges excluding feathers), tarsus length (from the junction of the tibiotarsus with the tarsometatarsus to its junction with the phalanges), and digit length (the middle toe from the webbing just below its junction with the tarsometatarsus to the distal end excluding the nail). I estimated adult sizes from measurements of museum specimens ( $N = 17$ ) at Mississippi State and Louisiana State universities.

I manipulated 5 broods of size 3 and 10 broods of size 4 during the 1977 breeding season so that the young were even-aged. Pipped eggs and young under the age of 3 days were removed from nests, matched according to developmental progress, and placed back into other nests where eggs and/or young had been previously removed. I weighed these nestlings every 2–7 days.

The timing of endothermy was estimated by removing chicks from their nests, placing them individually in an incubator set at 25°C or 10°C, removing them after a 5- or 10-min period, and recording body temperature to the nearest 0.5°C by inserting a thermometer down the nestling's throat to the pectoral girdle. Data were analyzed by relating body weight to temperature.

Behavioral development of Little Blue Herons was studied during approximately 600 h of field observations. Blinds were constructed atop scaffolding, allowing me to view nests at close range and to identify individuals by differences in body markings. These observations were supplemented with experiments similar to those designed by Emlen (1963) for Herring Gull (*Larus argentatus*) chicks. A 46 × 61-cm piece of plexiglass was fixed as the top of a table at a height of 92 cm and this apparatus was placed outside the heronry. The plexiglass platform had a portion of the gummed paper covering removed to provide a "visual cliff" (see Emlen's Fig. 3, 1963). Prior to testing, birds were taken from their nests, hooded, transported to the platform, and placed on and parallel with the line dividing the paper-covered portion and the transparent part of the plexiglass. I would then lie underneath the platform so that I could view the bird from below and perform these tests: 1) *visual cliff*—the response of the nestling to the visual

cliff; 2) *push resistance*—I placed the chick on the middle of the platform and slowly pushed it with a transparent shield towards the edge; 3) *edge withdrawal*—I placed the chick 5 cm from the edge of the platform; and 4) *jump-escape*—I withdrew from under the platform, walked 15 m from the platform, turned, waited 5–10 s, and ran slowly (ca. 2 m/s) back to the platform waving my arms. I scored my observations for these tests as: *visual cliff* test—no response (0), head turn (1), body turn (2); *push resistance* and *edge withdrawal* tests—no response (0), body turn (1), backwards push (2); *jump-escape* test—no response (0), jump during arm waving approach to platform (1), jump during initial testing or during withdrawal from platform (2). I repeated each test three times per chick unless the escape response made this impossible. Chicks were aged by bill length and grouped into age classes of 3-day intervals for analysis.

Data were analyzed using the SPSS Statistical Package (Nie et al. 1975) for descriptive statistics. I compared population parameters with the aid of the BMD Statistical Package (Dixon 1974). Analysis of covariance designs were treated as a regression problem with “dummy” variables (Neter and Wasserman 1974) and analyzed with an on-file program (LLS-SELECT) at the Mississippi State University Computer Center using the Linear Least Squares procedure of Daniel and Woods (1971) and the subset selection procedure of Lamotte and Hocking (1970). I calculated growth rates of body parts using Ricklefs' (1967) technique from data on the first- and second-hatched nestling.

## RESULTS

*Nestling mortality.*—Of 926 nests observed during the 3-year study, 164 (17.7%) were deserted before the young reached the age of 28 days. Of these 164 desertions, 146 (89.0%) were abandoned before hatching was completed (Fig. 1). No nests with young over the age of 28 days were deserted. Of 18 pairs that deserted after hatching, 12 deserted after predation of juveniles, 4 deserted after loss of nest support, and 2 deserted from unknown causes. Predation on juveniles was nocturnal and concentrated in one area of the heronry. Only part of the nestlings were eaten, usually the head, suggesting that the predator was probably an owl or small mammal (J. Ogden pers. comm.).

Partial brood mortality was more common than loss of the entire brood. Of the sample population of 3,750 eggs, the loss of young because of entire brood failure was 664 (17.7%) while the loss of young from partial brood mortality was 1,031 (27.5%) (Fig. 2).

In general, incubation began after the second egg was laid, producing an asynchronous hatch (Table 1). The most common pattern of hatching was 2 eggs on day 1 followed by later hatchings every 1–2 days. Brood reduction generally resulted from the death of late-hatching chicks. Differences among mortality rates by position in the hatching sequence are significant ( $\chi^2 = 20.87$ ;  $df = 4$ ;  $P < 0.01$ )—mortality increased with each later position in the hatching sequence (Fig. 3). The primary reason for the higher mortality among late-hatching chicks was their failure to compete successfully with older siblings for food. This resulted in lower growth rates and eventual starvation (Fig. 4, Table 2). The growth rates of late-hatching chicks, however, were affected by the survival of older siblings. When early-hatching chicks survived, younger siblings apparently could not compete successfully for food, grew slowly, and eventually died. When older siblings died, however, late-hatching chicks did compete successfully for food, grew nearly as fast as early-hatching chicks, and survived well.

Death of early-hatching chicks was relatively uncommon in successful nests (Fig. 3). Among the first-, second-, and third-hatched, 20% ( $N = 83$ ) failed to survive past the age of 19 days. The six of these nestlings that I was able to locate had died after falling from the nest, either injuring themselves or being unable to climb back to the nest (see also Meanley 1955).

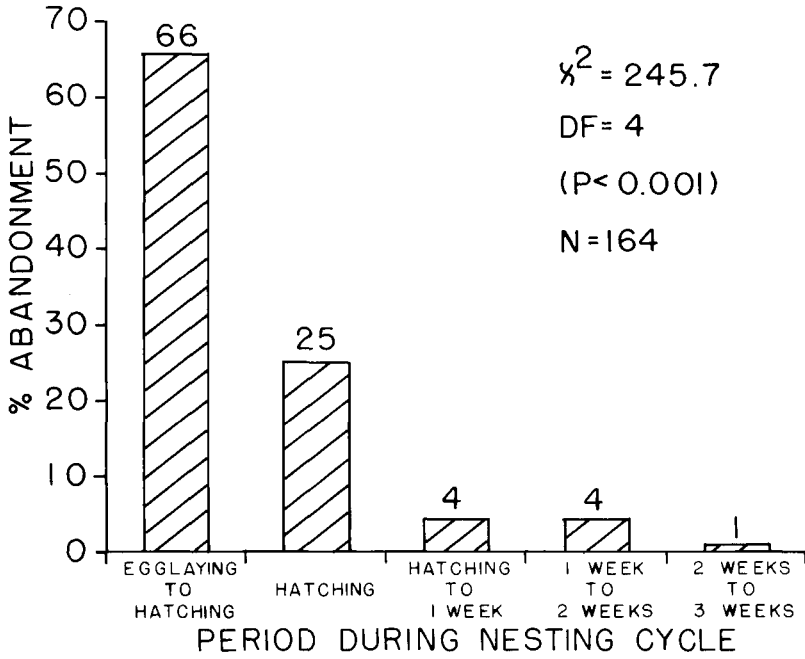


Fig. 1. Nest desertions by Little Blue Herons through the nesting cycle. Numbers above bar graph are percentage values.

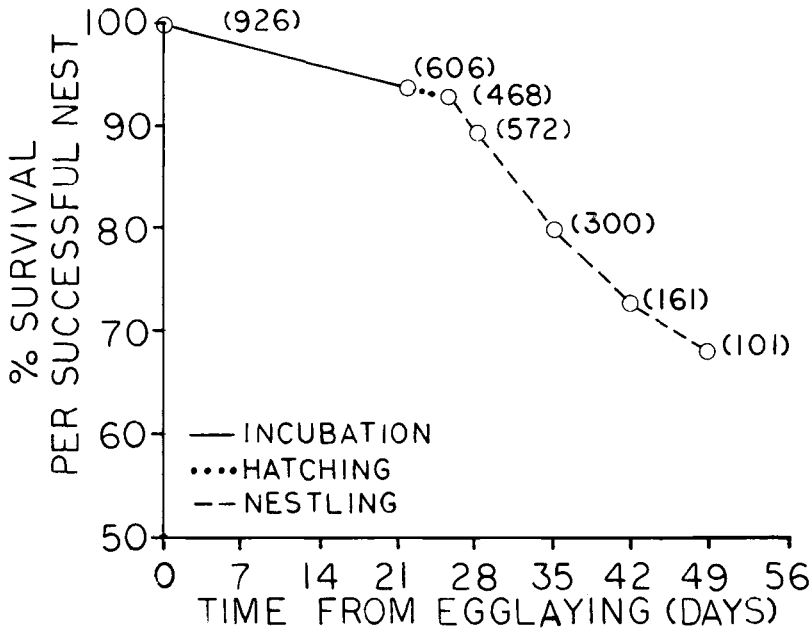


Fig. 2. Survival of Little Blue Heron eggs and nestlings per successful nest. Numbers in parentheses are sample sizes.

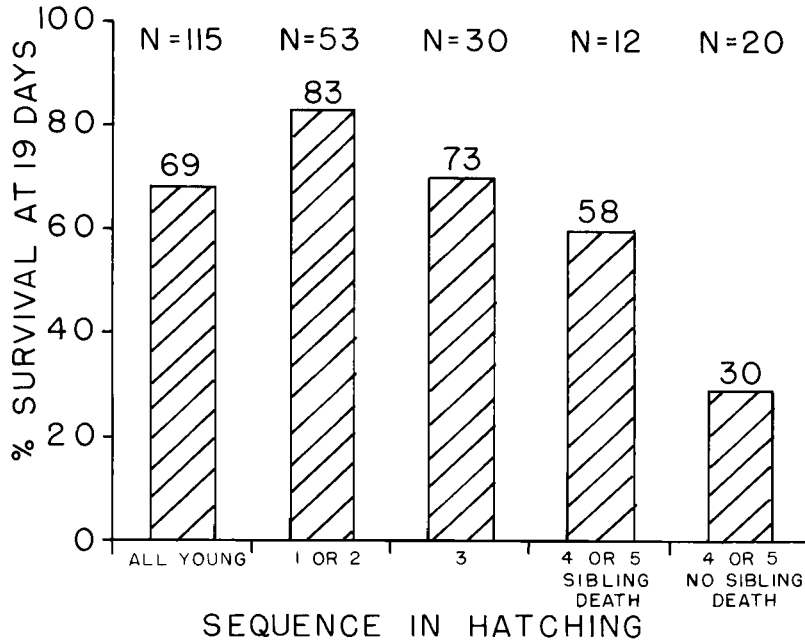


Fig. 3. Survival of Little Blue Heron nestlings by position in hatching sequence. Later hatchings (4 or 5) are divided into groups with and without death of older siblings. Numbers above bar graph are percentage values.

Because of the apparent effects of sibling competition for food, I was curious as to whether differences in growth rates among early- and late-hatching chicks resulted from insufficient food delivered to the nest to support all chicks or from an uneven distribution of food among nestlings. To distinguish between these alternatives, I manipulated 5 broods of size 3 and 10 broods of size 4 so that the young were even-aged. I assumed that young in even-aged broods had competitive abilities more nearly equal than young in asynchronously-hatched broods. Hence, if the growth rates of even-aged nestlings were lower than older chicks of uneven-aged broods, then the amount of food delivered limited the growth of late-hatching chicks. However, if the growth of even-aged chicks was equal to that of older chicks of uneven-aged broods, then food distribution limited the growth of late-hatching chicks. The growth rates of nestlings from even-aged broods of size 3 and 4 were not significantly different from those of the older chicks of uneven-aged broods (Fig. 4 and Table 2).

TABLE 1. Hatching sequence of Little Blue Herons.

Sequence in hatching	N	Time difference (days) in hatching from 1st hatched ( $\bar{x} \pm 1$ SD)	Range (days)
2nd	34	0.59 $\pm$ 0.61	0-2
3rd	32	1.78 $\pm$ 0.91	1-4
4rd	18	2.67 $\pm$ 1.19	1-6
5th	8	3.38 $\pm$ 1.19	2-5

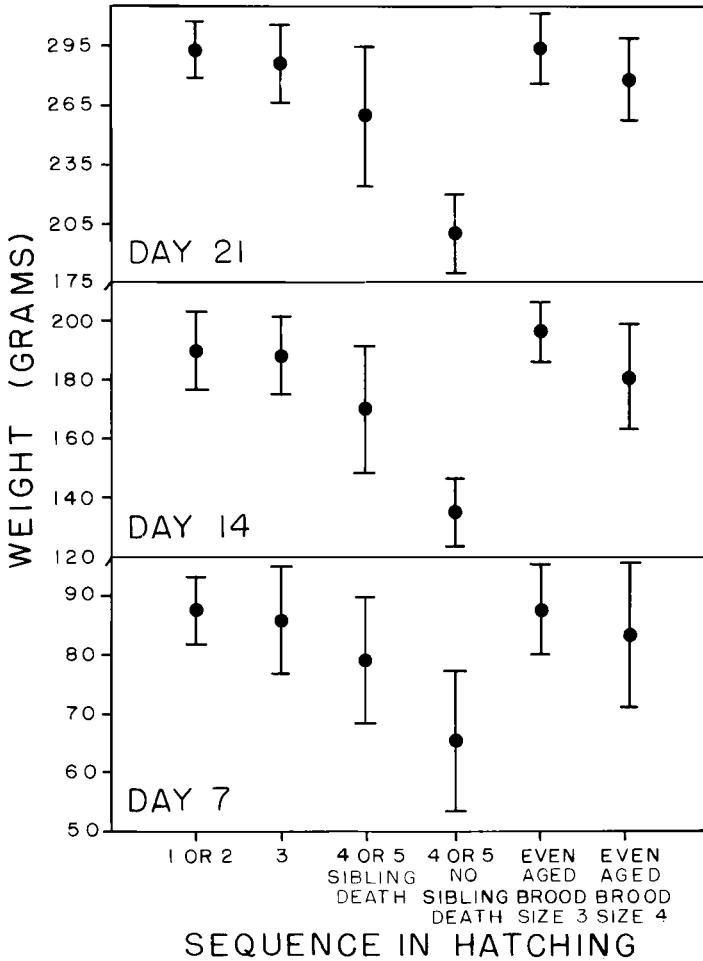


Fig. 4. Growth of nestling Little Blue Herons by position in hatching sequence for asynchronously-hatched broods and even-aged broods. Mean and 95% confidence interval are plotted. Regression equations for each group are given in Table 2. Division of later hatchings (4 or 5) same as in Fig. 3.

These results suggest that adults are unable to distribute food evenly among nestlings, rather than the amount of food delivered limiting the growth of late-hatching chicks.

*Nestling development.*—Nestling Little Blue Herons showed differential growth of body parts (Fig. 5), with a remarkably rapid development of the feet during the first 2 weeks. Four of the growth variables (digit, weight, wing, and tarsus) conform to the logistic curve and one (bill) to the Gompertz curve when data are fitted by Ricklefs' (1967) method (Table 3). Comparing the times required for 90% of the nestling's growth ( $t_{10-90}$  values), the digit shows the highest growth rates, followed by the wing, tarsus, and bill.

Endothermy was reached at a weight of about 225 g (age 16 days) during cold treatments (10°C for 10 min) and a weight of 160 g (age 11 days) for moderate temperatures (25°C for 5 min) (Table 4). However, these estimates should be con-

TABLE 2. Results of analysis of covariance comparing nestling growth vs. age, position in hatching sequence, experimental manipulation of hatching sequence, and death of early-hatching chicks.

Source	df	Mean sum of squares	F-value
Regression	6	360975.3	773.1**
Error	336	466.9	
Total	342		

Variables	B	STD error	t-value
X <sub>1</sub>	14.82	0.25	59.2**
X <sub>1</sub> X <sub>2</sub>	0.07	0.38	0.2
X <sub>1</sub> X <sub>3</sub>	-1.06	0.94	1.1
X <sub>1</sub> X <sub>4</sub>	-0.03	0.32	1.0
X <sub>1</sub> X <sub>5</sub>	-1.84	0.48	3.8**
X <sub>1</sub> X <sub>6</sub>	-4.98	0.85	5.9**

$Y = 27.4 + 14.8X_1 + 0.07X_1X_2 - 1.06X_1X_3 - 0.03X_1X_4 - 1.84X_1X_5 - 4.98X_1X_6$   
 where:  $y$  = weight (g);  $X_1$  = age (days) - 3;  $X_2$  = 1 if even-aged, brood size 3, 0 otherwise;  $X_3$  = 1 if even-aged, brood size 4, 0 otherwise;  $X_4$  = 1 if 3rd hatched, 0 if otherwise;  $X_5$  = 1 if 4th or 5th hatched, death of older sibling, 0 otherwise;  $X_6$  = 1 if 4th or 5th hatches, no death of sibling, 0 otherwise.

\*\* ( $P < 0.01$ ).

sidered maximal, or what Dunn (1975) calls the *physiological* age of endothermy. The *effective* age of endothermy is generally earlier because of the synergistic effects of exogenous factors on body temperature. Depending on the weather and the age of nestlings, adult Little Blue Herons will brood or shade, nestlings will huddle or disperse, and individuals will sunbathe or gular-flutter as means of conserving or dispersing body heat (see also Bartholomew and Dawson 1954, Hudson et al. 1974). By the age of 11 days, nestlings were individually able to thermoregulate from 0800 to 2000 except during adverse weather. An adult brooded the young at night, during morning hours, and during adverse weather until the age of 19 days.

The rapid development of the feet and the timing of endothermy coincided with the behavioral changes needed for movement from the nest. After day 12, nestlings did not avoid a visual cliff and the beginnings of escape behavior were apparent (Fig. 6). By day 17 the results for the visual cliff and escape-jump tests were nearly reversed from day 3. The results of the push resistance and edge withdrawal tests reversed in a similar, though not so clear, manner.

The Forward (= threat) display is the common stereotyped behavior used by herons during territorial encounters (Meyerriecks 1960). Some components of the Forward display were evident in nestling Little Blue Herons at age 5 days (e.g. bill jabbing, head and neck held erect) though other components (e.g. feather erection, wings spread) did not appear until the age of 13 days. By the age of 18 days, although there were still obvious size differences between adults and young, Forward

TABLE 3. Growth parameters for Little Blue Herons, calculated by the methods of Ricklefs (1967).

Variable	Growth form	Asymptote	Ratio to adult	Growth rate	
				$K$	$t_{10-90}$ (days)
Weight	Logistic	300 g	1.16	0.258	17.2
Digit	Logistic	58 mm	1.08	0.388	11.3
Wing	Logistic	74 mm	1.03	0.209	21.1
Tarsus	Logistic	79 mm	1.18	0.133	28.8
Bill	Gompertz	62 mm	1.26	0.088	31.8

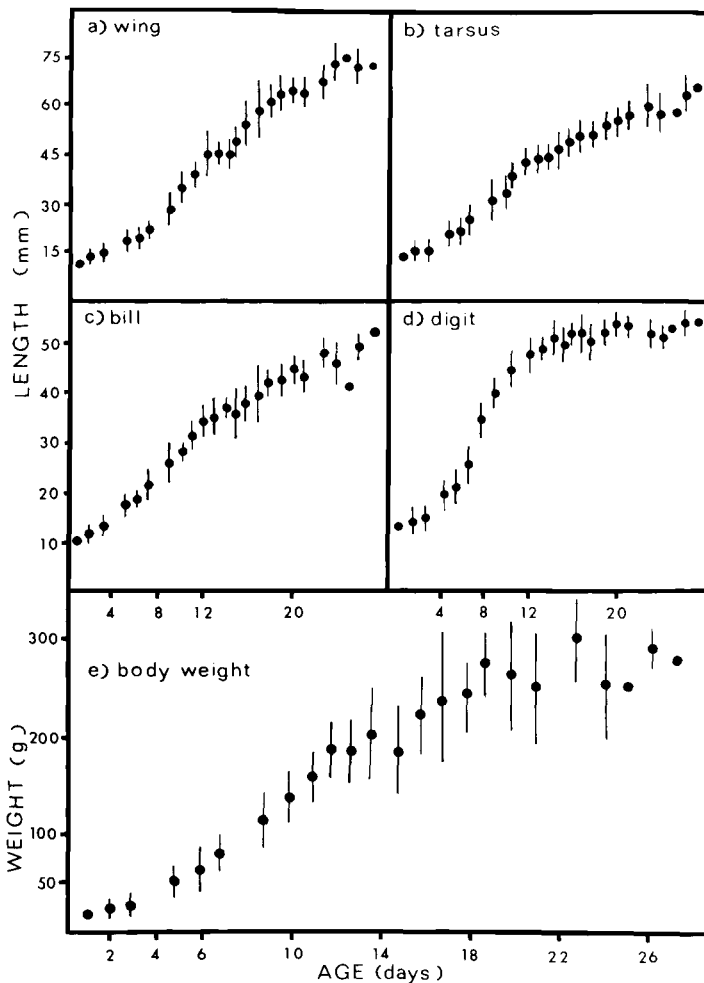


Fig. 5. Growth curves of body parts of nestling Little Blue Herons. Mean values  $\pm$  2 SD are shown.

TABLE 4. Results of analysis of covariance comparing body temperature vs. body size, temperature of chamber, and time in chamber.

Source	d.f.	Mean sum of squares	F-value
Regression	5	158.53	142.0**
Error	212	1.14	
Total	217		

Variables	B	STD error	t-value
X <sub>1</sub>	5.18	0.35	14.7**
X <sub>2</sub>	-2.79	0.79	3.5**
X <sub>3</sub>	4.64	0.79	5.9**
X <sub>1</sub> X <sub>2</sub>	0.77	0.41	1.9*
X <sub>1</sub> X <sub>3</sub>	-1.82	0.41	4.1**

$Y = 25.7 + 5.18X_1 - 2.8X_2 + 4.64X_3 + 0.8X_1X_2 - 1.82X_1X_3$   
 where: Y = body temperature (C°); X<sub>1</sub> = log<sub>10</sub> (body weight [g]); X<sub>2</sub> = 1 if chamber temperature 10°C, 0 if chamber temperature 25°C; X<sub>3</sub> = 1 if 5 min, 0 if 10 min.

\*\* (P < 0.01).

\* (P < 0.05).



displays by nestlings were usually successful in defending the nest site (see also Werschkul 1977c).

I assessed the responses of nestling Little Blue Herons to predators by observing their reactions to me during weighings. From the age of 1 to 6 days nestlings showed no apparent escape or protection responses to removal from the nest or handling. After the age of 7 days, Forward displays were frequently given when I approached and nestlings attempted to stab my hand with their bills when I reached into the nest. Nestlings first tried to escape at day 10, though they were easy to catch until day 14. After the age of 18 days, success at capturing nestlings depended on the location of the nest, the time of day, and the age of the chicks (see also McVaugh 1973). These observations parallel the relationship between nestling's age and predation rate. For the 12 nests suffering predation after hatching, 7 had an oldest nestling of 7 days or younger, 4 had an oldest nestling between the ages of 8 and 14 days, 1 had an oldest nestling between the ages of 15 and 21 days, and none occurred in nests with young older than 21 days.

*Parent-young interactions.*—I recorded the distance from the nest to parent between 1200 and 1300 through the nesting cycle (if a feeding was in progress the observation was discarded). The pattern of parent attentiveness after hatching was: brooding from day 1 to 10, one adult near the nest from day 11 to 18, and both parents absent from the nest after day 18 (Table 5).

After the age of 10 days young were fed once per adult visit. Before the age of 10 days young were fed more than once per adult visit. I assume adults deliver about the same amount of food to the nest on each visit and the multiple feedings before the age of 10 days represent one way adults provide food to young to match their ability to utilize and store food. Based on this assumption, I equate parental exchange rates, defined as the time between adult visits to the nest between 0600 and 2100, to feeding rates (Fig. 7). Parental exchange rates decreased after day 5, were nearly halved by day 11, and remained around 100 min until day 21. After day 21 they decreased until day 32, when quantitative observations stopped.

Feeding behavior changed with nestling development. During the first week food was regurgitated by adults into the nest where nestlings picked it up. Nestlings first started to grab the adult's bill at day 3 and this behavior was commonly observed after day 5. Bill grabbing and direct transfer of food predominated after day 7. At the age of 13 days chicks began to follow adults and were fed away from the nest. The change in feeding behavior from regurgitation into the nest, to bill grabbing, to active chase accentuated the impact of sibling food competition because of the nestlings' age differences. I did not quantify differential feeding of young, though I observed that older siblings were first to be fed and not all chicks were fed each feeding (see also Blaker 1969).

The young were capable of gliding flight after day 28 and sustained flight after day 35. After the age of 40 days, feedings were rare—a maximum of two per day. Adults continued to feed young until the eighth week, when they fledged. I was not always able to observe the exact date of fledging. However, I did note differences in fledging age of 9 days between nests and, in general, young from early-nesting birds stayed in the heronry longer than young from late-nesting birds.

Adult Little Blue Herons did not leave the nest when small avian egg predators such as Common Crows (*Corvus brachyrhynchos*) and Blue Jays (*Cyanocitta cristata*) entered the heronry although they did leave the nest when larger predators, like Red-tailed Hawks (*Buteo jamaicensis*), appeared. I found several partially-eaten

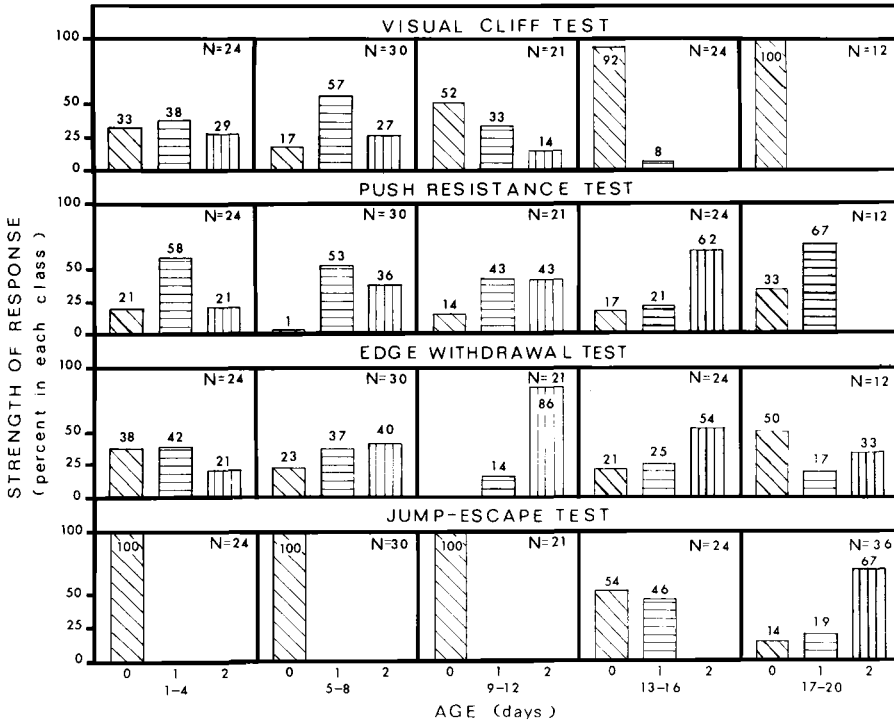


Fig. 6. Behavioral development of nestling Little Blue Herons. Numbers above bar graphs are percentage values.

adult Little Blue Herons on their nests after what I think was a raid by an owl. However, based on observations of adult behavior during the day, I doubt if the adults were protecting nestlings, but more likely were victims of nocturnal attacks. In general, herons have not been observed to defend the nesting area against large predators (Milstein et al. 1970, Krebs 1974, Werschkul 1977c), though they will defend against other herons and small egg predators (Werschkul 1977c, Burger 1978).

TABLE 5. Parent distances from the nest as a function of the age of the oldest nestling.

Age (days)	N	Parent behavior (%)			
		Brooding <sup>a</sup>	On nest <sup>b</sup>	Near nest <sup>c</sup>	Away from nest <sup>d</sup>
1-3	23	87.0	13.0	0.0	0.0
4-6	25	84.0	16.0	0.0	0.0
7-9	14	83.4	16.6	0.0	0.0
10-12	17	11.8	47.1	41.1	0.0
13-15	11	9.1	27.3	54.5	9.1
16-18	17	5.8	5.8	47.1	41.1
19-21	7	0.0	0.0	28.6	71.4
22-24	5	0.0	0.0	0.0	100.0
>25	23	0.0	0.0	0.0	100.0

<sup>a</sup> Includes shading.

<sup>b</sup> Within 1 m of nest.

<sup>c</sup> Between 1 m and 10 m of nest.

<sup>d</sup> Greater than 10 m from nest.

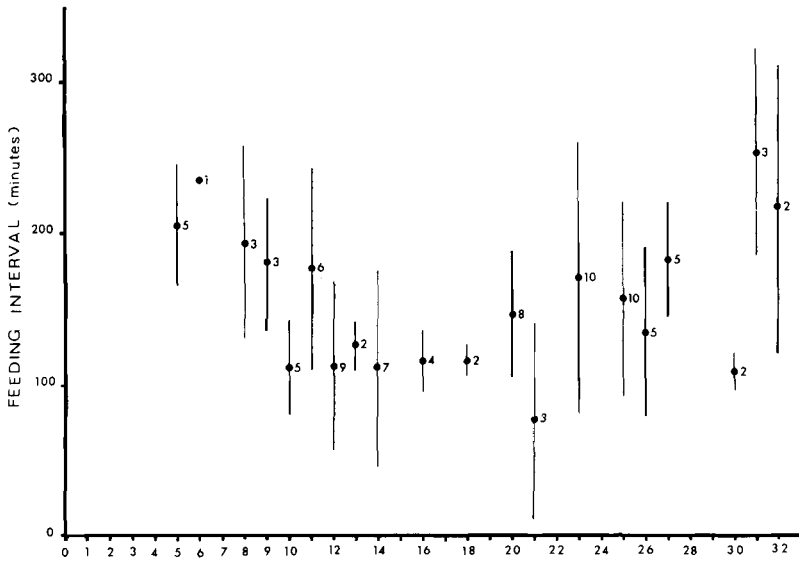


Fig. 7. Plot of feeding intervals vs. the age (days) of the oldest chick. Mean  $\pm$  SD are shown. Numbers to the right of mean are sample sizes. Age is that of first-born chick.

*Interactions among siblings.*—I never observed nestlings to push younger siblings out of the nest (*contra* Meanley 1955). However, siblings would fight with one another before and after feedings, attempting to gain access to adults. At this time, nestlings occasionally fell from the nest site though they were usually able to climb back. It is probable that these exchanges between siblings represent one way a dominance order is established (D. Mock pers. comm.). A second form of interactions among siblings appears to me to be a form of play (Ficken 1977), where nestlings exchanged bill jabbing and grasping (possibly ritualized as Bill Duel in adults, see Mock 1976). I have observed minor injuries to younger siblings during these exchanges. Hence, these exchanges among nest mates may reinforce a dominance system established during feedings as well as provide an opportunity for young to develop the motor skills necessary after fledging for feeding and defense.

#### DISCUSSION

Parental care for nestling Little Blue Herons can be divided into three phases (following Milstein et al. 1970): brooding (ages 1–10), guardian (ages 11–18), and post-guardian (ages 19–56). Age is determined from the hatching of the first chick. During the post-guardian phase both adults forage away from the nesting area, returning to feed young during the day and roost at night. Adults are able to leave the nesting area when young are older than 19 days because of the development of thermoregulation, rapid growth of the feet and the concurrent emergence of terrestrial locomotory skills, and the early escape response of the young. Except for food, nestlings are essentially independent of adults after the age of 19 days. By effectively shortening the duration of nestling dependence on adults, the pattern of nestling development serves as a preadaptation to large body size by allowing a longer time period for

growth. In terms of the Little Blue Herons' life history, and probably that of many other wading bird species, this developmental pattern is one way the evolutionary conflict between selection for larger body size and reducing the duration of the nestling period is resolved.

Still, it would be a mistake to confuse selective pressures for rapid nestling development with possible evolutionary advantages from the emergent properties of rapid nestling development. The pattern of nestling development in the Little Blue Heron has not evolved in response to selective pressures on adult size but rather in response to selective pressures on young. Failure of nestling motor skills, often grouped as "accidental death" (see Meanley 1955, Summerour 1971), accounted for 100% of the known mortality I observed among early-hatching chicks from nests that were successful in raising at least one chick. This suggests that selective pressures favoring early development of terrestrial locomotion are strong—the high risk reflects harsh penalties associated with delayed maturity. The most likely advantages of rapid development of locomotory skills by nestling Little Blue Herons are to increase food delivery by allowing both adults to forage simultaneously, to avoid predators, and to increase competitive abilities during feedings.

*Food delivery.*—The ability of adults to forage simultaneously during the post-guardian phase should allow an increase in food delivery to nestlings (Owen 1955, Siegfried 1972). My observations on feeding intervals (Fig. 7) do not support this idea. On the contrary, the time between feedings increased during the post-guardian phase in the Little Blue Heron. It is possible that the amount of food delivered per feeding increased during this phase, but if this phase were timed to allow an increase in food delivery, one would expect increased energy demands by nestlings. Instead, nestling weight is near asymptote by day 18 (Fig. 5e) and the expected energy demands, for birds with an adult size of Little Blue Herons (Ricklefs 1968), are probably just after  $t_{50}$  or at 12–15 days.

Adults might increase their intake of food during the post-guardian phase if their body reserves were depleted during the guardian phase when food delivery to nestlings was high. I observed male Little Blue Herons to fast during nest construction and egg-laying, apparently to protect against promiscuous behavior by neighboring birds (Werschkul in prep.). Fasting, or a reduction in food consumption by adults during the guardian phase, would allow food delivery to parallel the energy needs of nestlings. Then with the emergence of chick independence at 18 days and the reduction in nestling energy demands, adults could increase their own intake. In this way, the development of early locomotory skills could increase food delivery to nestlings. However, this increased food delivery would be a result of rapid development rather than a cause.

*Predator avoidance.*—It is unreasonable to expect adult Little Blue Herons to protect nestlings against large predators since they are iteroparous and other types of parental care are necessary for the chick's survival (Skutch 1971). For this reason there are clear advantages for nestlings to develop ambulatory skills and an early escape response. The development of the feet and locomotory skills occurs by the end of the guardian phase and correlates with the emergence of an escape response at 13 days. Even during the guardian phase adults protect nestlings against other herons and from thermal stress, but not from large predators. The development of terrestrial locomotion decreases the vulnerability of nestlings to large predators from 30 days (age of first flight) to 15 days. Early development of ambulatory skills among nestlings dependent on adults for food is common when they are liable to predation

(Welty 1975) and there can be little doubt one of the ultimate selective advantages for the rapid development of the feet and escape response by Little Blue Herons is a decreased exposure to predators.

*Sibling competition.*—Nestling Little Blue Herons are active in obtaining food from adults by bill grabbing after day 5 and by following adults after day 13. These changes in feeding behavior allow greater monopolization of food, which in turn, intensifies sibling competition: the older and more mobile young are fed more often, the younger and less developed are fed less often. My study indicates a major cause of brood reduction is starvation, particularly of the youngest chick (see also Blaker 1969, Milstein et al. 1970, Siegfried 1972). Hence, natural selection should favor increased competitive abilities.

*Other factors.*—Additional factors probably selecting for early development of locomotory skills are restrictions on nest size and support of older and larger nestlings (W. Graul pers. comm.) and the frequent loss of nests late in the nesting cycle from construction deficiencies, loss of supporting structures, stick piracy, and/or poor weather (Werschkul 1977c, 1977d).

#### CONCLUDING REMARKS

In general, selective pressures on juveniles and on adults can differ and, in certain situations, may be in conflict. Selection for rapid nestling development and large adult body size is one example of this. For the Little Blue Heron, the resolution of this conflict appears to be the differential development of the physical and behavioral tools necessary for fledging (e.g. thermoregulation, locomotion, feeding). As a result, the period of nestling dependence (excepting food) has been reduced to 19 days, although the young continue to mature and do not "fledge" until day 56. There are probably numerous examples of this general type of conflict in avian evolution. Importantly, when selective pressures on juveniles and adults conflict, then adaptations by juveniles will constrain the direction of adaptations by adults, i.e. adaptations by juveniles are selective pressures on adults and vice versa.

Asynchronous hatching has traditionally been interpreted as one way parents adjust brood size to food availability (Gibb 1950, Owen 1955, Lack 1956, Siegfried 1972, Hussell 1972, O'Connor 1977b). When food availability is high, all young survive; when it is low, only the youngest die. My observations on Little Blue Herons suggest that late-hatching chicks survive only when an older sibling dies. In this way, late-hatching chicks are a form of insurance for adults against the death of early-hatching chicks as well as a way that adults can adjust brood size to food availability. Though never explicitly stated, the hypothesis that asynchronous hatching acts to adjust brood size to food availability assumes that when food is abundant chicks will consume only what they need and all chicks are fed. My observations on the growth of even-aged broods do not support this assumption and suggest that the ability of adults to distribute food evenly, not food availability, limits the growth of late-hatching chicks. It is possible that even-aged broods beg more than asynchronously-hatched broods and because of this are fed more (D. Mock pers. comm.). If this is so then the growth of even-aged broods may not be comparable with the growth of asynchronously-hatched broods.

In those species where asynchronous hatching, brood reduction, and sibling competition have been documented (Lack 1954, Emlen 1956, Ricklefs 1965, Parsons 1970, 1975), investigators have either ignored adaptive responses by nestlings or have looked at behavioral adaptations (Meyburg 1974). Morphological adaptations

improving competitive abilities among siblings have recently been recognized (O'Connor 1977a) and no doubt are widespread. An important question raised by my observations on Little Blue Herons is in what way do these adaptations to sibling competition influence nesting success? Unfortunately, before the results presented here can be applied convincingly to this problem observations are needed on: (1) growth during years of differing food availability, (2) parental feeding effort and brood size, and (3) brood position, fledging weight, and post-fledging survival. Still, the success of even-aged broods suggests to me that the question of how parents minimize the adverse effects of adaptations by nestlings to sibling competition is of interest and may prove fundamental to understanding how parents use sibling competition to maximize their genetic contribution. Further, the evolution of reproductive strategies is influenced by factors other than high fertility (Brockelman 1975), and fertility may be lowered when unpredictable food resources during the nestling period create a high competitive environment among siblings.

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