

Mayfield's (1961, 1975) alternative index and daily survival probabilities (which has not been used for red-wings) reduces these difficulties by integrating a measure of time into the calculation. The major assumption required for the technique's use (i.e., that the rates of loss of eggs during incubation and nestlings during nestling period be consistent) can be validated for red-wings by the work of Young (1963) and Robertson (1972). For Williamstown Lake, probabilities of survival may be divided into component parts as follows (see Mayfield [1975] for details): (1) probability of nest (with some contents intact) surviving incubation $1 - (3/85.5)^{12} = 0.652$; (2) probability egg is fertile $1 - 6/40 = 0.85$; (3) partial egg losses $1 - (0/300.5)^{12} = 1$; (4) probability of egg becoming a nestling $a \times b \times c = 0.55$; (5) probability of a nest (with some contents) surviving nestling stage $1 - (3/75)^9 = 0.693$; (6) partial nestling losses $1 - (4/235)^9 = 0.857$; and (7) probability of an egg producing a fledgling $d \times e \times f = 0.329$.

The daily survival probability was the lowest of the three survival estimates derived in this study (33% as compared to 37% and 41% for fledging success and nesting success, respectively). Because of the small sample size from Williamstown Lake, I consider the survival probability calculation to be more accurate since nests found following commencement of incubation were included and the parameter of time has been quantified.

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Growth, diet, and mortality of nestling Great Blue Herons.—Patterns of growth and development have been described for a number of Ciconiiformes (Owen, *Proc. Zool. Soc. London* 133:597–617, 1960; Kahl, *Condor* 64:169–183, 1962; Siegfried, *Living Bird* 11: 193–206, 1973; McVaugh, *Living Bird* 14:163–184, 1975; Kushlan, *Auk* 94:164–167, 1977, *Condor* 79:31–36, 1977; Werschkul, *Auk* 96:116–130, 1979). However, growth has not been documented for the Great Blue Heron (*Ardea herodias*) and the diet of nestlings has been reported mainly for inland populations (Kirkpatrick, *Am. Midl. Nat.* 24:594–601, 1940; Kushlan, pp. 365–369 in *Wading Birds*, Natl. Audubon Soc., 1978). Additionally, only Pratt (*Condor* 74:447–453, 1972) has provided a partial description and schedule of nestling mortality in this species. In this study, I describe growth during the first month of life, compare growth between years in the same colony and with adult measurements, and fit growth to common growth equations. Also, I describe the diet of nestlings and discuss the timing and causes of nestling mortality in light of current ideas on the adaptive significance of asynchronous hatching and brood reduction.

Study area and methods.—Great Blue Herons were studied on Boot Island (45°08'N, 65°16'W), Nova Scotia, between April and August in 1977 and 1978. This 144-ha island is located in the Southern Bight of the Minas Basin at the mouth of the Gaspereau River. The river mouth provides one of three major foraging areas for the herons. Nests are located 9–12 m above ground in the tops of white spruce (*Picea glauca*). Numbers of breeding pairs decreased from 42 in 1977 to 26 in 1978. Clutch-sizes ranged between four and six with a mode of five eggs in both years. Mean clutch-size was 4.6 and 5.0 in 1977 and 1978, respectively. An average of 2.6 young fledged per breeding pair in 1977 and 3.1 young in 1978.

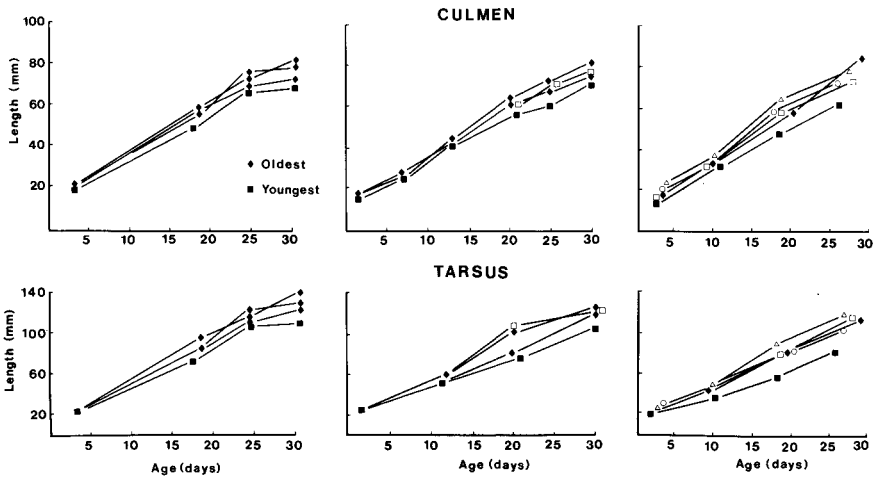


FIG. 1. Growth of culmen and tarsus in three broods of Great Blue Herons. Left: three oldest hatched on same day, youngest hatched 2 days later. Center: two oldest hatched on same day, youngest hatched 7 days later. Right: youngest hatched 5 days after oldest.

Twenty-three and 36 nestlings from 12 and 16 nests in 1977 and 1978, respectively, were measured every 2–3 days. Seventeen of the young measured were the first in their brood to hatch, 13 hatched last, and 29 hatched neither first nor last. Day 0 is considered the day of hatching. To increase sample size, measurements taken on days 0 and 1 were combined to give an average age of 0.5 days. In the same way data from days 28 and 29 were combined to give an average age of 28.5 days. Most nestlings were not handled after the age of 30 days as they may leave the nest and perch precariously when disturbed.

Visits to the colony were restricted to a maximum of 2 h per day. Weather permitting, nest checks were conducted during the morning in 1977. In 1978, they were undertaken during the high tide periods when the island could be visited by boat. Nestlings were lowered to the ground where the following measurements were taken: body weight (using hand-held Pesola spring balances), exposed culmen and tarsal length (to the junction with the base of the middle toe with vernier calipers), wing chord, proximal wing length (the distance from the back of the elbow to the distal tip of the longest primary), and length of the 10th primary from its insertion to its distal tip (with rulers). Colored nail polish and pipe cleaners were used to mark young nestlings individually in 1977 and 1978, respectively. When about 2 weeks old, nestlings were banded with standard U.S. Fish and Wildlife Service aluminum bands.

Adult measurements for *A. h. herodias* were obtained from 63 museum specimens from the National Museum of Canada (Ottawa), Royal Ontario Museum (Toronto), and the American Museum of Natural History (New York).

Some adults and nestlings regurgitated when disturbed or handled. Whenever possible, food items from these regurgitations were identified to species level and their lengths and weights were taken.

Data for growth variables were tested for normality using the Kolmogorov-Smirnov test (STAT PACK V4, Western Michigan University). STAT PACK V4 was also used for regres-

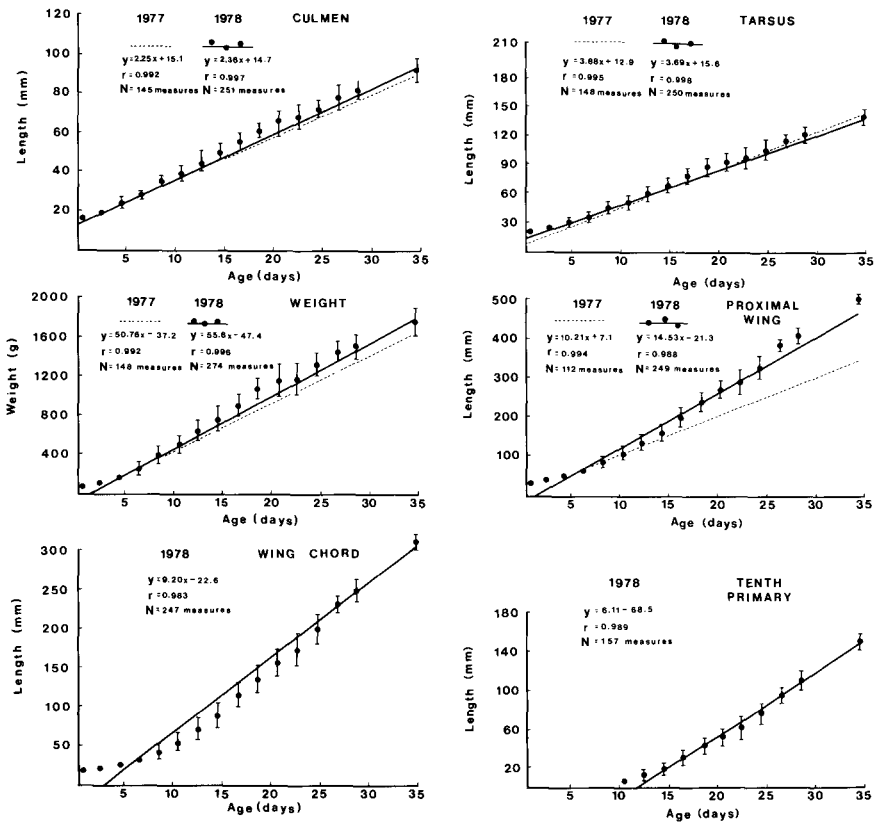


FIG. 2. Growth of nesting Great Blue Herons. An average of 9 and 16 nestlings (1977 and 1978, respectively) were measured at each age. Lines were fitted by regression, and vertical bars represent \pm SD for 1978.

sion analysis. Growth measurements were fitted to three common equations—logistic, Gompertz, and von Bertalanffy (Ricklefs, *Ecology* 48:978–983, 1967).

Nestling growth.—I found that full nestling emergence from an egg whose shell had a star-shaped crack or had a small hole usually took 48 h or less. Although hatching is generally asynchronous (sometimes spread over 7 days), two or more eggs in a clutch may hatch on the same day. The semi-altricial nestlings (Nice, *Trans. Linn. Soc.* 8, 1962) emerge down covered and are fed by both parents until 2–3 weeks after fledging. Fledging occurs at about 7–8 weeks of age.

Nestlings last to hatch in their respective clutches grew more slowly than those that hatch first (Fig. 1 and Table 1). To compare growth between years I constructed growth curves wherein each age is represented by nestlings from all positions in a brood (Fig. 2). The regression lines thus represent the growth of an “average” nestling.

External sexing of nestlings was not possible. If sexual dimorphism in growth occurs it

TABLE 1
CULMEN GROWTH OF FIRST- AND LAST-HATCHED NESTLINGS

Hatch order	N	Regression equation	<i>r</i>	SD ^a (slope)	SD ^b (intercept)
First	17	2.5x + 12.3	0.998	0.04	0.73
Last	13	2.2x + 15.8	0.996	0.05	0.87

^a*t* = 4.28, *P* < 0.001.

^b*t* = 10.86, *P* < 0.001.

should become apparent with increasing age. I constructed histograms for culmen and tarsal length, weight and wing chord for all nestlings 28.5 days old (*N* = 15) from 1978. Bimodal distributions that would suggest dimorphism were not evident for any of these variables. I concluded that no measurable dimorphism in growth occurs up to age 28.5 days.

Correlation coefficients obtained from the regression analysis indicate strong linear relationships between age and all variables measured through the first month of life (Fig. 2). The slopes for weight and proximal wing length differed significantly between 1977 and 1978 (*P* < 0.001) such that changes in body weight and wing length were more rapid in 1978.

Adult measurements.—Measurements of adult Great Blue Herons are given in Table 2. I combined male and female measurements for two reasons. First, a significant difference was found between the sexes only in wing chord length. Second, birds of undetermined sex were frequently encountered in the museum specimens that I examined.

The growth of various nestling body parts is expressed as a percentage of the adult measure in Fig. 3. At 44 days of age (about 1 week prior to fledging), 96% of the adult tarsal length is achieved. Additionally, 86% of the adult body weight, 83% of wing chord length and 78% of the culmen length are attained. Differential rates of growth are also seen in this figure.

Growth equations.—The correlation coefficients obtained for all measured body parts indicate that a simple linear relationship between age and a given part can be used to adequately describe growth through the first 30 days of life. How can growth be best described after the first month of life? Growth measurements were fitted to three common growth equations: the logistic, Gompertz and von Bertalanffy. The standard deviations indicated that the logistic growth curve provided the best fit. However, the predicted asymptote was close to the actual asymptote only for the tarsus. Here, the logistic equation predicted an asymptote 4% below the actual value of 173 mm.

Diet.—Ninety-five piscine food items from six species were identified from regurgitations

TABLE 2
MEASUREMENTS OF ADULT GREAT BLUE HERONS FROM EASTERN NORTH AMERICA

	N ^a	Mean ± SD
Culmen (mm)	53	137.1 7.5
Tarsus (mm)	62	173.3 11.5
Wing chord (mm)	63	463.3 15.9
Weight (g)	37	2229.1 762.1

^a 8–16 males, 10–15 females, sex of others unknown.

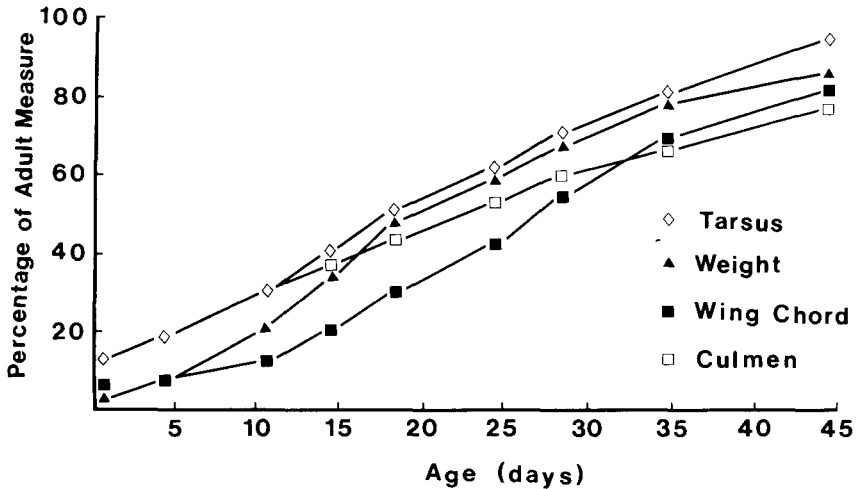


FIG. 3. Growth of nesting Great Blue Herons in 1978 expressed as a percentage of adult measurements. On average, 16 nestlings were measured at each age.

(Table 3). The results show a shift with time in the type of prey species delivered to the nestlings. Owen (1960) reported such a shift for the Grey Heron (*Ardea cinerea*) in England. These changes may be associated with changes in prey availability. Size extremes ranged from 1-g, 46-mm mummichog to a 400-g, 637-mm American eel. Prey of increasingly large size were brought to the nestlings as the season progressed. Small and well digested items were regurgitated by the youngest nestlings and larger, less digested ones by older nestlings. Kirkpatrick (1940) obtained regurgitated prey 50–400 mm in length and 28–398 g in weight from Wisconsin Great Blue Heron nestlings. Hoffman (pp. 365–369 in *Wading Birds*, Natl. Audubon Soc., 1978) found prey in Ohio to range between 78 and 228 mm.

Nestling mortality.—In 1978, 10% of all nestlings in the heronry died before fledging. In

TABLE 3
REGURGITATED FOOD ITEMS OF GREAT BLUE HERONS, 1977–1978

	Atlantic silverside (<i>Menidia menidia</i>)	Mummichog (<i>Fundulus heteroclitus</i>)	American eel (<i>Anguilla rostrata</i>)	Gaspereaux (<i>Alosa pseudo-harengus</i>)	Pollack (<i>Pollachius virens</i>)	Yellow perch (<i>Perca flavescens</i>)
15 May–15 June ^a	25	4	8	8	0	8
16 June–15 July ^a	0	17	11	4	10	0
% total items collected	26	22	20	13	10	8
Mean weight (g)	5	4	95	83	32	12

^a $\chi^2 = 52.28$, $df = 5$, $P < 0.001$.

TABLE 4
NESTLING MORTALITY IN RELATION TO AGE AND ORDER OF HATCH, 1977 AND 1978

Number dead	Age at death (days)	Order of hatch					
		1st	2nd	3rd	4th	5th	last
22	1-10	1	2	2	1	1	15
3	11-20	0	0	0	0	0	3
0	21-30	0	0	0	0	0	0
5	31-40	0	2	1	1	0	1
Total	30	1	4	3	2	1	19

1977, 16% of the young died. The hatch order and age at death are given for 70% of the dead nestlings in Table 4. Sixty-three percent of those that died were the last to hatch in their clutches. Furthermore, 73% of the nestlings died within their first 10 days of life.

Discussion.—An asynchronous hatch usually results in size hierarchies and differential growth within a brood. This pattern of hatching has been thought to facilitate partial loss of the brood when food supply is restricted. The loss of one or two of the smallest siblings might be preferable to all siblings being affected by food shortage (Lack, *Ibis* 89:302-352, 1947; Owen 1969; Ricklefs, *Ibis* 118:179-207, 1976; O'Connor, *Anim. Behav.* 26:79-96, 1978; Werschkul and Jackson, *Ibis* 121:97-102, 1979). Hessel (Ecol. Monogr. 42:317-364, 1972) and Bryant (*Ibis* 120:16-26, 1978) suggest that size hierarchies may spread out the food needs of individual siblings and thus space the demands upon adults. Size hierarchies and brood reduction occur frequently in the nests of Boot Island Great Blue Herons. The youngest nestlings in a given brood grow more slowly and survive less well than their eldest sibling. In those nests for which I have data, the youngest nestling died within 2 weeks of hatching in 19 of 46 nests, and 63% of all the dead nestlings hatched last in their brood. These results clearly show the influence of asynchronous hatching. Siblings are sometimes 7 days apart in age. There is no preferential feeding of the nestlings because the parents feed the young by regurgitating food into the floor of the nest, and aggression between siblings is pronounced at feeding times. The primary cause of nestling mortality appears to be starvation of youngest nestlings because of their failure to compete successfully with older siblings for food. Werschkul (1979) observed the same pattern in the Little Blue Heron (*Egretta caerulea*). On Boot Island mortality decreased after the first 10 days until the nestlings were 5 weeks old. This corresponds to the age that birds begin vigorously exercising their wings and moving out of their nests onto adjacent branches, whereupon some fall. Seventeen percent of the nestlings that died succumbed in this manner.

My results resemble those obtained by McAloney (*Can. Field-Nat.* 87:137-140, 1973) from Tobacco Island, Nova Scotia. Ninety percent of the Great Blue Heron nestlings that died in his study were the last to hatch. Total nestling mortality on Tobacco Island was 7%. Boot Island mortality was 16% in 1977 and 10% in 1978. In contrast to these Nova Scotia results, Pratt (1972) reported mortality ranging from 19-45% between 1967 and 1970 for Great Blue Heron nestlings in California. Most of the deaths occurred when the young were 4-5 weeks old. Owen (1960) found nestling mortality to be as high as 46% in the Grey Heron, and he stated that it was always the smallest, last-hatched young that died.

Boot Island herons commonly forage in three nearby estuaries. These estuaries are available for foraging at low tide which occurs twice every 24 h. However, weather conditions are far less predictable, and rain and high winds have a detrimental effect upon foraging

success (Bovino and Burt, *Auk* 96:628–630, 1979; Quinney and Smith, *Can. J. Zool.* 58: 1168–1173, 1980). The asynchronous hatch and consequent brood reduction may be a mechanism that enables herons to reproduce successfully in areas with highly variable foraging conditions.

In summary, nestling Great Blue Herons are close to adult size by the time they fledge. Culmen and tarsal growth show much less variation between years than body weight and wing length. Culmen and tarsal lengths are also useful indicators of nestling age. Nestlings that hatch last in their respective clutches grow more slowly and survive less well than those that hatch first, but overall nestling mortality is low on Boot Island.

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Downy Woodpecker sexes select different cavity sites: an experiment using artificial snags.—Primary cavity users such as woodpeckers typically roost and nest in cavities which they have excavated themselves. Secondary cavity users do not dig, but roost and nest in cavities fashioned by other birds (Thomas et al. *in Wildlife Habitats in Managed Forests*, J. W. Thomas, ed., USDA For. Serv. Agric. Handbook No. 553, 1979). This group also readily accepts nest boxes, which has allowed extensive manipulative research into their breeding biology, territoriality, and population regulation (Von Haartman *in Avian Biology*, Vol. 1, D. S. Farner and J. R. King, eds., Academic Press, New York, New York, 1971).

This report introduces artificial snags made of polystyrene as a research tool for manipulating populations of woodpeckers. Habitat selection and phenology of excavation in Downy Woodpeckers (*Picooides pubescens*) using artificial snags will be reported elsewhere (Peterson and Grubb, unpubl.). Here, I address the question, important for future research, whether Downy Woodpeckers as a species have a preferred snag height in which to dig roost cavities.

For primary cavity users, available snags of dead and rotting wood appear to be a resource that limits population density (Short, *Wilson Bull.* 91:16–28, 1979). Downy Woodpecker sexes have sex-specific foraging niches, presumably in response to limited food resources (Grubb, *Condor* 77:175–182, 1975; Williams, *Am. Midl. Nat.* 93:354–367, 1975). Thus, I also attempted to determine whether the sexes might segregate the roost-site resource by showing preference for snags of different height and by digging cavities at different distances from the snag top.

The artificial snags consisted of polystyrene (“bead board”) cylinders 22.5 cm in diameter painted dark brown. During Oct.–Dec. 1980, I set out 16 trios of these snags in central Ohio woodlots. I drilled a hole 0.75 m up the middle of each cylinder, then slid it down over a metal fence post driven into the ground, where it was held vertically. Each trio was composed