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GROWTH AND SEXUAL DIMORPHISM OF THE BOAT-TAILED GRACKLE

G. THOMAS BANCROFT

ABSTRACT.—At hatching, male and female Boat-tailed Grackles (*Quiscalus major*) are similar in size. By day 12, just before fledging, they differ in manus and tarsal lengths, tarsal thickness, and weight, but not in culmen, primary remex 7, and tail lengths. Male and female nestlings attain asymptotic weights of 102.4 g and 65.6 g, respectively, at a rate faster than predicted from the general passerine pattern. Furthermore, these asymptotes are only 54.8% and 65.3%, respectively, of adult weight. The combination of a faster growth rate and an asymptote below adult size means that grackles fledge sooner than would be expected for the general passerine pattern. Clutches of three eggs hatch asynchronously; the hatching of the third chick does not decrease growth rates of the early-hatching chicks. Third-hatched young fledge at weights significantly below those of early-hatching young. Compared to males hatching from the first or second egg, males from the third egg require several more days to attain sizes larger than females.

The pattern of growth represents an important component of an animal's life history. Bird species differ widely in the rate at which young attain independence and adult size. Much of this variation is correlated with body size (Ricklefs 1968) and, presumably, fitness. For species in which the sexes differ in size, the pattern of growth often differs between sexes. Typically, at hatching, males and females of many size-dimorphic species do not differ significantly in size, but by fledging, one sex is significantly larger (Ricklefs 1968, Newton 1978, Moss 1979, Howe 1979, Fiala 1981). Frequently the smaller sex develops its plumage and motor skills sooner than the larger sex (Holcomb and Twiest 1970, Newton 1978, Moss 1979, Richter 1983). The larger sex may be more variable in growth and take longer to reach adult size (Howe 1979, Richter 1983).

Asynchronous hatching leads to a size hierarchy among the nestlings (Howe 1976, Bryant 1978), which influences how the parents feed the nestlings and the nestlings' subsequent growth. I have found little information about the effects of asynchronous hatching on the development of sexual dimorphism.

Boat-tailed Grackles (*Quiscalus major*) are sexually dimorphic as adults; this dimorphism develops during the nestling period (McIlhenny 1937). I could find no detailed study of their growth. In central Florida, Boat-tailed Grackles typically lay clutches of two or three eggs (Bancroft 1983). Clutches of two, and the first two eggs in clutches of three, usually hatch on the same day, but several hours apart. In clutches of three, the third egg hatches one day later. Relative to adult size, grackles have a short nestling period (13–15 days). This suggests that they grow rapidly and/or fledge before they reach adult size. I investigated the development of sexual dimorphism in Boat-tailed Grackles and examined the effect of brood size and asynchronous hatching on their growth.

METHODS

I studied Boat-tailed Grackles at ten locations during four field seasons, 1978–1981. All colonies were in western Hillsborough County, Florida, except the Alligator Lake colony which was near Safety Harbor, in the eastern part of adjacent Pinellas County. All grackle colonies were situated in cattail (*Typha latifolia*) stands in and around bodies of water. The study areas are described elsewhere (Bancroft 1983).

I located grackle colonies early in the spring, either before egg-laying began or soon after the first few clutches had been laid. I visited some colonies daily and others every second to third day. I found most nests during their construction and marked the nests individually with numbered flags. I marked eggs with a permanent marker and marked the young by clipping one claw shortly after hatching. I reclipped the claw when the nestling was four or five days old. The claw had almost fully regrown by the time the nestlings were ready to fledge, but it could still be used for identification. I banded nestlings with U. S. Fish and Wildlife bands and, at some locations, also with celluloid color bands. During 1978 and 1979, I banded nestlings 14 days after hatching, but this often resulted in early fledging, so in 1980 and 1981 I banded nestlings when they were 11 or 12 days old.

I recorded measurements of seven variables on individually marked young of known age, sequence of hatching, and sex. Because adults

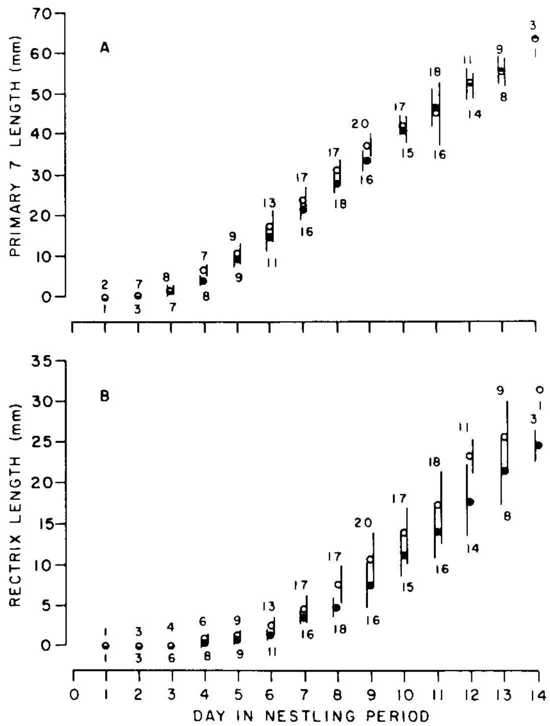

FIGURE 1. Lengths of primary remex 7 (A) and central rectrix (B) in nestling Boat-tailed Grackles relative to day in the nesting period for males (closed circles) and females (open circles). Means are represented by circles. Vertical lines extend one SD on either side of the mean for males (left) and females (right). Male sample sizes are above the lines and female sample sizes are below the lines.

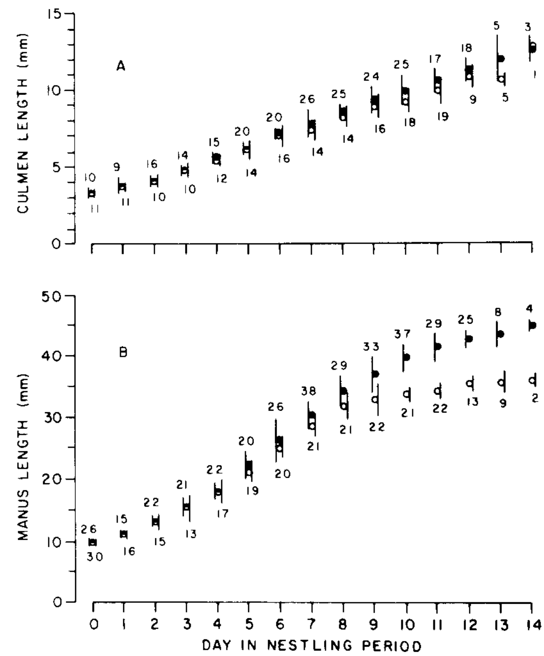

FIGURE 2. Culmen (A) and manus (B) lengths of nestling Boat-tailed Grackles relative to day in the nestling period for males (closed circles) and females (open circles). Other symbols as in Figure 1.

stopped feeding nestlings while I was in the colony, I tried to limit my visits by not completely measuring all young. I measured 805 different nestlings from one to 15 times. Culmen, manus, tarsal, primary remex 7, and central rectrix lengths and tarsal thickness were measured to the nearest 0.1 mm with dial calipers. I recorded weight, usually to 0.1 g, with 10-, 50-, 100-, or 300-g Pesola balances. The culmen was measured from the distal edge of the nares to the tip of the bill, and the manus from the proximal end of the carpometacarpus to the tip of the fleshy part of the manus. I measured the tarsus as the diagonal from the intertarsal joint to the joint with the middle toe, and tarsal thickness at the narrowest anterior-posterior point. The primary remex and rectrix were measured from the skin surface to the tip of the ensheathed or fully-grown feather.

I could sex known-age nestlings that were healthy and growing normally when they were older than 10 days by tarsal length, manus length, tarsal thickness, or weight. Gonadal inspection confirmed all sexing by external measurements of healthy individuals. Younger individuals or those that were stunted were sexed by laparotomy.

I compared mean sizes on consecutive days in the nestling period for separate sexes and the difference in mean size between sexes on each day in the nestling period using one-way analyses of variance for unequal sample sizes (Sokal and Rohlf 1981). Sizes were considered significantly different if the probability of a larger F value was less than 0.05.

RESULTS

The distribution of down feathers at hatching was similar to that described for icterids by Wetherbee (1957). The average number of down feathers found in each region on five specimens 1–3 days old are given parenthetically. A row of downs extended from between the eyes to the back of the coronal region (18) of the capital tract. I found a shorter inner row only in the coronal region (8). Two feathers were found in a third outer row of the coronal region in three specimens. I found a single row of downs on each side of the occipital region (6), as well as downs in the humeral (11), femoral (17), and caudal tracts (12) and on the anterior (7) and posterior (7) edge of the crural tract. Downs formed a double row along the spine from between the wings to the pelvic girdle (22) and beyond in a single or double row to the base of the tail (21). They also occurred on the upper greater (11) and upper

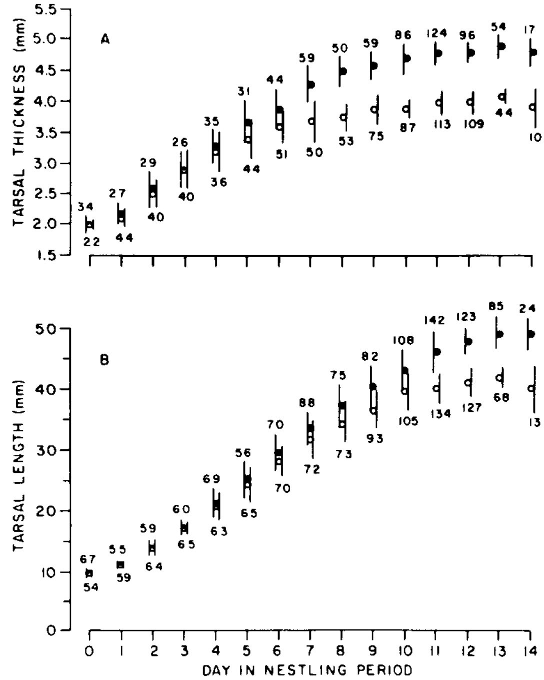

FIGURE 3. Tarsal thicknesses (A) and lengths (B) of nestling Boat-tailed Grackles relative to day in the nestling period for males (closed circles) and females (open circles). Other symbols as in Figure 1.

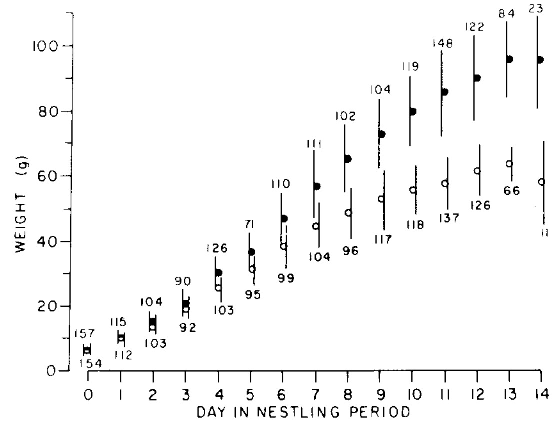

FIGURE 4. Wet weights of nestling Boat-tailed Grackles relative to day in the nestling period for males (closed circles) and females (open circles). Other symbols as in Figure 1.

middle secondary (8) coverts. Down feathers appeared to have been present for the primaries, secondaries, upper greater primary coverts, and alula, but I could not count them accurately. Only two specimens had down feathers in the abdominal region (9) of the ventral tract, and only two had down feathers in the marginal region (2) of the alar tract.

Primary and secondary juvenal feathers emerged through the skin at 2 days-of-age (Fig. 1) and juvenal feathers of the body tracts emerged at 3 days. The tail was measurable by 4 days (Fig. 1). At fledging, most feathers on all tracts still were actively growing. From day 4 through day 9, primaries of females, on average, were longer than those of males, and on all but days 5 and 6, the difference was significant. Not until late in the nestling period did primary length in males equal that of females. From day 6 though day 12, central rectrices of females were, on average, significantly longer than those of males (Fig. 1). The body feathers also developed faster in females than males. At day 13, just before fledging, primary remex 7 had attained 45% of its juvenal feather length for males (124.0 mm, $n = 2$), and 54% of juvenal feather length for females (102.1 mm, $n = 2$). At day 13, the tail was still relatively short, having attained 17% of juvenal feather length for males (129.5 mm, SD = 6.8, $n = 11$) and 24% of juvenal feather length for females (108.0 mm, SD = 8.8, $n = 31$). Fledglings were generally out of the nest a week or more before they began to fly regularly.

At hatching, culmen length averaged 3.4 mm for males and 3.3 mm for females (Fig. 2), representing 11% of adult male length (32.0 mm, SD = 1.0, $n = 7$) and 13% of adult female length (25.9 mm, SD = 3.1, $n = 70$). From age 9 days through 11 days, culmens averaged significantly longer in males than in females, but by 12 days the lengths were not significantly different. Lack of a difference may reflect small sample size for these later nestling ages. At fledging, male culmens had reached 39% of adult length and females had reached 49% of adult length. Nine males captured when two to four months past fledging had culmens averaging 25.7 mm (SD = 3.1) or 80% of adult length. During this same time period, females had culmens averaging 22.5 mm (SD = 1.8, $n = 36$) or 87% of adult length.

At hatching, the manus averaged 9.8 mm for males and 9.7 mm for females (Fig. 2). By 7 days-of-age, the manus of males was significantly longer than that of females. The rate of manus growth for females began to level off at 9 days and length did not increase significantly each day thereafter. Manus length of males increased significantly each day through day 12 and by 14 days the manus averaged 8.9 mm longer than that of females.

At hatching, tarsal thickness averaged 2.0 mm for both sexes (Fig. 3). Mean tarsal thicknesses for males and females were not significantly different until day 5, after which males had significantly thicker tarsi than females. Growth rates for females slowed by day 7, after which thickness did not increase significantly with each successive day. For males, thickness increased significantly during each day through day 11. At fledging, tarsal thickness of all males not stunted or starving exceeded 4.4 mm whereas all females had tarsi less than 4.5 mm thick.

At hatching, tarsi averaged 9.8 mm for males and 9.7 mm for females (Fig. 3), representing 19.0% of adult male length (51.6 mm, SD = 2.2, $n = 7$) and 23.2% of adult female length (41.8 mm, SD = 3.2, $n = 69$). The development of sexual dimorphism in tarsal length is illustrated by the increase in length per day for each sex. Through day 2, tarsi of males and females grew at the same rate, but afterward those of males grew faster than those of females. Growth rate for both sexes increased to a plateau between day 4 and day 7, and then decreased. The difference in growth rates between the sexes meant that by day 6, males had significantly longer tarsi than females (Fig. 3). By day 13, mean tarsal lengths of both sexes were within the adult range.

Boat-tailed Grackle eggs averaged 8.1 g at laying, which represented 8.1% of female weight (Bancroft, in press). The weight of young at hatching was correlated with egg weight and newly hatched young averaged 79.6% of fresh egg weight (Bancroft, in press). Eggs that produced males did not differ significantly in weight from those that produced females. Wet weights of day-0 nestlings averaged 7.0 g for males and 6.9 g for females (Fig. 4). Since some of these individuals had been fed before weighing, these means were not those of newly-hatched young. Males were significantly heavier on succeeding days through day 13, and females were significantly heavier on succeeding days through day 10 (Fig. 4). Healthy young frequently fledged when disturbed at day 13. Thus, day-14 weights probably are slightly lighter than the population average because some birds had fledged. I did not attempt to get a large sample of day-14 weights. From day 2 through fledging, males weighed, on average, significantly more than females. Males gained weight slightly faster than females through day 3, thereafter males gained weight much faster than females. Thus, sexual difference in weight increased throughout the nestling period so that, by 13 days, males averaged 32.1 g (50.1%) more than females (Fig. 4).

Based on live birds captured at the study sites, the mean wet weight of eight definitive-plumage males was 194.3 g (SD = 7.2), and the mean wet weight of 69 females that were at least one year old was 100.5 g (SD = 5.6). Thus, day-0 males and females were 3.6% and 6.9% of adult weights, respectively. By day 13, when young often fledged, males had attained 49.5% and females had attained 63.8% of adult weight. When three to five months old, eight males had a mean wet weight of 160.3 g (SD = 11.0), which was 82.5% of adult weight, and 37 females averaged 93.3 g (SD = 8.5) which was 92.8% of their adult weight.

Growth for most passerines is best described by a logistic equation (Ricklefs 1967, 1968). I used the non-linear regression procedure (Gaus-Newton option) of Statistical Analysis System (SAS) to calculate the asymptote, growth constant, and the inflection point in the growth curve (Helwig and Council 1979). The 95% confidence interval of each parameter is given parenthetically. For male and female Boat-tailed Grackles, the asymptotes were 102.1 g ($\pm$3.6) and 65.6 g ($\pm$1.9), respectively. The asymptote of males was 52.5% of adult weight, and that of females was 65.3% of adult weight. However, males take more than one year to reach adult weight (Selander and Giller 1961). Yearling males weighed 178.0 g (SD = 18.1, $n = 4$), therefore males grew to 57.4% of this weight. Regardless, females grew to adult size faster than males.

The growth constant is a measure of the rate at which a bird grows to its asymptotic weight. Both sexes had similar growth constants of 0.378 ($\pm$0.025) for males and 0.393 ($\pm$0.028) for females. The 95% confidence limits show that these values were not significantly different. This growth rate was reflected in the 11.6 days (males) and 11.2 days (females) required to grow from 10% to 90% of the asymptotic weight. Thus, even though males attained an asymptote that was 36.5 g heavier than females and both sexes started at the same weight, both sexes took the same amount of time to grow from 10% to 90% of the asymptote. This implies that males accumulated tissue at a much faster rate than females. The difference in weight between the mean weight on one day and that on preceding day is the average weight of tissue accumulated over that 24-hour period (Fig. 4). Males gained weight only slightly faster than females through day 3. Thereafter, males began gaining weight more rapidly than females. Peak rate of growth for each sex corresponds to the inflection point in the logistic curve (Fig. 4). Based on least squares regression analysis (non-linear), the inflection point was 6.47 ($\pm$0.27) and 5.18 ($\pm$0.22) days after hatching for males and females, respectively. Females gained weight at a maximum of 6.6 $g \cdot day^{-1}$ between day 5 and day 6, whereas males grew to maximum of 10.1 $g \cdot day^{-1}$ between day 6 and day 7. The rate of weight gain decreased rapidly soon after reaching the maximum for females, whereas males maintained a high rate of weight gain through day 11.

Males and females hatched at the same weight, but in the same period attained asymptotic weights 36.5 g apart. Their similar growth constants indicated that they reached their asymptotes at similar rates. Because the sexes started at the same weight, however, females, were closer to their asymptotes than males. Figure 5 shows the accumulated increase in weight as represented by the percentage of the asymptote attained. Weight at day 0 was 6.9% and 10.5% of the asymptotes for males and females, respectively. Males began one full day behind females in the percentage of the asymptote attained. This gap broadened to 1.5 days at day 3 and was maintained through day 13. Thus, females grew to their asymptotic weight at 13 days, whereas males did not reach their's until day 14 or 15.

I studied color-banded fledglings to determine survivorship until they reached independence, relative to fledging weight. Fledglings could be censused until they were quite mobile (about day 30) because the colony was on a cattail island. The mean weight, at fledging, of males (90.5 g, $n = 24$) and females (63.3 g, $n = 24$) that survived more than 25 days did not differ significantly from the mean weight, at fledging, of males (93.5 g, $n = 30$, $F = 0.76$, $P > 0.38$) and females (61.7 g, $n = 29$, $F = 0.50$, $P > 0.48$) that were not seen again.

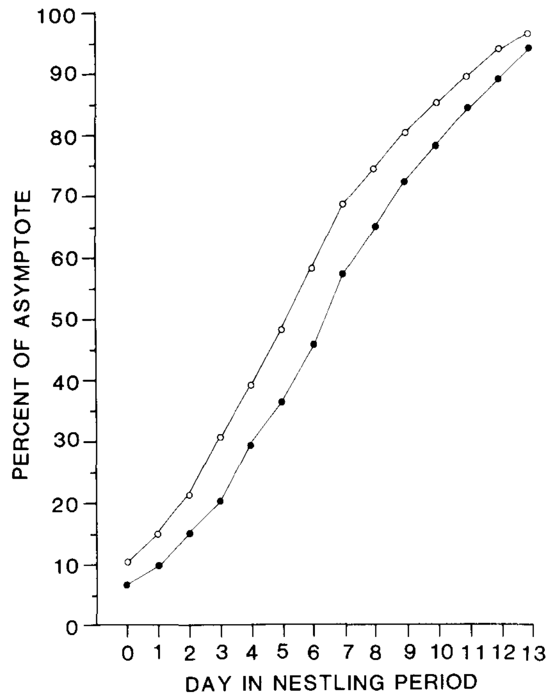

FIGURE 5. Accumulated increase in wet weight of nestling Boat-tailed Grackles as a percentage of the asymptote achieved. Asymptote calculated from the logistic equation. Closed and open circles are for males and females, respectively.

ASYNCHRONOUS HATCHING, BROOD SIZE, AND GROWTH

Hatching asynchrony resulted in size hierarchies within broods because some nestlings had been fed and had had the opportunity to grow before others hatched. Thus, on day 1, weight varied significantly relative to sequence of hatching in broods of both two and three (Fig. 6). To determine the effects of asynchronous hatching and brood size on growth, I assigned all nestlings the age of the oldest nestling. Although nestlings were not always the same absolute age within a brood, they were classified as the same age for this analysis.

For each sex, mean daily weights of nestlings in broods of two did not differ significantly from mean daily weights of the two oldest individuals in broods of three (Fig. 6). In broods of two, I did not find sexual dimorphism in weight until day 7. For broods of three, the first- and second-hatched males did not weigh significantly more than first-hatched females until day 7. For each sex, third-hatched nestlings weighed significantly less than first-hatched young throughout the nestling period. Third-hatched nestlings were two to three days behind first-hatched females. Males and females from the third egg weighed significantly less at fledging than fledglings of their sex from the first or second egg.

Tarsal length on each day for each sex was not significantly different between broods of two and the two oldest young in broods of three (Fig. 7). Considering only the two oldest nestlings, tarsal lengths were not significantly longer in males than females until day 9, in broods of both two and three. Third-hatched young had, on average, smaller tarsi than the two oldest individuals throughout the nestling period. The absolute difference in length increased during the middle part of the nestling period. At fledging, tarsi of the third-hatched young for each sex were, on average, still significantly shorter than those of the older individuals. Tarsi of third-hatched young did not show sexual dimorphism until day 10. Third-hatched males did not have tarsi significantly longer than those of females until day 13.

Growth rates of males and females did not differ relative to sequence of hatching (Table 1). First-hatched females reached the inflection point in the logistic curve sooner than any male or than females hatching from later eggs. Nestlings from the third egg reached the inflection point more than a day later than other young, partly because they had hatched one day later. First-hatched males in broods of two had higher asymptotes than males hatching from second or third eggs in broods of three. For females, asymptotic weights did not vary with sequence of hatching in broods of two,

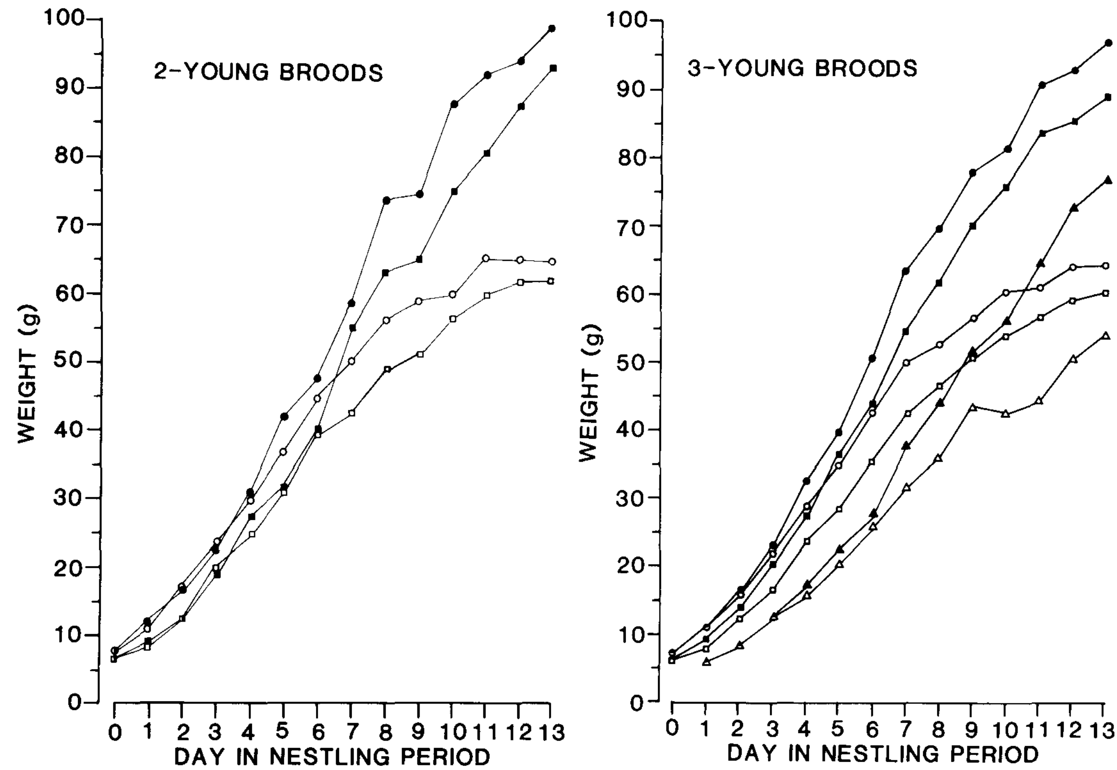

FIGURE 6. Mean daily wet weights for nestling male and female Boat-tailed Grackles relative to sequence of hatching in broods of two or three young. Closed and open symbols are for males and females, respectively. Circles, squares, and triangles represent first-, second-, and third-hatched young, respectively. Sample sizes for each mean range from 11 to 49 in broods of three and from five to 25 in broods of two.

but did vary significantly in broods of three. Males had asymptote weights significantly heavier than females. Asymptotic weights for males did not vary with sequence of hatching. For males and females separately, comparisons of first-hatched young between broods of two and three or second-hatched young between broods showed no differences in growth rate or asymptotic weight.

Because means were significantly different, I examined relative variability in growth by comparing coefficients of variation (C.V.) in weight on day 12 by an F_{max} test based on the square of the ratio of C.V.s (Lewontin 1966). Asynchronous hatching increases variability in growth (Table 2). Compared with first-hatching young, third-egg young had significantly higher C.V.s in mean weight for males ($F = 6.68$, $P < 0.01$) and females ($F = 6.89$, $P < 0.01$) on the day the first-hatched individual was 12 days old. This greater variation was partly attributable to the variation in hatching spread of the clutches (Bancroft 1983). Nestlings from the third egg might be up to two days younger than those from the first egg.

Based on the total sample, C.V.s in weight were not significantly different between sexes on day 12 (Table 2). Males hatching from the second egg, but not from the first or third, were significantly more variable in weight than females (Table 2). Comparing mean weight of third-hatched young to that of young from the first two eggs also did not suggest a greater variability in growth of males, although males from the third egg apparently suffer higher mortality than equivalent females (Bancroft 1983). At day 12, third-hatched males had 81.3% of the mean weight of males from the first two eggs, whereas the mean weight of equivalent females was 81.9% of that of females from the first two eggs (Table 2).

DISCUSSION

Boat-tailed Grackles grow relatively rapidly; their nestling period is shorter than expected for their size. Based on asymptotes of 102.1 g for males and 65.6 g for females, Ricklefs' (1968) allometric equation predicts that males and females should take 14.3 and 12.6 days to grow from 10% to 90% of their respective asymptotes. The observed values of 11.6 days and 11.2 days indicate that grackles grow faster than the general passerine trend. Their incubation period is also a relatively short 13.1 days. Based on fresh egg weight and female body weight, allometric equations (see Rahn and Ar 1974, Rahn et al. 1975) predict an incubation period around 19 days (Bancroft,

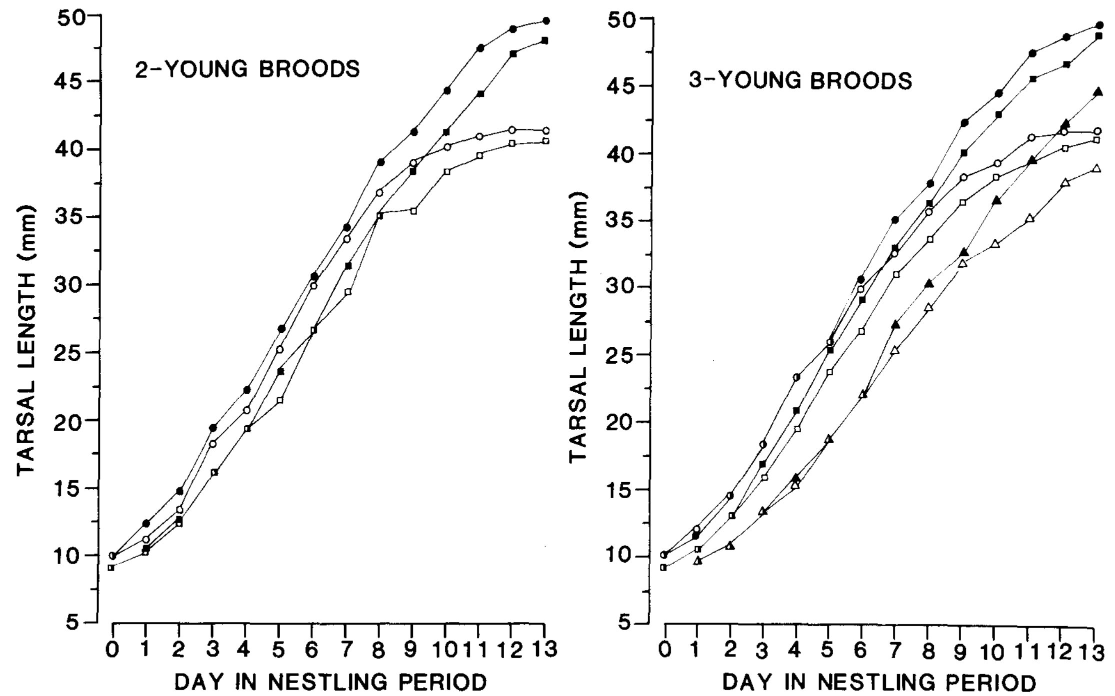

FIGURE 7. Mean daily tarsal lengths for nestling male and female Boat-tailed Grackles relative to sequence of hatching in broods of two or three young. Other symbols as in Figure 6. Sample sizes for each mean range from 10 to 39 in broods of three and from three to 21 in broods of two.

in press). The entire nestling period appears to be shorter than might be expected for a passerine of grackle size.

When Boat-tailed Grackles fledge (day 13), their juvenal plumage is incomplete, and many feathers and body components are still growing. Mean tarsal lengths at fledging are within the range of adult size; the leg may attain adult size quickly so that the fledglings can grasp the cattails when they leave the nest. Young grackles remain fairly inactive for at least a week after they leave the nest, which may be enough time for the flight feathers to finish growing.

The ratio of the asymptotic weight at fledging to adult weight is a measure of development by fledging time. Boat-tailed Grackles have ratios of 0.55 and 0.65 for males and females, respectively. The ratio for males was less than that of 56 passerines listed by Ricklefs (1968) and only male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) have a lower ratio than female Boat-tailed Grackles. Fledging weights of Great-tailed (*Quiscalus mexicanus*) and Common grackles (*Q. quiscula*) suggest that the ratios of their asymptotes to adult body weight for each sex would be similar to that of Boat-tailed Grackles. Great-tailed Grackles in Texas weigh about 110 g (males) and 70 g (females) at day 13 just before fledging (Gotie and Kroll 1973), whereas first-year males weigh 180 to 200 g and first-year females weigh about 115 g (Selander and Giller

TABLE 1. Parameters of the logistic growth curve for Boat-tailed Grackles relative to sex and brood size.[1]

	Males			Females		
Sequence[2]	K[3]	A[4]	I[5]	K[3]	A[4]	I[5]
Brood of two						
1	0.384 ± 0.048	107.3 ± 6.9	6.38 ± 0.49	0.448 ± 0.033	67.2 ± 1.6	4.43 ± 0.19
2	0.375 ± 0.052	100.3 ± 7.8	6.84 ± 0.59	0.415 ± 0.070	65.6 ± 4.3	5.16 ± 0.51
Brood of three						
1	0.403 ± 0.040	101.9 ± 4.7	6.06 ± 0.35	0.437 ± 0.029	65.9 ± 1.5	4.60 ± 0.18
2	0.402 ± 0.027	94.6 ± 3.1	6.25 ± 0.24	0.416 ± 0.023	62.6 ± 1.4	5.35 ± 0.17
3	0.359 ± 0.049	91.0 ± 9.0	8.08 ± 0.72	0.391 ± 0.032	55.9 ± 2.1	6.24 ± 0.29

[1] For the equation: weight = $A/[1 + e^{K(age - I)}]$.
[2] Sequence of hatching within the brood.
[3] Growth rate constant of logistic curve ± 95% confidence interval.
[4] Asymptote of the logistic curve ± 95% confidence interval.
[5] Age at the inflection point in the logistic curve ± 95% confidence interval.

TABLE 2. Mean weight and variation in weight on day 12 in the nestling period for males and females in broods of three for Boat-tailed Grackles in central Florida.

Sequence	Males				Females				F^1
	N	Mean	Variance	CV	N	Mean	Variance	CV	
1	36	93.5	69.7	8.9	39	64.3	32.4	8.8	1.02^{ns}
2	28	85.5	183.4	15.8	40	59.6	38.4	10.4	2.31*
3	17	73.2	283.8	23.0	25	50.7	137.2	23.1	1.01^{ns}
Total	81	86.5	208.7	16.7	104	59.2	85.8	15.6	1.15^{ns}

[1] *F* test of relative variation in mean weight between males and females calculated as the square of the ratio of coefficients of variation (Lewontin 1966, Sokal and Rohlf 1981).
^{ns} Not significant; * $P < 0.05$.

1961). Common Grackles in Michigan average 67.8 g (males) and 63.0 g (females) at day 12 whereas adults average 124.7 g and 102.0 g, respectively (Howe 1979).

Other icterids also leave the nest before they have attained adult weights. Yellow-headed Blackbirds have asymptotic weights that are 63% (males) and 74% (females) of adult weight, and Red-winged Blackbirds (*Agelaius phoeniceus*) have asymptotic weights that are 67% (males) and 74% (females) of adult size (Ricklefs 1968). Clearly, icterids fledge at weights considerably below those of adults or first-year birds. Before fledging, many passerines attain weights much closer to adult weight. Of the 56 passerines listed by Ricklefs (1968), 42 (75%) had asymptotes equal to or greater than 80% of adult weight (two additional species had estimates that were both above and below 80% of adult weight).

Fledging before growth is complete requires that some body parts be sufficiently strong and developed to function properly. The evolution of grackles has emphasized maturation of the legs and early growth of the plumage; these characteristics may have required shifting energy allocations from other components. When Boat-tailed Grackles fledge, tarsal size is near that of adults, indicating that leg development is advanced. Young grackles cannot fly well for several weeks after fledging. Although the juvenal plumage is not fully grown at fledging, it is complete enough for the birds to thermoregulate and fly short distances (pers. obs.). The decrease in rate of weight gain and attainment of an asymptote below adult size may reflect a shifting of energy from cell division and weight gain to the maturation of legs and plumage.

Many icterids nest in marshes and tend to have higher daily rates of nest mortality than many other birds (Ricklefs 1969a; Robertson 1972, 1973; Caccamise 1976; Orians 1980; Bancroft 1983). Their low fledging weights and short incubation and nestling periods would tend to reduce nestling mortality.

Growth rate is a compromise between factors that select for shortening the growth period and those that select for lengthening it (Lack 1968, Case 1978). Because growth requires energy, the duration of the growth period and the size attained during growth affect the energy requirement of the young. Faster growth requires more energy per unit time for each offspring. The growth rate would be highest for a brood of one when the parents deliver food as often as possible (Ricklefs 1969b). Brood sizes larger than one would select for slower growth rates. Providing the nutrients and energy needed for faster growth might require the parents to forage more frequently. Thus, they would be absent from the nest more often, which might decrease survivorship of young by increasing their exposure to mortality factors (Case 1978). Feeding the nestlings more often increases the likelihood of a visual predator's finding the nest (Skutch 1949). These factors, which depend upon growth rate, would favor slower growth (Lack 1968, Case 1978) if the latter did not result in more predation because of the longer nest period.

Predation should generally select for shortening the period spent in the nest. Since growth constants (K) are not correlated with daily mortality rates, Ricklefs (1969b, 1979) judged that greater predation has not favored faster growth rates. He concluded that growth rates are always at a physiological maximum and that interspecific differences in growth rate reflect species differences in physiology. Ricklefs did not consider the possibility that nestling mortality might be dependent on growth rate. Case (1978) showed that taking nestling mortality into account makes intermediate growth rates the best. By using K as the only measure of growth rate, Ricklefs did not consider the influence of asymptotic weights below adult weight on the duration of the nestling period. If Boat-tailed Grackles attain adult size during the nestling period, the general passerine pattern of growth predicts that they would need 16.9 days (males) or 14.2 days (females) to grow from 10% to 90% of these weights. Having an asymptote below adult weight clearly shortens the time young remain in the nest, but not all species with high rates of nest predation have high growth rates (Ricklefs 1969a, 1976).

BROOD SIZE AND SEXUAL DIMORPHISM

Studies of several species have shown a negative correlation between brood size and growth (Lack 1948, 1956; Lack and Lack 1951; Koskimies 1950; von Haartman 1954; Paynter 1954; Perrins 1965; Klomp 1970; Bryant 1978). For male and female Boat-tailed Grackles considered separately, growth rates of the first- and second-hatched young do not differ with brood size. Third-hatched chicks of both sexes, however, have relatively lower asymptotic weights, which indicates that the addition of a third offspring does not depress fledging weights of the first two. Asynchronous hatching does substantially delay the development of sexual dimorphism in third-hatched young. Males hatching from the third egg require several more days to become larger than females. Presumably, asynchronous hatching is important in creating a size hierarchy which insures that first-hatched chicks receive all the food they need. If food is scarce, the first two hatchlings still receive enough food to be able to fledge at the greatest weight possible.

Fledging weight varies significantly with sequence of hatching in Boat-tailed Grackles, unlike Common Grackles and Yellow-headed Blackbirds (Howe 1976, Richter 1984). For several species, the probability of survival after fledging is correlated with fledging weight (Perrins 1965; Howe 1976, 1979). This suggests that for Boat-tailed Grackles the light third-hatched chick may have lower survivability, although fledgling survival is not wholly dependent on fledging weight. At fledging, half of the third-hatched males weighed less than 77% of mean weight of first-hatched males, and half of the third-hatched females weighed less than 85% of the mean weight of first-hatched females.

Survival until fledging for young in successful nests also varied significantly with sequence of hatching. In broods of three that fledged some offspring, only 52% of the third-hatched chicks fledged, compared to 90–93% of those fledged from first and second eggs (Bancroft 1983). Starvation was the principal cause of mortality for these young (Bancroft 1983). The males' greater size appears to make them more vulnerable to food shortage and starvation. The sex ratio of third-hatched fledglings was skewed significantly toward females (Bancroft 1983), suggesting that males suffered higher rates of starvation. In addition, among nestlings that hatched from the second egg, growth was significantly more variable in males than females.

In sexually dimorphic species, the smaller sex appears to mature faster than the larger sex (Holcomb and Twiest 1970; Newton 1978, 1979; Moss 1979; Fiala 1981; Richter 1983, 1984). For Boat-tailed Grackles, females are closer than males to their asymptotic weights at hatching and attain their asymptote one to two days sooner than males. Lengths of primaries and rectrices of females are, on average, longer on many days than those of males, which suggests that plumage develops more rapidly in females. At fledging, primary and tail lengths and weights of females are closer to adult level than those of males. Comparison of water indices (water content/lipid-free dry weight) of tissue suggests that tissues of fledging females are closer to maturity than those of males (Bancroft 1983). Just before fledging, three males had water indices averaging 3.8 (SD = 0.3) and five females had indices averaging 2.9 (SD = 0.2). Females tend to fledge at a younger age than males. Females that hatch from the first egg often leave the nest if it is visited 12 days after hatching, whereas males rarely depart at that age. These findings suggest that in Boat-tailed Grackles, female nestlings allocate energy to maturation of tissues and plumage, while males are still allocating a large proportion of their energy to gaining weight.

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Department of Biology, University of South Florida, Tampa, Florida 33620. Present address: National Audubon Society, Research Department, 115 Indian Mound Trail, Tavernier, Florida 33070. Received 24 August 1983. Final acceptance 11 May 1984.