INTERSEXUAL DIFFERENCES IN FOOD CONSUMPTION BY HAND-REARED GREAT-TAILED GRACKLE (*QUISCALUS MEXICANUS*) NESTLINGS

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ABSTRACT.—I monitored food consumption by hand-reared Great-tailed Grackle (*Quiscalus mexicanus*) nestlings to test the hypothesis that males and females consume similar amounts of food but males direct more of their energy into characters that result in greater mass increase. Growth patterns of hand-reared nestlings reflected those of naturally reared nestlings: males were heavier and had longer tarsi, and females had longer 9th primaries on days 6–12 post-hatching. Males, on average, consumed 15.8% more food than females throughout this period; the amount of food consumed per unit mass increase was similar for both sexes. The results suggest there may be substantial cost differences to parents in rearing offspring of different sex. The nestling sex ratio for this and other sexually size-dimorphic species is generally close to one, and Fisher's (1930) theory that differential investment in sons and daughters should result in a skewed sex ratio at the end of parental care is not supported.

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FISHER (1930) suggested that the total investment by parents in rearing offspring of each sex should be equal. Subsequently, the relative number of young of each sex at the end of parental care should reflect the costs of rearing them. Because the costs of raising males and females in most species are probably similar, sex ratios in most populations are generally close to one (Charnov 1982). In some species, however, the young of one sex may be significantly larger than the other. If individuals of the larger sex are more costly to rear, then parents should equalize investment between the sexes by producing greater numbers of the less expensive sex.

Although Fisher's ideas have been confirmed mathematically (Kolman 1960; Verner 1965; Leigh 1970; Charnov 1975, 1982), empirical evidence has been restricted largely to studies of invertebrates (reviewed by Charnov 1982). Investigations of altricial birds in which nestlings exhibit sexual size dimorphism have been less supportive of Fisher's predictions. The sex ratio of nestlings is generally close to unity both at hatching (Porter and Weinmeyer 1972, Newton 1979, Fiala 1981, Bancroft 1983, Richter 1983, Weatherhead 1983, Bortolotti 1984) and at fledging (Willson 1966, Newton and Marquiss 1979, Patterson and Emlen 1980, Bancroft 1983; but see Fiala 1981). Indeed, in many dimorphic raptors (Hickey 1942, Balfour and Cadbury 1979, Picozzi 1980, Collopy 1986) and at least one passerine (Dhondt 1970), fledgling sex ratios may actually be biased in favor of the larger sex.

Differences in the costs of rearing males and females in dimorphic species might be less than previously thought (Fiala 1981, Richter 1983, Bancroft 1984). This would be true if both sexes require similar amounts of food despite size differences, or if parents somehow compensate for the demands of the larger sex at no extra cost to themselves despite food-requirement differences. The first option might be true if the sexes differ in their allocation of energy to the different components of growth and development. Thus, while the larger sex might put more energy into components that result in an increase in body mass, the smaller may direct similar amounts of energy into development that results in less body mass increase. On the other hand, if food-requirement differences are significant, parents might compensate by bringing larger, but not necessarily more, food items to the larger sex.

I hand-reared Great-tailed Grackle (*Quiscalus mexicanus*) nestlings from day 6 through day 12 post-hatching to test the first hypothesis. Great-tailed Grackles are a highly dimorphic species in which adult males are approximately twice as heavy as females (Selander 1958). I attempted to determine whether males require more food than females of similar age, whether sexes differ in their energy requirements per unit mass, and

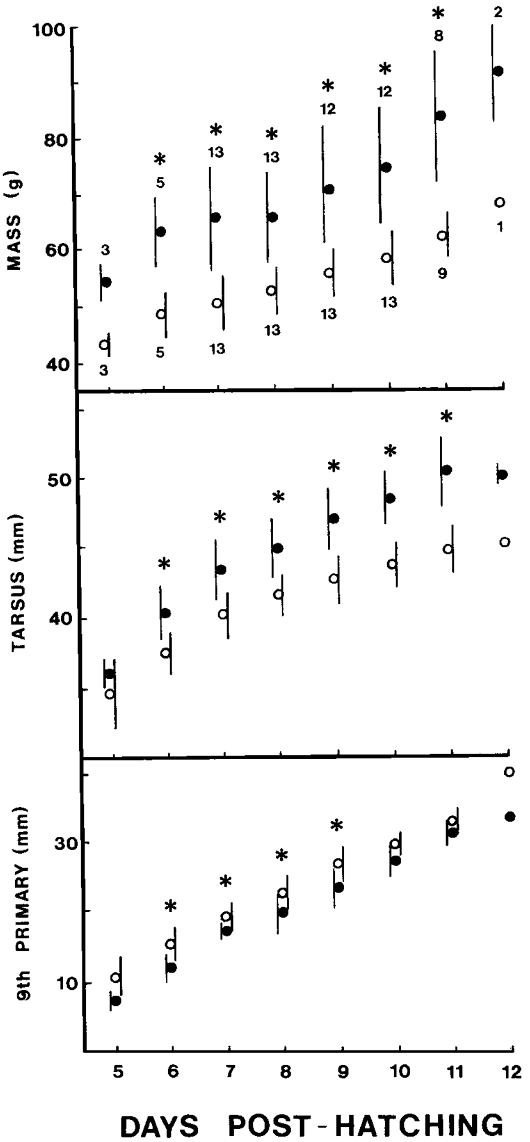

Fig. 1. Differences in mass, tarsus, and 9th primary (±1 SD) in hand-reared male (●) and female (○) Great-tailed Grackle nestlings. Sample sizes (given at the top) are the same for the three variables. Asterisks indicate significant differences at $P < 0.05$ (t-tests).

whether sexes convert similar proportions of food into increasing body mass.

MATERIALS AND METHODS

The study was conducted between 25 May and 22 June 1986 at the Welder Wildlife Foundation near Sinton, Texas. Groups of 5-6-day-old nestlings were taken from nests on the evenings of 25 May ($n = 9$), 1 June ($n = 10$), and 15 June ($n = 12$) and placed in pairs in natural nests that had been brought into the laboratory. Nests were kept outside in the shade during the day except during extreme heat or rain. During the evening nestlings were returned to the laboratory, where the temperature was maintained at 22-26°C. Moist towels and a heating pad were placed over the nests to maintain humidity.

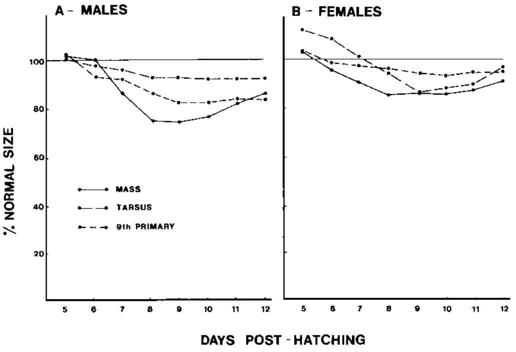

Fig. 2. Mass, tarsus, and 9th primary shown as a percentage of normal growth for Great-tailed Grackle nestlings. Normal growth was determined from naturally reared nestlings, and sample sizes range from 5 to 35. Sample sizes for hand-reared nestlings are as in Fig. 1.

Nestlings were fed a homogeneous mixture of catfish chow, wild-bird starter, egg, gelatin, vitamins, molasses, and water (after Lanyon and Lanyon 1969) through calibrated syringes. Nestlings were fed every 10-20 min from 0630 to 2030 until they stopped gaping. Thus, nestlings dictated how much food they received. Fecal sacs were collected from individuals after each feeding to calculate digestive efficiency.

Nestlings were weighed before feeding each morning and again at 2030. Tarsus and 9th primary lengths (mm) were recorded each evening.

All birds in the first group and birds of uncertain sex in groups 2 and 3 were sexed by dissection at the end of the 5-6 days in captivity. Birds whose sex was obvious by their growth patterns were returned to natural nests.

RESULTS

Males were significantly heavier and had significantly longer tarsi than females on days 6-11 (Fig. 1). Females, however, had significantly longer 9th primaries than males on days 6-9 (Fig. 1). Although these results are similar to differences between the sexes in natural nests (Teather unpubl. data), the growth of all three

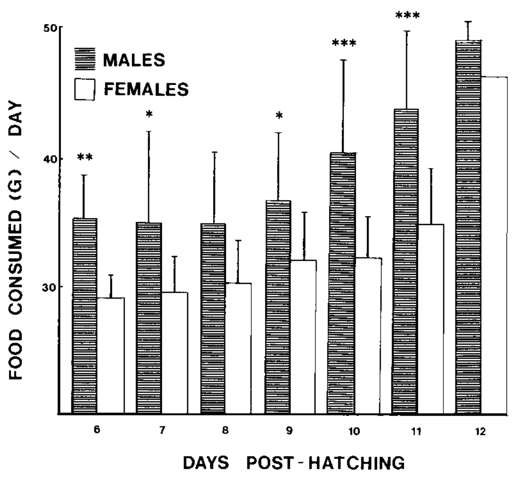

Fig. 3. Average amount of food consumed per day (±1 SD) by male and female nestlings from day 6 to day 12 post-hatching. Asterisks indicate significance level (* $0.1 > P > 0.05$, ** $0.05 > P > 0.01$, *** $P < 0.01$; t-tests). Sample sizes are as in Fig. 1.

variables was depressed in hand-reared nestlings (Fig. 2).

The relationship between body mass and energy requirements generally follows a power function (reviewed by Power 1983). I found, however, that the amount of food consumed vs. body mass was best described by a linear relationship (food consumed $= 7.26 + 0.44 \cdot$mass; $r = 0.790$, $P < 0.001$). Subsequently, because males were larger, they consumed more food than females of similar ages throughout the study period (Fig. 3). The average amount of food consumed by males between days 5 and 12 was 272.5 g, which was 15.8% more than the amount consumed by females (235.4 g). During the same period males weighed 30.0% more than females. Therefore, although males consumed more food than females, the difference was not directly proportional to the difference in body size. Females, in fact, consumed slightly more food than males of equal mass (Fig. 4).

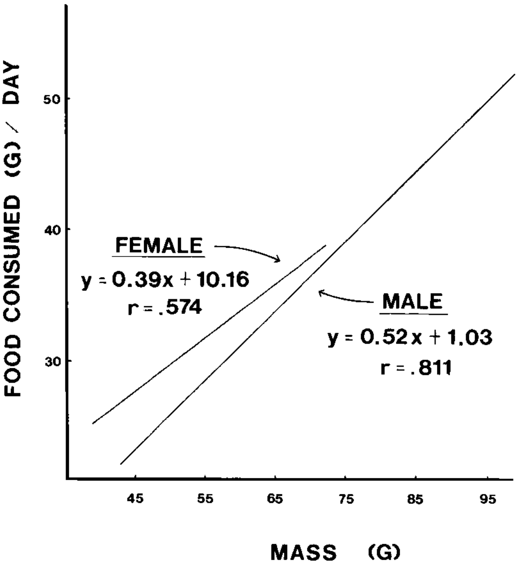

Fig. 4. Food consumed per day as a function of body mass. Regressions for males and females are significantly different ($F = 3.30$, $P = 0.04$).

TABLE 1. Relationship between amount of food consumed and mass increase for males and females. Values represent the ratio [dry mass of food consumed (g) − dry mass of feces (g)/mass increase per day (g) and are given ±1 SD. Probability values were calculated from t-tests on arcsine transformations. Sample sizes are as in Fig. 1.

Days post-hatching	Males	Females	P
6	1.63 ± 0.62	2.63 ± 1.57	0.236
7	1.61 ± 1.21	1.82 ± 1.39	0.688
8	1.30 ± 0.42	1.14 ± 0.17	0.201
9	1.13 ± 0.47	1.09 ± 0.24	0.782
10	1.14 ± 0.18	1.32 ± 0.21	0.030
11	1.59 ± 1.27	1.43 ± 0.47	0.731
12	0.94 ± 0.16	1.44	0.236

To determine whether males and females differed in the amount of food consumed per unit mass gained each day, I calculated the ratio [dry mass of food consumed (g) − dry mass of feces (g)]/mass gained (g). No consistent differences were found between values obtained for males and females over the study period (Table 1).

DISCUSSION

Male Great-tailed Grackle nestlings consumed more food than females of equal age and therefore required a greater absolute amount of food to be reared to fledging. The difference in food consumption over the 5–6-day study period was probably a minimum estimate for two reasons. First, the growth of hand-reared males was depressed more than that of females, and, thus, differences in food requirements of nestlings reared in natural nests are probably larger. Second, because the disparity in size between the sexes continues to increase while the nestlings are under parental care (approximately another 2 weeks after fledging), food consumption differences probably continue to increase. These results agree with those of Fiala and Congdon (1983), who showed that the gross energy intake of male Red-winged Blackbirds (*Agelaius phoeniceus*), during days 0–10, was approximately 1.3 times that of females. In contrast, male and female European Sparrowhawk (*Accipiter nisus*) nestlings, despite large size differences, consume similar amounts of food (Newton 1978), and male and female Golden Eagle (*Aquila chrysaetos*) nestlings do not differ in food consumption or energy metabolized (Collopy 1986).

Although males consume more food than females, requirements may not be proportional to their size. My results suggest that at constant mass females actually consume slightly more food than males. This differs from male Red-winged Blackbirds, which consume slightly more food than females of similar mass (Fiala 1981). Unfortunately, nestlings in both studies suffered from reduced growth rates so the relationship between mass and food consumption remains unclear.

An alternative is that dimorphic nestlings might channel energy into different characters. Thus, while energy of the larger nestling is directed to structures that result in increased body mass, the smaller sex may divert energy to physiological characters that enable it to compete with its larger brood mates. This may explain why feather development is more advanced in females than in males in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Boat-tailed Grackles (*Quiscalus major*) (Richter 1983, Bancroft 1984). Data from my study do not support this interpretation. Despite more advanced feather development in females, the mass gained per unit food consumed was similar for both sexes. Although it might be argued that the variability between nestlings masked potential differences, it is more likely that feather growth is not more costly to females than males. Female feather development, although initiated earlier (Teather unpubl. data), proceeds at a rate similar to males. Thus, on a daily basis both sexes probably direct similar amounts of energy to feather development. Any added costs to the female should occur only during the initial stages of feather growth.

Although male Great-tailed Grackles require more food than females, the sex ratio remains near one throughout the nestling period (Selander 1960, 1961), an observation consistent with studies of other dimorphic altricial nestlings (see references in introductory paragraphs). These results appear to contradict Fisher's (1930) prediction that there should be an overproduction of the less expensive sex during the period of parental care. There are three possible explanations for this. First, higher food consumption by the larger sex may not be accompanied by increased costs to parents. This would be true if parents met the demands of larger nestlings by feeding them larger, and not necessarily more, food items. This might occur if some food items were too large to be fed to the smaller sex or if parents opportunistically captured food items of varying size and distributed these to offspring according to nestling size.

Second, selection favoring overproduction of the smaller sex might be offset by selection favoring overproduction of the larger sex. Fisher's prediction that the less expensive sex should be produced in greater numbers is based on the assumption that the mortality rate of both sexes is similar while under parental care. Fisher also predicted, however, that if mortality rates of sons and daughters differed, the sex ratio should be initially biased in favor of the sex that suffers the greatest mortality. Indeed, there is some evidence, at least from passerines, that the larger sex experiences higher nestling mortality rates under certain conditions (see below). Mortality rates of males and females also may differ during the period between fledging and independence, although I know of no data that address this question.

Last, although there may be substantial cost differences in rearing sons and daughters, initial sex ratios are a function of random segregation of sex chromosomes and not subject to parental control. If this is the case, parents would be expected to adjust their food provision to the overall energy demands of the brood. Because energy demands would be higher in nests containing a higher proportion of the larger sex, production of the larger sex should suffer under stressed or food-limiting conditions. Examination of the few populations with skewed sex ratios at fledging support this interpretation. In nearly all cases, the fledgling sex ratio was skewed toward the smaller sex, and this was a result of higher mortality of the larger sex under experimentally or naturally stressed conditions (Howe 1977, Cronmiller and Thompson 1981, Fiala 1981, Bancroft 1983, Roskaft and Slagsvold 1985; but see Dhondt 1970).

To evaluate precisely the importance of adaptive sex-ratio manipulation in altricial birds, further data are required on energy requirements and mortality rates of each sex throughout the dependent period, how food is distributed to nestlings, and sex ratios of offspring after periods of food abundance and food stress.

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