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GAPES OF SEXUALLY DIMORPHIC BLACKBIRD NESTLINGS DO NOT SHOW SEXUALLY DIMORPHIC GROWTH

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ABSTRACT.—Within broods of many altricial birds, one or more nestlings is often predictably smaller than the rest. This occurs both because of hatching asynchrony within broods and also because one sex rapidly becomes larger than the other in sexually dimorphic species. If parents rely on competitive, size-based cues from nestlings in deciding which to feed, this size asymmetry presents a major predictable problem to younger or smaller nestlings. A recent study of sexually dimorphic Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) suggested that the gape, a prominent feature of the begging signal of hungry young, may grow more rapidly in female nestlings than males. In this paper, I report similar data on nestling gape growth in another sexually dimorphic species, the Red-winged Blackbird (*Agelaius phoeniceus*), and show that the apparent relatively faster gape growth of females in both Yellow-headed and Red-winged blackbirds is an artifact of the analytical method used in the comparison. Gapes of males and females grow in exactly the same relation to their mass and, to the extent that the mass of females is less at a given age, females will have smaller gapes. I further analyze gape growth in a group of undernourished nestling Red-winged Blackbirds to evaluate the related prediction that, when resources for growth are limited, nestlings should conserve the growth of those morphological characteristics such as gapes that directly influence feeding. The data yield little support for this hypothesis. The specialized and prominent nestling gapes, however, may have important functions beyond feeding competition. *Received 23 November 1992, accepted 28 January 1993.*

SIBLING COMPETITION WITHIN BROODS of altricial birds is often thought to be mediated by begging behavior directed at the parent, particularly in species that lack the bill structure to be overtly siblicidal (Mock 1984, Drummond et al. 1986, Mock et al. 1991). Begging has both auditory and visual signal components, the latter being composed of neck extension, the size and color of the mouth during "gaping," and body movements during begging. In several passerines, parent birds may respond differentially to the nestling having the nearest open beak (Ryden and Bengsston 1980), begging with greatest intensity (Ryden and Bengsston 1980), raising its head highest or, perhaps, being first to beg (Teather 1992). Gaping behavior and vocalizations are characteristic of even very young hatchlings (Nice 1962, Tinbergen and Keunen 1975, Bengsston and Ryden 1981, Choi and Bakken 1990). With its distinctive width and often colorful rictal flanges, the gape appears to be an important nestling characteristic, one that might influence parental feeding choices when nestlings are young. For species with sexually size-dimorphic nestlings, gape-size-dependent feeding would, however, seem to be disadvantageous for the smaller sex. If parents do preferentially feed nestlings with relatively larger gapes, one might expect selection on the smaller sex for allocation of resources to the growth of the gape, as well as to the development of other key "competitive" structures or behaviors involved in begging (Stamps 1990).

Such selection could be intensified in many species of altricial birds because the nestlings within a brood hatch asynchronously (Clark and Wilson 1981, Slagsvold 1985, Magrath 1990). If brood size is three or more, almost 25% of nestlings of the smaller sex will find themselves the youngest with at least one older sibling of the larger sex. In such cases, they would have a particularly difficult time getting enough food. Thus, the regular occurrence of age asymmetry within broods could intensify selection for rapid, early gape development in the smaller sex.

Both Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Richter 1984, Ortega and Cruz 1992) and Red-winged Blackbirds (*Agelaius phoeniceus*; Holcomb and Twiest 1970, Fiala 1981) show significant sexual dimorphism in mass by the second or third day of nestling life, a difference that increases until males are about

30% larger and heavier than females by fledging (Holcomb and Twiest 1970, Ortega and Cruz 1992). No differential death of female nestlings with brothers has been detected in studies of two sexually dimorphic icterids: Red-winged Blackbirds (Fiala 1981); and Great-tailed Grackles (*Quiscalus mexicanus;* Teather 1989). In fact, a preponderance of females among fledglings has been reported in many studies of dimorphic birds, including Red-winged Blackbirds (reviewed in Fiala 1981, Weatherhead and Teather 1991), Great-tailed Grackles (Teather and Weatherhead 1989), and others (Slagsvold et al. 1986). This raises the question of how smaller female nestlings with brothers succeed so well in getting enough food (Stamps 1990, Gowaty and Droge 1991).

Ortega and Cruz (1992) recently identified differentially fast growth of the gape as one potential way in which female Yellow-headed Blackbird nestlings successfully compete and survive in nests with larger and sometimes older brothers. Their analysis of age-specific mass and gape widths showed that males had absolutely larger gape widths than females at most ages, but that the mass-to-gape-width ratio (MGWR) was statistically significantly smaller for females at all but one age (day 2) from hatching to fledging. This led Ortega and Cruz to conclude that greater gape growth relative to overall body size could be a specific adaptation by female Yellow-headed Blackbirds, enabling them to compete successfully with larger brothers.

This result, if true, would be exciting and theoretically provocative with respect to predictions on sex-specific competitive strategies (Stamps 1990). However, it appears to be a statistical artifact of the behavior of ratios. In this paper, I present an analysis of similar data on sex-specific growth of Red-winged Blackbird gapes, and show that the gapes of males and females grow on exactly the same trajectory with respect to mass. I further illustrate that, given this result and the larger mass of males, the MGWR at a given age will differ between sexes, although such a difference is meaningless with respect to specific growth adaptations.

I then extend the analysis to test for a related possibility. If gapes are important in parental feeding decisions, underfed, slow-growing nestlings should differentially allocate resources to their growth in order to minimize their competitive disadvantage in getting food. My analysis of growth in nestlings that were severely growth-retarded due to hypothermia and lack of food during cold rains in 1992, however, provides little support for the hypothesis of selective conservation of gape growth by starving nestlings.

BACKGROUND AND METHODS

Study site and measurements.—Red-winged Blackbirds nesting at the Cornell Experimental Ponds, Ithaca, New York, have been under study since 1988 (e.g. Westneat 1992). Nests are usually found during building and eggs are individually marked as laid. After the clutch is complete, daily visits cease until 11 days after the first egg is laid. Pipped eggs are rechecked frequently enough that hatching nestlings are usually found within 3 to 4 h of hatching. I recorded egg mass for most eggs in 1991 and 1992. Using egg mass in conjunction with empirically based estimates of the mass contribution of the shell, how fast hatchlings' down dries and fluffs, how color of nestlings, and curve of the body changes in the first hours posthatching, etc., one can estimate time of hatching very closely. Ages of nestlings at the time of daily growth measures are calculated to the nearest hour, based on the known or estimated hatching time (age at hatching = 0).

Two years of data, 1991 and 1992, are the basis of this report. In 1991, the weather was warm and settled, and growth of nestlings rapid. In 1992, cold and rain apparently resulted in slow-growing nestlings and high mortality. The nestlings hatched in the two years are treated separately here and in the results as healthy nestlings (1991) and undernourished nestlings (1992).

In 1991, as one step in an ongoing study of sex-specific behavioral and morphological development in Red-winged Blackbird nestlings, I measured their gape width and length at the ages of 48 h (±4 h) and 96 h (±4 h), using vernier calipers accurate to 0.1 mm. Gape width was measured as the maximum distance between the points of the fleshy corners of the bill and represents the widest measure across an opened gape (Fig. 1). The measurement used by Ortega and Cruz (1992) was width "at loral feathering" (cf. Baldwin et al. 1931), but this seemed imprecise when nestlings are young with only sparse down. Care was taken to touch, but not compress the fleshy corners. Gape length was measured as the maximum distance between the tip of the bill and the furthest point of the fleshy fold of one rictal flange (Fig. 1). This distance forms one of four sides of the open gape. Other measures taken on all nestlings included mass and tarsal length.

Nestling growth comparisons.—In 1992, a week of cold, rainy weather with high temperatures well below

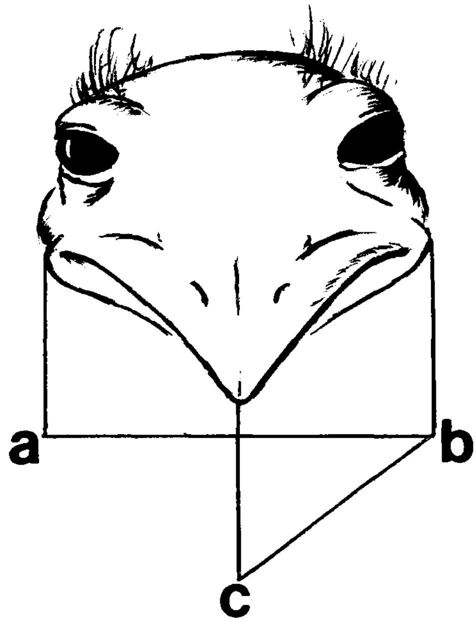

Fig. 1. Measures of nestling gape width (a–b) and gape length (c–b) used.

15.5°C followed the May hatching of the first Red-winged Blackbird nests on the study area. It resulted in extremely slow growth and ultimately the death of the 21 nestlings (six whole broods) that hatched just before or during the period. In 1992, masses and measures were recorded daily. In addition, nestling body temperature was determined at the time of measuring, as a variable in a more complete motor assessment. These nestlings often had body temperatures of 21° to 25°C in the nest, rather than the normal temperatures of 34° to 35°C characteristic of healthy nestlings later in the same season. Thus, the nestlings suffered not only from lack of food, but also from hypothermia. Most lived at least four days but the few reaching 10 days (near fledging age) came down with a fatal enteric infection (Clark and Berlin unpubl. data).

This group of nestlings provided a test for the idea that, in the face of little food, growth of gapes might be conserved more than growth of structures that were not important to getting fed. Tarsus length is a linear measure that is probably unrelated to begging effectiveness in the first four to five days. At this age, begging nestlings raise their bodies vertically to achieve greater height, rather than standing up on their tarsi.

I compared the increase in mass, gape width and tarsus length of the undernourished 1992 nestlings with that of the healthy 1991 nestlings, predicting that gape growth should be more normal than tarsal growth. The gape analysis was restricted to nestlings of 1.9 to 5.0 days of age both to make the age interval comparable in the two years and because gape width is hard to measure accurately on new hatchlings. Because 1992 nestlings could not be sexed in the field (see below), I compared their growth with that of the 1991 male and female nestlings combined. Tarsal growth relative to mass normally differs by sex; the tarsal growth of 1992 nestlings also was compared to that of 1991 females as the sex closest to them in mass. In the case of tarsal growth, all nestlings less than five days of age were used because daily measures were available in both years.

Sexing of nestlings.—Normally growing nestlings that survived to at least seven days of age were sexed by a combination of tarsus length and mass. They were judged to be males if they had a tarsus length of 27.5 mm or greater in conjunction with a mass of 33 g or greater at eight days of age or older, a combination of the criteria used by Holcomb and Twiest (1970), Fiala (1981), and Yasukawa et al. (1990). I also checked that presumptive males actually showed the characteristically rapid growth in tarsal length beyond seven days of age. Tarsal growth of normal females slows at this age. In this population, the tarsi of adult females do not exceed 28.5 mm and few exceed 27.5 mm (Westneat unpubl. data). The major source of error with these rules is the likelihood of labelling underweight males as female (Fiala 1981).

In 1991, nestling growth was generally excellent, none starved and sexing was likely to be quite accurate. Starvation as a cause of death was generally inferred when a nestling or nestlings disappeared from the nest after growing slower than the remaining siblings, or when all were growing very slowly and one disappeared. Starved nestlings were in fact often discovered before they were removed by parents. They were usually obviously thin before and at death. Starvation was also clear when whole broods were found dead in the nest after little growth, as in 1992. Nestlings taken by predators while too young to sex confidently were not used in the analysis of sex differences.

The undernourished nestlings of 1992 grew too slowly and died too soon to be sexed. In the analyses, they are treated as a group with an expected sex ratio not different from that in 1991.

Statistical analysis.—Data were analyzed for differences in means with one-way ANOVA after using Bartlett's test for homogeneity of variances. ANCOVAs and tests for homogeneity of slopes were carried out using SYSTAT (Wilkinson, 1989).

RESULTS

Growth patterns of healthy nestlings.—This analysis is based on 55 nestlings (18 broods) for which I have gape measurements on at least

TABLE 1. Gape widths and lengths (±SD) of male and female Red-winged Blackbird nestlings at day 2 and day 4.

Gape measure (mm)	Male	Female	P[a]
Day 2 (n = 13 males and 25 females)			
Width	12.70 ± 0.73	12.14 ± 0.60	<0.02
Length	10.93 ± 0.42	10.40 ± 0.62	<0.02
Day 4 (n = 11 males and 24 females)			
Width	14.49 ± 0.41	13.72 ± 0.39	<0.001
Length	13.54 ± 0.39	12.82 ± 0.60	<0.001

[a] One-way ANOVAs. Bartlett's test for homogeneity of group variances ($P > 0.10$).

one of the two days. Some nestlings were taken by predators before their 96-h developmental assessment; none died of starvation. Of the 38 nestlings that could be sexed, 13 were males and 25 were females.

Age-related changes in the morphology of the gape may provide some clues as to when gapes are most important in parent-offspring interactions. The gape width of hatchling Red-winged Blackbird nestlings is striking and exceeds the gape length. At day 2, the ratio of width:length averaged 1.14 ± SD of 0.08 (range 1.0–1.30, n = 52); by day 4, it was 1.07 ± 0.06 (range 0.94–1.21, n = 36). By day 6, gape length equaled or exceeded width and the fleshy edges were less soft and colorful, as noted for Yellow-headed Blackbirds by Ortega and Cruz (1992). At this time, the nestlings' eyes begin to accommodate and focus at different distances (Howland and Clark unpubl. data). Nestlings can then more actively compete for food, being capable of following their parent's bill by eye and directing their heads appropriately, as reported for Brewer's Blackbirds (*Euphagus cynanocephalus*; Balph 1975). Thus, if gape size or other simple passive nestling characteristics figure in parental feeding decisions, it is likely that they would be most salient during the first five days of nestling life. The following analyses deal with nestlings of five days or less.

To explore differences in the growth of gapes in males and females, I compared masses and gapes of known males and females at the two ages: day 2 and day 4. Gape width (GW) is plotted against the cube root of mass (Mass$^{1/3}$) to avoid comparing linear with cubic measures. In both age categories, males had significantly wider and longer gapes than did females (Table 1). However, if gape width is subjected to an ANCOVA by sex with mass$^{1/3}$ as the covariate, it is clear that the gape widths of both sexes fall on a single line (Fig. 2) with no differences in slope or intercept (Mass$^{1/3}$ × Sex, $F_{1,73} = 0.38$, ns; Sex, $F_{1,74} = 0.41$, ns). The same is true for gape length (Mass$^{1/3}$ × Sex, $F_{1,73} = 0.001$, ns; Sex, $F_{1,74} = 1.53$, ns). Thus, the maximum presented gape size varies with the mass of the nestling, but does not differ between the sexes for nestlings of the same mass. Since females weigh less at any given age, they will generally present smaller gapes than their same-aged brothers.

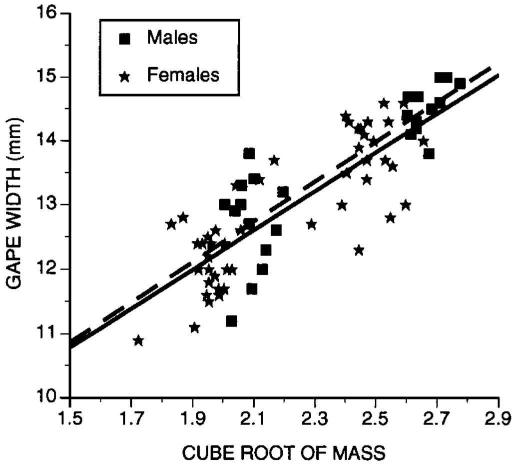

Fig. 2. Normal (1991) male and female gape widths increased similarly in relation to cube root of body mass. Note that lines will cross the Y-axis above origin. Dashed line for males, $Y = 6.18 + 3.12X$, $R^2 = 0.73$; solid line for females, $Y = 6.22 + 3.04X$, $R^2 = 0.66$.

I duplicated the analysis of Ortega and Cruz (1992), using mass as they did, rather than mass$^{1/3}$ as used above. As Ortega and Cruz reported, the MGWR plotted against exact age was higher for males through 4.2 days at least. However, this is simply because the regression line for gape width versus mass does not pass through the origin. Note that the Y-intercept of the extrapolated line relating gape width to mass is positive when mass equals zero (Fig. 3A). Using the points plotted in Figure 3A, I have computed the MGWRs and plotted these against mass (Fig. 3B), showing that as mass increases the ratio also increases. (Note that, if the Y-intercept were negative rather than positive, the ratio would decrease with increasing mass. Only if the line passes through the origin will the

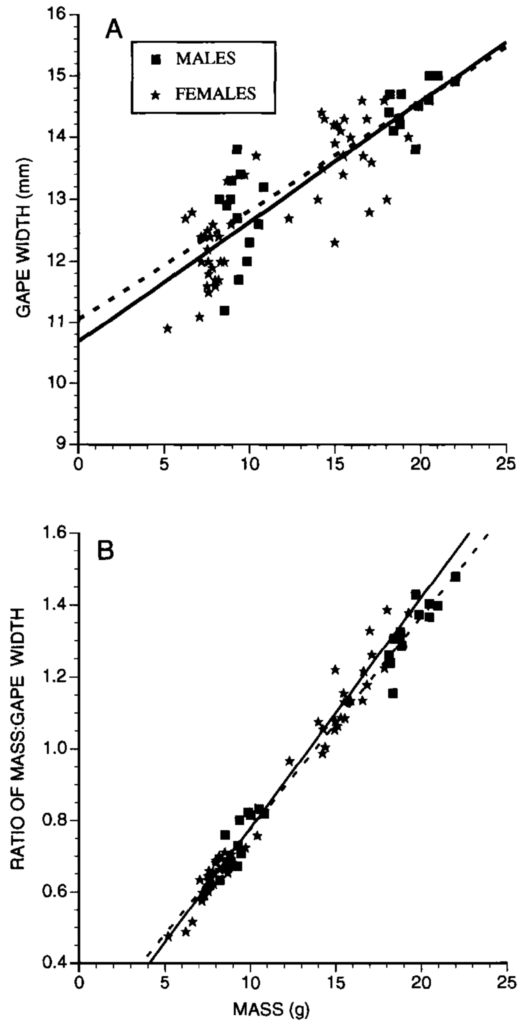

Fig. 3. (A) Growth of male versus female gape widths in relation to mass. (B) Ratios of same data plotted against mass. Ratio will increase with increasing mass similarly for both males and females (dashed line for males; solid line for females).

ratio *Y*:*X* remain constant along its length.) Because males are consistently heavier than females at the same age beginning at day 2 (Sex, $F_{1,39}$ = 22.77, $P < 0.001$), the ratios of males plotted against age will fall on a line above the ratios of females at the same ages (ANCOVA: Age × Sex, $F_{1,70}$ = 1.37, P = 0.246; Sex, $F_{1,71}$ = 38.06, $P < 0.001$). Females do not differ from males in the allometry of gape growth. The apparent sex difference in ratios with age is an outcome of the artifactual result that heavier nestlings will generally have higher ratios than lighter nestlings. The same result pertains if mass is replaced by mass$^{1/3}$ in this analysis.

Growth allocation under restricted-resource conditions.—The undernourished nestlings of 1992 had a strikingly and significantly lower rate of mass gain up to five days compared to healthy nestlings (Year × Age, $F_{1,345}$ = 62.76, $P < 0.001$), and the few that survived to 10 days never caught up (Fig. 4). While the slope of their gape-width growth with age did not differ from that in 1991, the intercept did (Fig 5; Year × Age, $F_{1,133}$ = 1.14, ns; Year, $F_{1,134}$ = 17.31, $P < 0.001$). Thus, gapes in 1992 were significantly narrower at all ages up to five days.

The slope of gape width versus mass$^{1/3}$ did differ significantly between the two years (Year × Mass$^{1/3}$, $F_{1,133}$ = 13.78, $P < 0.001$), with the lines for the two years crossing. Thus, gape widths of the undernourished nestlings are smaller than expected for the lightest birds and exceed 1991 gape widths for the heaviest ones (Fig. 6). However, the few 1992 nestlings that reached such masses already were much older than the 1991 nestlings of the same mass (compare Figs. 2 and 6).

Unlike gape width, the growth allometry of the tarsus normally differs by sex. The tarsi of 1991 females grew significantly more slowly with age than those of males (Sex × Age, $F_{1,183}$ = 10.40, P = 0.001). The tarsi of 1992 nestlings grew more slowly with age than those of male and female 1991 nestlings combined (Year × Age, $F_{1,208}$ = 84.43, $P < 0.001$); more slowly even than 1991 females alone (Year × Age, $F_{1,208}$ = 20.01, $P < 0.001$). Up to five days, the mass of normal males increases faster relative to their tarsal growth than the mass of females, resulting in males having a significantly lower rate of tarsal growth with respect to mass than normal females (Sex × Mass$^{1/3}$, $F_{1,183}$ = 4.85, P = 0.029). The tarsal growth of 1992 nestlings with respect to mass was indistinguishable from that of normal females (Year × Mass$^{1/3}$, $F_{1,208}$ = 1.73, ns; YEAR, $F_{1,208}$ = 1.49, ns) and similar to 1991 males and females combined (Fig. 7; Year × Mass$^{1/3}$, $F_{1,279}$ = 0.08, ns; Year, $F_{1,280}$ = 0.06, ns).

Thus, as expected, the undernourished nestlings gained mass more slowly and were smaller at all ages than healthy nestlings. Both gape width and tarsus length, however, seemed less affected than was total mass. While both gape and tarsus grew more slowly than normal, both increased more rapidly relative to mass than the gapes and tarsi of the healthy 1991 nestlings.

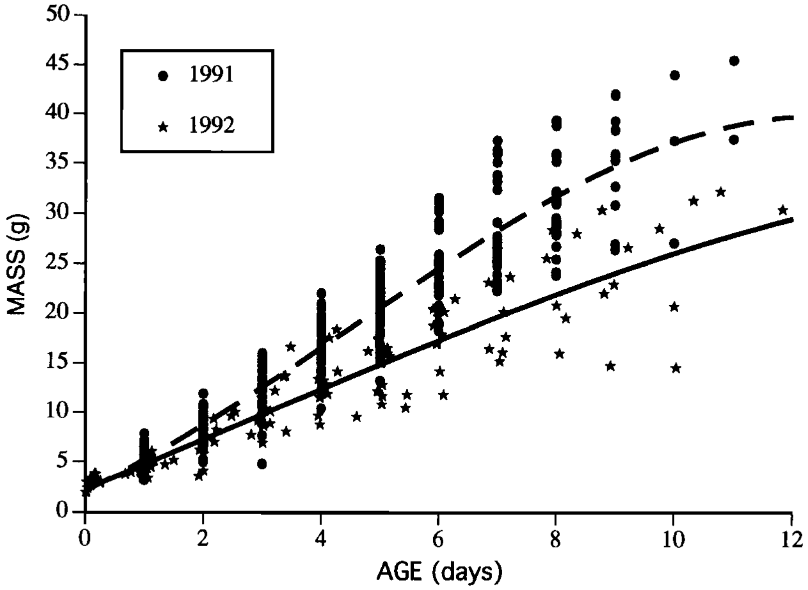

Fig. 4. Nestling mass gain with age was more rapid in 1991 (dashed line) than in 1992 (solid line). All ages up to fledging shown, but many 1992 nestlings died before day 7. Normal mass gain over entire nestling period conforms best to a polynomial curve, but mass gain from days 0 to 5 fits a straight line (1991, $R^2 = 0.89$; 1992, $R^2 = 0.86$; $P < 0.001$ for both). My analyses are based on linear regression.

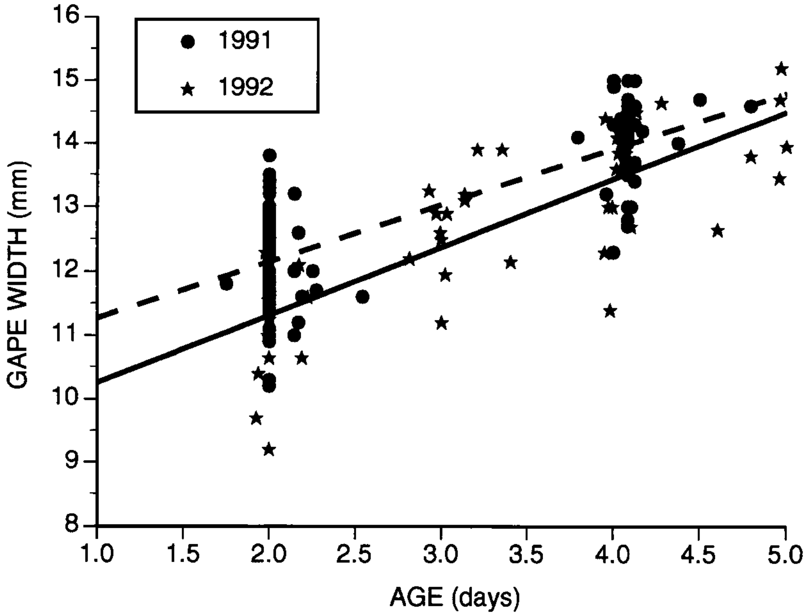

Fig. 5. Gapes of growth-retarded nestlings (solid line) were significantly smaller at all ages than gapes of normal nestlings (dashed line) at all ages from day 1.9 through day 5. Slopes, however, were statistically similar (1991, $Y = 9.19 = 1.06X$, $R^2 = 0.63$; 1992, $Y = 10.30 + 0.88X$, $R^2 = 0.59$).

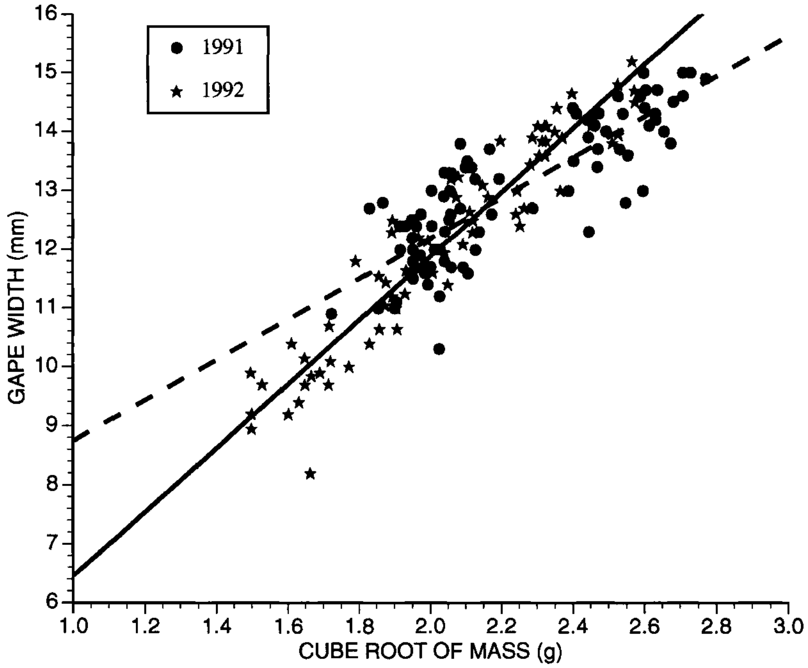

Fig. 6. Growth-retarded nestlings (1992, solid line) and normal nestlings (1991, dashed line) had a significantly different relationship between gape width and mass$^{1/3}$. Gape widths of 1992 nestlings were larger for their mass$^{1/3}$ at higher masses, but these nestlings also were much older than 1991 nestlings of the same mass (1991, $Y = 1.02 + 5.42X$, $R^2 = 0.88$; 1992, $Y = 5.30 + 3.43X$, $R^2 = 0.70$).

DISCUSSION

My study demonstrates that specially accelerated growth of the gape does not compensate for the size of the smaller female nestlings in two sexually dimorphic icterid species. The females' gape size increases relative to mass by the same allometric rule as the gape size of their male siblings. Data presented by Ortega and Cruz (1992) is in agreement with this conclusion, once the misinterpretation of the MGWR ratio is rectified.

Underweight or starving nestlings constitute another class of nestlings that might suffer from having smaller gapes. I predicted that gape width growth might be less affected by food shortage than the growth of body parts unrelated to competition for food. Conceivably, the growth allometry of undernourished 1992 nestlings in comparison with that of normal 1991 nestlings might be taken as supporting evidence. Gape width of undernourished nestlings did increase more steeply than normal with respect to mass and, while the tarsus did also, its rate of increase did not exceed that of healthy nestlings. There are, however, several reasons to be suspicious of this as confirmation of the hypothesis. Mass is a composite measure of actual body dry mass, gut and crop contents, and degree of hydration. The degree of hydration, as well as gut and crop contents, may be reduced in undernourished nestlings because food is also their water source. Thus, mass at a given time is likely to be more depressed than any bone or beak dimension. In fact, mass gain can almost stop and the nestlings continue to survive (see Fig. 4). Apparently, during such a period, some growth of bones and beak continues. The fact remains that gapes and tarsal lengths fell far behind those of normal nestlings of the same age. The use of tarsal length for comparison, when the sexes of 1992 nestlings are unknown, leaves some doubt about the actual change in slope. If, by some improbable statistical accident, most of the broods in 1992 nest were all males, the appropriate comparison for 1992 tarsal growth would have been with male tarsal growth in 1991. Growth in 1992 could then have been significantly faster than in 1991, similar to the result for gapes. The comparison of gape-

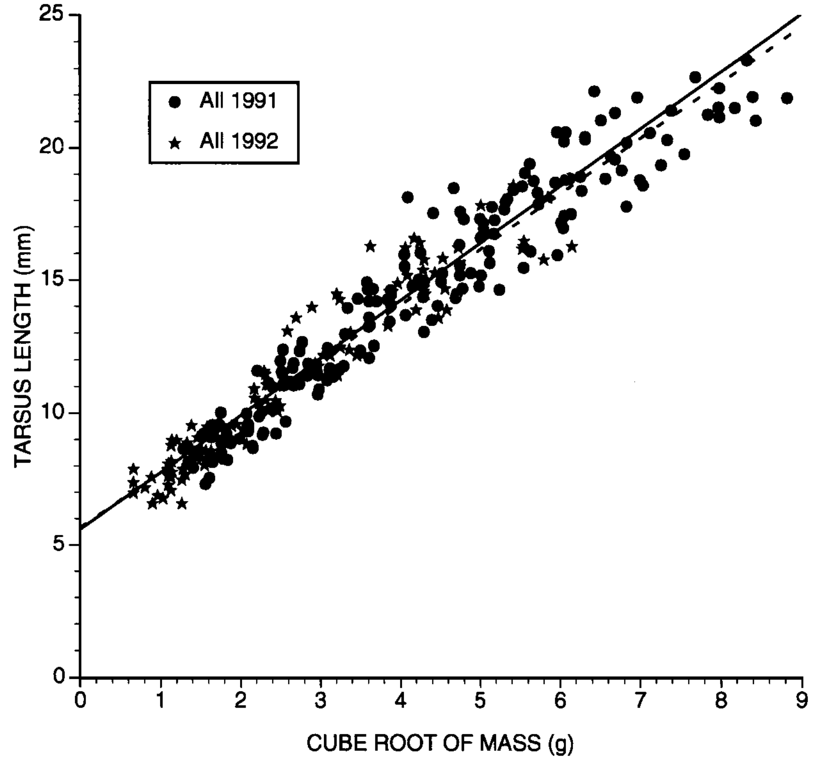

Fig. 7. Tarsal growth with increasing mass$^{1/3}$ of growth-retarded nestlings (1992, dashed line) was similar to that of normal nestlings (1991, solid line) (1992, $Y = 5.597 + 2.16X$, $R^2 = 0.92$; 1991, $Y = 5.66 + 2.10X$, $R^2 = 0.93$).

width growth and tarsal growth would then no longer lend any support to the hypothesis of competition-driven adaptive variation in growth.

The data presented here and by Ortega and Cruz (1992) are pieces of a more general puzzle concerning the interaction of avian parents and offspring. Several major questions have been the subject of considerable theoretical and empirical attention. First, given that parents provide care such as food directly to individual offspring, and that each nestling is assumed to behave in its own interests primarily (O'Conner 1978), how can parents use the behavioral and morphological characteristics of their young to assess accurately how much care is needed by each young (MacNair and Parker 1979, Parker and MacNair 1979, Harper 1986, Hussell 1988)? In cases where sexes differ in rate of growth, size, and costs (e.g. Fiala and Congdon 1983, Teather and Weatherhead 1988), how can parents apportion food equably (by need) between nestlings of different sex? Finally, when parents show sex-specific feeding preferences, how do they recognize the nestling's sex and what is their reproductive payoff for the preference (Stamp 1990, Gowaty and Droge 1991)?

Begging of altricial birds often is assumed to have a large role in the parents' assessment of their nestlings' food needs (Harper 1986, Hussell 1988). Collective vocal behavior of a brood can influence the number of feeding trips to the brood (von Haartman 1953, Bengsston and Ryden 1983, Hussell 1988), but it is less clear how individual begging characteristics determine the allocation of food within a brood. Parents may put food in the most-widely-opened beak (Illies 1975). Teather (1992) has shown that the Red-winged Blackbird nestling with greater head height and, more variably, the one begging first on a feeding visit is most likely to receive food. Begging intensity (a composite measure of type and duration of movements) and position with respect to the parent also play roles (Ryden and Bengsston 1980). Furthermore, there probably are other nestling characteristics that could provide the parent with information on the amount or kind of food needed (Stamps et al. 1985, 1989, Hussell 1988).

The morphology and ontogeny of gapes suggest that they should be important in parent-offspring interactions. The gapes of young nestlings are characteristically large relative to the rest of the body, with fleshy, colored rictal flanges that accentuate the size of the opened mouth (Skutch 1976, O'Conner 1984; see Harrison 1978). As the young become capable of recognizing the parent and tracking its feeding movements, these flanges begin to diminish in size relative to the rest of the bill (O'Conner 1977 and above). It is at about this age (i.e. day 7) that Red-winged Blackbird females show the first clear signs of differentiating their own from other nestlings (Peek et al. 1972).

The results presented above and in Ortega and Cruz (1992) fail to support the idea that the relative gape size exerts a strong influence over food allocation. This does not mean, however, that gapes do not inform and influence the parent, perhaps by acting as an initial stimulant of a switch to feeding from incubation, or perhaps by reflecting the health of young nestlings. Although gapes tend to be species-specific in appearance, species recognition alone does not explain their occurrence because they are not limited to birds that experience interspecific brood parasitism.

One possibility receiving little attention is that parent birds can determine the relative ages of their nestlings using rictal flanges and adjust what they bring, how they evaluate the begging behavior of the nestling, or how much of one load they feed it. Birds obviously are capable of adjusting the size of food items as the nestlings grow (O'Conner 1984, Quinn 1990, pers. obs. for American Robins [*Turdus migratorius*] and Red-winged Blackbirds.). Female Budgerigars (*Melopsittacus undulatus*) are capable of discriminating the ages of their nestlings although these lack passerine-type gapes or bright oral flanges. They feed the younger nestlings ground-up seed while the older ones, fed within the same hour, receive regurgitated whole seed (Stamps et al. 1985). A similar phenomenon has been reported for Bullfinches (*Pyrrhula pyrrhula;* Newton 1967). Other food characteristics, such as the amount of chitin in insects offered, also may be adjusted.

Thus, the characteristics of nestling gapes are worthy of further study as signals to the parent about the age-specific food needs of the nestlings. It seems less likely that the relative gape size is a major determinant of food allocation within a brood. In looking for explanations of such nestling traits associated with feeding, one should consider the breadth of information the traits may carry. Choi and Bakken (1990) have suggested, for instance, that hatchling vocalizations signal thermal stress as much as hunger. The study of nestling begging behaviors should be placed in a broader context than simply food competition among siblings.

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