Wilson Bull., 105(1), 1993, pp. 159–166

BEHAVIORAL DEVELOPMENT OF MALE AND FEMALE RED-WINGED BLACKBIRDS

KEVIN L. TEATHER[1]

ABSTRACT.—When sexual size dimorphism occurs among nestlings, individuals of the smaller sex are thought to develop locomotory skills and plumage more quickly than their larger, opposite-sexed siblings. It follows that certain aspects of the behavioral development of nestlings should be sex-specific. I tested the prediction that female Red-winged Blackbird (*Agelaius phoeniceus*) nestlings develop behaviors associated with muscle development and self-maintenance prior to males. Videotaped observations from 14 nests suggest that female nestlings engaged in higher levels of preening, and possibly scratching and wing-flapping, near the end of the nestling period than did males of the same age. There was little difference in the frequency of stretching for either sex, although there was evidence that males engaged in more leg stretching and females in more wing-leg stretching at certain ages. *Received 17 March 1992, accepted 20 Aug. 1992.*

Investigations of growth patterns of altricial nestlings have been largely restricted to morphological (e.g., changes in mass and feather length) and physiological (e.g., development of endothermy) characters. Behavioral development, while mentioned sporadically in descriptive studies of growth and development, has figured much less prominently in ecological or evolutionary studies. Part of the problem, no doubt, stems from the difficulty in directly observing and quantifying behavioral development without disturbing parent-offspring interactions. Certain behaviors, such as those directly related to feather and muscle development, may reflect the physiological state of the nestling and thus may be a useful gauge of developmental patterns. In this investigation, I compare the development of male and female nestlings of a sexually dimorphic species to determine whether sex-specific differences in morphological development are reflected in predictable differences in behavioral development.

In many sexually dimorphic species, mass differences between the sexes appear early in development, with males weighing significantly more than the females within a few days of hatching (e.g., Fiala and Congdon 1983, Bancroft 1984, Teather and Weatherhead 1988). A similar trend is apparent for bone development; the tarsus, for example, is significantly longer in male Great-tailed Grackles (*Quiscalus mexicanus*) by three days of age (Teather and Weatherhead 1988). Feather development, on the other hand, proceeds more quickly in females. Primary feathers of female Boat-tailed Grackles (*Q. major*) emerge significantly earlier and remain

[1] Dept. of Zoology, Cambridge Univ., Cambridge, UK CB2 3EJ. (Present address: Augustana Univ. College, Camrose, Alberta, Canada T4V 2R3).

longer than those of males until just prior to fledging when feather growth of males overtakes that of females (Bancroft 1984). For many dimorphic species, regardless of whether males or females are larger, it has been suggested that the smaller sex develops locomotory skills more quickly (e.g., Beebe 1960, Newton 1978, Richter 1983). Consequently, the smaller sex, probably because of its more rapid development of feathers and advanced locomotory skills, usually fledges before the larger sex (e.g., Holcomb and Twiest 1970, Newton 1978, Richter 1983, Bancroft 1984, Delannoy and Cruz 1988).

Here I quantify patterns of stretching, preening, spontaneous begging (begging in the absence of parents), scratching, and wing-flapping in nestling male and female Red-winged Blackbirds (*Agelaius phoeniceus*), a species that exhibits sexual size dimorphism early in development (Fiala and Congdon 1983). Because stretching is probably related to the degree of muscle development, I predict that if females develop locomotory skills more quickly, they should stretch more often and earlier than males. Similarly, because feather development and fledging time are advanced in females, I expect preening behavior, scratching (a behavior thought to supplement preening [Ficken 1962]) and wing-flapping to be initiated earlier in females. In addition, since males require more food for growth than females (Teather, 1992), the frequency of spontaneous begging (begging when parents are absent) should be higher in males.

METHODS

I studied a colony of Red-winged Blackbirds between 1 May and 15 July 1991 in a 4-ha marsh near Portland, Ontario. Each day, I checked the colony for new nests, eggs, and nestlings. Upon hatching, nestlings were marked uniquely on one tarsus, using a felt-tipped waterproof marker. Nests were thereafter visited at least every second or third day until nestlings were approximately ten days old.

Fourteen nests were chosen for videotaping on the basis of (a) ease of camera set-up (filming was restricted to nests that were below waist height), (b) brood size (three or four nestlings), and (c) nestling health (broods in which nestlings were underweight for their age/sex group were not filmed). At least three days prior to filming, artificial cameras were placed within 2 m of nests to habituate parents to their presence. When nestlings were 5–9 days old, artificial cameras were replaced with videocameras between 06:00 and 09:00 h EST and parent-nestling interactions filmed for 1.5 to 3 h. All nestlings were marked uniquely with a small spot of colored acrylic paint on the tops of their heads. At the end of filming, nestlings were weighed, and their tarsus lengths, eighth primary lengths, and gape widths (commissural widths) were recorded. Sex of nestlings was determined by weight and tarsus measurements (see Teather, 1992) which are significantly different shortly after hatching (Fiala and Congdon 1983).

Nestling behaviors were replayed and reviewed at slow speed. I noted the frequency (number/h) that individual nestlings (1) stretched legs, (2) stretched wings, (3) stretched legs and wings simultaneously (wing-leg stretch), (4) preened (the number of minutes during which nestlings were observed to preen), (5) scratched, (6) wing-flapped, and (7) sponta-

TABLE 1

NUMBER OF MALES AND FEMALES AND TOTAL TIME OF OBSERVATION FOR THE FIVE AGE GROUPS

Age (d)	Males		Females	
	Number	Time (h)	Number	Time (h)
5	4	11.3	3	8.6
6	11	30.9	17	47.9
7	14	34.3	21	58.3
8	8	22.5	15	38.0
9	6	16.8	8	20.9

neously begged. Possible age-related patterns and sex-related differences for behaviors were tested by Spearman rank correlations and Mann-Whitney *U*-tests, respectively.

RESULTS

Table 1 lists the sex, number of nestlings, and total number of observation hours for ages five through nine days. Of the 14 nests, four were filmed on one day, two on two days, five on three days, and three on four days. Nine of the broods contained three nestlings, while the remaining five contained four nestlings. The overall sex ratio was 20 males : 27 females.

Males were larger than females in terms of mass, tarsus length, and commissural width for all ages during the study (Fig. 1). Mass and tarsus lengths of opposite-sexed nestlings continued to increase and diverge during the study period, while gape widths remained relatively constant for ages five to seven days for both sexes and decreased thereafter. There was no consistent difference between males and females in the length of eighth primaries during this period.

If stretching is correlated with muscle activity, the frequency of this behavior may be useful as an indirect measure of the degree to which muscle development proceeds in nestlings. One obvious prediction from this is that nestlings should stretch with increasing frequency as they become older. With the exception of leg stretching by males, this was the case (Fig. 2A–C). Leg stretching by females ($r_s = 0.366$, $P = 0.004$), wing stretching by both males and females (males: $r_s = 0.331$, $P = 0.026$; females: $r_s = 0.453$, $P < 0.001$), and wing-leg stretching by both sexes (males: $r_s = 0.449$, $P = 0.003$; females: $r_s = 0.714$, $P = 0.001$) increased with age. While there were no differences between males and females in the frequency of wing stretching, males consistently stretched their legs more often than females from ages five through eight days although the difference approached significance on only two of these days. No difference

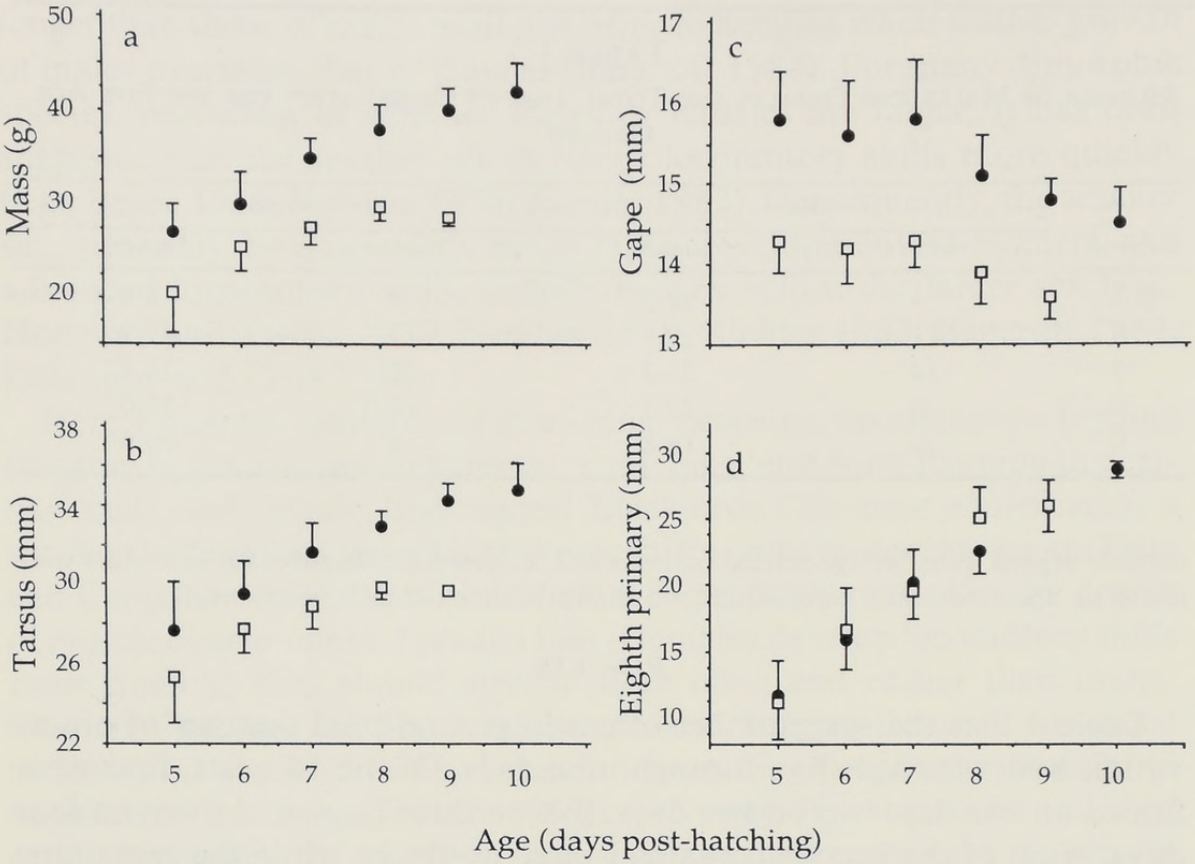

FIG. 1. Differences in (a) mass, (b) tarsus length, (c) gape width and (d) eighth primary length for five to ten-day old male (closed circles) and female (open squares) Red-winged Blackbird nestlings. Vertical lines represent one standard deviation.

was observed in the frequency of body stretching until nine days of age when females stretched more often than males.

The development of preening skills is expected to coincide closely with the development of feathers. Preening activity was observed at low frequency when nestlings were five days old and may have occurred before that age. However, it was uncommon in either sex until seven days of age, after which the amount of preening done by female nestlings exceeded that by males (Fig. 2D).

Scratching and wing-flapping were observed infrequently and only when nestlings were seven to nine days old. Both behaviors appeared more common in females, although sample sizes were too small for statistical comparisons. Only one male, at seven days of age, was observed to scratch, and none was observed wing-flapping. Females scratched at a mean frequency of 1.1/h at both eight and nine days of age and wing-flapped at frequencies of 0.35 and 0.80/h on days eight and nine, respectively.

Finally, there was no difference in the number of times males or females begged in the absence of parents for any age cohort or over the entire observation period (Fig. 2E). In neither sex did the frequency of spon-

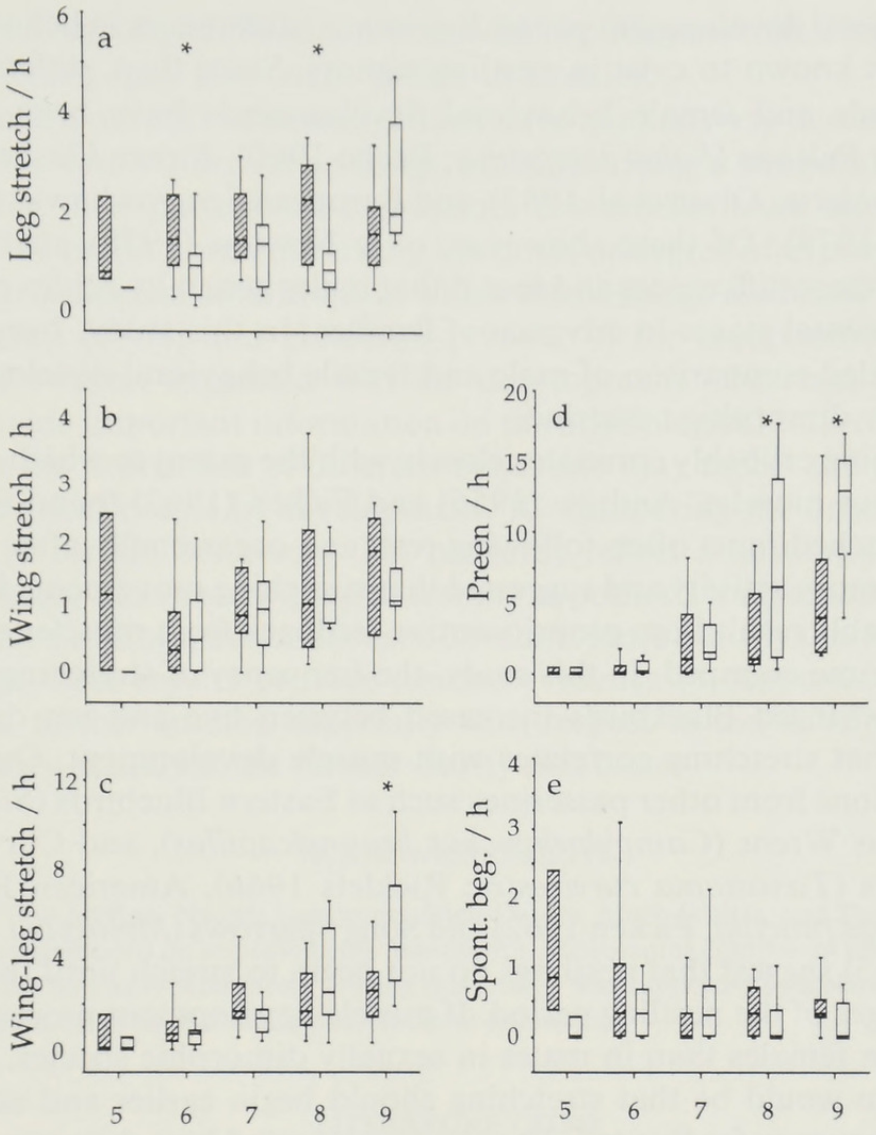

FIG. 2. Sex-specific patterns of development in Red-winged Blackbirds with respect to (a) leg stretching, (b) wing stretching, (c) leg-wing stretching, (d) preening and (e) spontaneous begging. Box plots (males: hatched, females: open) provide 10th, 25th, 50th, 75th, and 90th percentiles. Asterisks denote differences when $P < 0.10$ based on two-tailed Mann-Whitney *U*-tests.

taneous begging change significantly between age groups (Spearman rank correlations, $P > 0.10$ for each sex).

DISCUSSION

Although females are often said to develop more quickly in dimorphic icterines (see Richter 1983), this perception is most often based on advanced plumage maturation and earlier fledging by females (e.g., Holcomb and Twiest 1970, Richter 1983, Bancroft 1984) rather than on differences

in behavioral development per se. Intersexual differences in behavior have long been known to exist in nestling raptors. Since then, differences between male and female behavioral developments have been noted in Peregrine Falcons (*Falco peregrinus*; Beebe 1960), Brown Goshawks (*Accipiter fasciatus*; Olsen et al. 1982), and European Sparrowhawks (*A. nisus*; Newton 1978). Of these, however, only Newton (1978) attempted to quantify these differences and found that males generally achieved certain developmental stages in advance of females. In this study, I present the first detailed comparison of male and female behavioral development in a sexually dimorphic passerine.

Stretching probably correlates closely with the extent to which nestlings use various muscles. Andrew (1956) and Ficken (1962) found that nestlings stretched most often following rest, and occasionally after a period of locomotory activity and suggested that stretching movements following rest probably result from proprioceptive feedback from muscles after they have become cramped. In this study, the frequency of stretching by nestling Red-winged Blackbirds increased between five and ten days, suggesting that stretching correlates with muscle development. Qualitative observations from other passerines such as Eastern Bluebirds (*Sialia sialis*), Cactus Wrens (*Campylorhynchus brunneicapillus*), and Curve-billed Thrashers (*Toxostoma curvirostre*; Ricklefs 1966), American Redstarts (*Setophaga ruticilla*; Ficken 1962) and Song Sparrows (*Melospiza melodia*; Nice 1943) suggest that nestlings do not begin to stretch until the mid or latter stages of the nestling period. If muscle development proceeds more quickly in females than in males in sexually dimorphic species, a logical prediction would be that stretching should begin earlier and occur at a higher frequency for this sex. The results presented here, however, suggest that males, rather than females, may stretch leg muscles at a higher frequency earlier in development while there is no difference between the sexes in the frequency of wing stretching throughout the nestling period. The only support for this prediction comes from a slightly higher frequency of wing-leg stretching by females late in the nestling period.

The development of preening skills is likely to be closely tied to plumage development. Although there were no apparent differences in the development of eighth primaries of male and female redwings in this study, more detailed analyses of feather development in sexually dimorphic species suggests that feathers emerge earlier and remain longer in the smaller sex until shortly before fledging (Holcomb and Twiest 1970, Newton 1978, Moss 1979, Richter 1983, Bancroft 1984). Because feather development proceeds more quickly in female icterines, preening behavior should also be advanced in this sex. This appears to be the case; females engaged in more preening behavior that did males at eight and

nine days of age. In addition, limited evidence suggests that wing-flapping and scratching may also occur earlier in females.

Although a number of investigations have qualitatively described some of the behaviors of altricial nestlings, often providing a temporal sequence concerning their patterns of expression, few studies have attempted to test specific predictions concerning the onset or degree of expression with respect to ecological conditions in which the nestlings are found (although see Ricklefs [1966] and Holcomb [1966a, b] for exceptions). Ricklefs (1966), however, suggested that the development of certain behaviors may provide important information on the physiological state of nestlings and that the expression of different behaviors may reflect the passing of certain critical points in development. By comparing the onset and frequency of certain behaviors that probably reflect a nestling's developmental stage, I have attempted to test the hypothesis that, among sexually dimorphic nestlings, the smaller sex develops more quickly than the larger. Although these results provide limited evidence in support of this hypothesis, further studies, especially with respect to the development of locomotory skills, should further clarify this issue.

ACKNOWLEDGMENTS

I thank Sue McRae, Naomi Langmore, Nick Davies, Mark Forbes, and Patrick Weatherhead for suggestions on improving the manuscript. Videotaping equipment was generously loaned to me by Pat Weatherhead. During this study I was supported by a Natural Sciences and Research Council of Canada post-doctoral fellowship.

LITERATURE CITED

ANDREW, R. J. 1956. Normal and irrelevant toilet behavior in *Emberiza* spp. Brit. J. Anim. Behav. 4:85–91.

BANCROFT, G. T. 1984. Growth and sexual dimorphism of the Boat-tailed Grackle. Condor 86:423–432.

BEEBE, F. L. 1960. The marine Peregrines of the northwest Pacific coast. Condor 62:145–189.

DELANNOY, C. A. AND A. CRUZ. 1988. Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). Auk 105:649–662.

FIALA, K. L. AND J. D. CONGDON. 1983. Energetic consequences of sexual size dimorphism in nestling Red-winged Blackbirds. Ecology 64:642–647.

FICKEN, M. S. 1962. Maintenance activities of the American Redstart. Wilson Bull. 74: 153–165.

HOLCOMB, L. C. 1966a. Red-winged Blackbird nestling development. Wilson Bull. 78: 283–288.

———. 1966b. The development of grasping and balancing coordination in nestlings of seven species of altricial birds. Wilson Bull. 78:57–63.

——— AND G. TWIEST. 1970. Growth rates and sex ratios of Red-winged Blackbird nestlings. Wilson Bull. 82:294–303.

MOSS, D. 1979. Growth of nestling sparrowhawks (*Accipiter nisus*). J. Zool. (Lond.) 187: 297–314.

NEWTON, I. 1978. Feeding and development of Sparrowhawk (*Accipiter nisus*) nestlings. J. Zool. (Lond.) 184:465–487.

NICE, M. 1943. Studies in the life history of the Song Sparrow II. Trans. Linn. Soc. (N.Y.) 6:1–328.

OLSEN, P. D., J. OLSEN, AND N. J. MOONEY. 1982. Growth and development of nestling Brown Goshawks, *Accipiter fasciatus,* with details of breeding biology. Emu 82:189–194.

RICHTER, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. Am. Nat. 121:158–171.

RICKLEFS, R. E. 1966. Behavior of young Cactus Wrens and Curve-billed Thrashers. Wilson Bull. 78:47–56.

TEATHER, K. L. 1992. An experimental study of competition between male and female nestlings of the Red-winged Blackbird. Behav. Ecol. Sociobiol. 31:81–87.

——— AND P. J. WEATHERHEAD. 1988. Sex-specific energy requirements of Great-tailed Grackle (*Quiscalus mexicanus*) nestlings. J. Anim. Ecol. 57:659–668.