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DIFFERENTIAL GROWTH PATTERNS OF NESTLING BROWN-HEADED COWBIRDS AND YELLOW-HEADED BLACKBIRDS

CATHERINE P. ORTEGA[1] AND ALEXANDER CRUZ

Environmental, Population and Organismic Biology Department, University of Colorado, Boulder, Colorado 80309, USA

ABSTRACT.—As nestlings, male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) are significantly larger than female Yellow-headed Blackbirds in several measurements, and both male and female Yellow-headed Blackbirds are significantly larger than Brown-headed Cowbirds (*Molothrus ater*). We investigated the mechanisms by which female Yellow-headed Blackbirds are able to survive in nests with their larger siblings and how cowbirds are able to survive in the nests of hosts much larger than themselves. Growth was monitored of nestling Yellow-headed Blackbirds and Brown-headed Cowbirds, which were experimentally cross-fostered into Yellow-headed Blackbird nests, in Boulder County, Colorado during the 1986 breeding season. Measurements were recorded for weight, tarsometatarsus length, culmen length, gape width (width of bill at loral feathering), and length of ninth (outermost) primary. Nestling weight, tarsometatarsus length, and culmen length were larger in male than female Yellow-headed Blackbirds, and larger in both male and female Yellow-headed Blackbirds than cowbirds. Gape width differed significantly between male and female Yellow-headed Blackbirds throughout much of the nestling period; gape width in both were significantly wider than that of cowbirds. However, cowbirds had a significantly larger gape relative to their weight than did male Yellow-headed Blackbirds, and female Yellow-headed Blackbirds had a significantly larger gape relative to their weight than did males of the species. The relatively larger gape may enable females to compete with larger male siblings and enable cowbirds to compete with foster siblings much larger than themselves. Additionally, feather development was faster in female Yellow-headed Blackbirds than in males and was even more accelerated in cowbird nestlings. We used museum specimens of adults to calculate proportions of adult weight attained by nestlings. Cowbirds attained a greater proportion of their adult weight and adult ninth-primary length by fledging age than did Yellow-headed Blackbirds, and female Yellow-headed Blackbirds attained a greater proportion of their adult weight and adult ninth-primary length by fledging age than did their male siblings. *Received 29 October 1990, accepted 10 January 1992.*

GROWTH rates vary greatly among animals and, although few grow at the highest potential rate (Needham 1964), they may grow at the maximum potential rate (Ricklefs 1969). Sibling competition may be a major component in the selection for rapid growth (Werschkul and Jackson 1979) and, in some species, may result in brood reduction (Bortolotti 1986). Brood reduction may occur through siblicide (Mock 1984) or asynchronous hatching (Lack 1954, Richter 1982, Mead and Morton 1985). Among sexually dimorphic, altricial birds that also hatch asynchronously, one might expect a high degree of sibling competition resulting in a biased sex ratio. While some investigators of sexually dimorphic birds have found skewed sex ratios of nestlings or fledglings (Howe 1977, Slagsvold et al. 1986, Teather and Weatherhead 1989), others have reported that sex ratios were not significantly skewed (Selander 1960, Fiala 1981, Bancroft 1983, Weatherhead 1983). Interestingly, in all the above-listed studies with skewed sex ratios, the sex ratios were female-biased. Explanations for female-biased sex ratios include: depending on hatching sequence, males suffer higher mortality during food shortages (Slagsvold et al. 1986, Teather and Weatherhead 1989); and males are more costly to raise (Howe 1977, Slagsvold et al. 1986). None of the above-listed studies, however, have shown how females may compete with their larger male siblings for food.

Richter (1983) reported no significant bias in sex ratios for Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), a sexually dimorphic, asynchronously hatching species. He demonstrated a significant difference between nestling growth rates of males and females, but suggested that there may be little disparity in

[1] Present address: Department of Biology, Fort Lewis College, Durango, Colorado 81301, USA.

energetic requirements between the sexes. Differences also have been noted in nestling growth rates between the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) and smaller hosts (Marvil and Cruz 1989). Generally, cowbird nestlings are larger than their host siblings, often becoming sole occupants of their host nests, because they gain an advantage over their host siblings in competing for food through vigorous begging vocalizations and more rapid growth (Payne 1977). Additionally, the shorter incubation period of cowbird eggs usually results in the cowbird hatching first. When hosts are smaller than cowbirds, particularly when the cowbird hatches first, the host nestlings rarely survive (Mayfield 1977, Marvil and Cruz 1989); yet, when cowbirds are smaller than the host or not very much larger, both parasite and host nestlings are able to fledge (Smith 1981, Ortega and Cruz 1988, 1991, Weatherhead 1989). By cross-fostering cowbird eggs from Red-winged Blackbird (*Agelaius phoeniceus*) nests to Yellow-headed Blackbird nests, Ortega and Cruz (1991) showed that cowbirds could fledge from nests of Yellow-headed Blackbirds, which are not naturally parasitized by cowbirds.

The purpose of this study was to investigate mechanisms by which female Yellow-headed Blackbirds survive in nests with their larger male siblings and how cowbirds are able to survive and fledge from nests of hosts much larger than themselves. We show that cowbirds, as nestlings, have features that may be specifically adapted for a brood-parasitic mode of life, allowing them to effectively compete with larger hosts. We further show that the same features probably enable female Yellow-headed Blackbirds to compete with their larger brothers.

Study Areas and Methods

Yellow-headed Blackbird nests were investigated in three cattail (*Typha latifolia* and *T. angustifolia*) marshes in eastern Boulder County, Colorado during 1986. One marsh (at Walden Ponds) was a reclaimed gravel pit (surface area 9.3 ha) and was encompassed by patches of cottonwoods (*Populus sargentii*) and willows (*Salix* spp.), as well as weedy fields. Approximately 100 Yellow-headed Blackbirds and 30 Red-winged Blackbirds nested in this marsh. Two other marshes (approximately 4.0 and 1.6 ha), with a small road in between, supported at least 800 nesting Yellow-headed Blackbirds and 50 nesting Red-winged Blackbirds. These two marshes were surrounded by weedy fields and agricultural land.

Yellow-headed and Red-winged blackbird nests were found and identified with individually numbered tags. We visited each nest every one to three days, at which time nest contents were recorded. Yellow-headed Blackbird and cowbird nestlings were weighed and measured during each visit and were individually marked by color coding their tarsi with a permanent felt-tip pen. We selected (more or less at random) nonparasitized nests from which to measure birds, but all nestlings in selected nests were measured. Most parasitized nests were included for nestling measurements.

Experimental parasitism.—We cross-fostered 23 cowbird eggs from Red-winged Blackbird nests to 23 Yellow-headed Blackbird nests during the egg-laying stage and early incubation. Only one cowbird egg was added to each Yellow-headed Blackbird nest, and eggs transferred between nests were, to the best of our knowledge, the same age (i.e. within a day or two). The growth rate of Yellow-headed Blackbirds was similar in nonparasitized and experimentally parasitized nests (Ortega 1991); therefore, we pooled measurements for nestling Yellow-headed Blackbirds in parasitized and nonparasitized nests.

Measuring nestlings and adults.—Nestlings were weighed to the nearest 0.1 g with 10-g, 50-g, and 100-g Pesola spring scales, using the smallest scale possible. We measured to the nearest 0.01 mm tarsus length, culmen length, width of bill at loral feathering (from here on referred to as gape width), and length of ninth (outermost) primary according to Baldwin et al. (1931) with a Mitutoyo metal dial caliper. In addition, we measured museum specimens of 20 adult male and 18 adult female Yellow-headed Blackbirds, and 14 adult male and 16 adult female cowbirds (*M. ater artemisiae*, the subspecies most commonly found in Colorado) for tarsus length, culmen length, bill width, and wing chord; weight from specimen labels was noted.

Sexing nestlings.—Yellow-headed Blackbird nestlings were sexed on the basis of plumage, weight, and measurements. By the time of fledging, differences in plumage between males and females became apparent. Females showed darker backs with buff-colored wing bars, whereas males acquired lighter, tawny backs with white wing bars. The difference in plumage corresponded with two distinct weight classes that Richter (1983), through independent discriminant analysis, used to distinguish sexes of Yellow-headed Blackbird. Individuals that could not be confidently sexed (i.e. those that were lost to follow-up before reaching the age of approximately 10 days) were not used in the statistical analyses.

Although wide ranges in cowbird weights and measurements were recorded, we could not assign gender with confidence, since both the *artemisiae* subspecies and the smaller *M. ater obscurus* are found in Colorado (Ortega and Cruz, unpubl. manuscript). Measurements of female *artemisiae* nestlings may

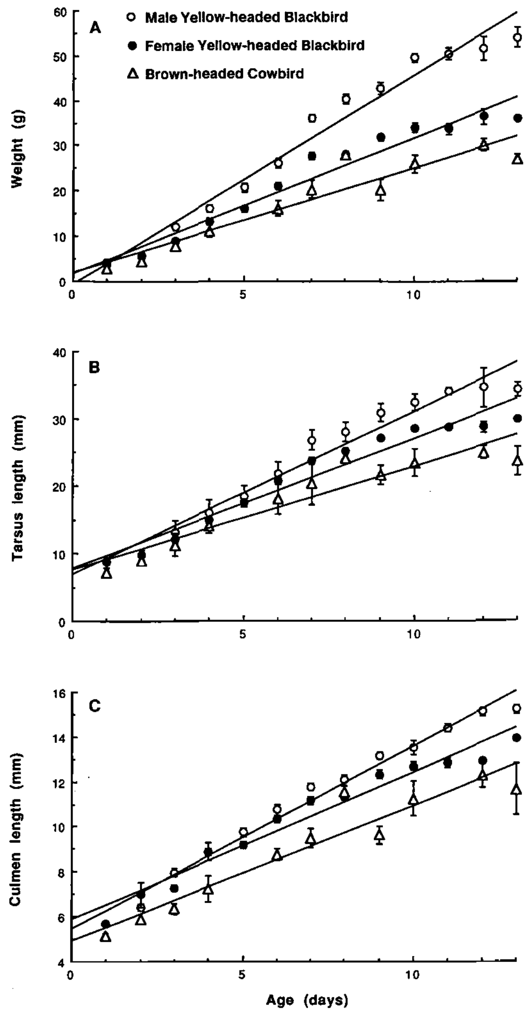

Fig. 1. Changes with age for nestling male and female Yellow-headed Blackbirds, and Brown-headed Cowbirds of: (A) weight (g), with r^2 of 0.9391, 0.9225, and 0.8501, respectively; (B) tarsus length (mm), with r^2 of 0.9487, 0.9437, and 0.8778; and (C) culmen length (mm), with r^2 of 0.9426, 0.9057, and 0.8640.

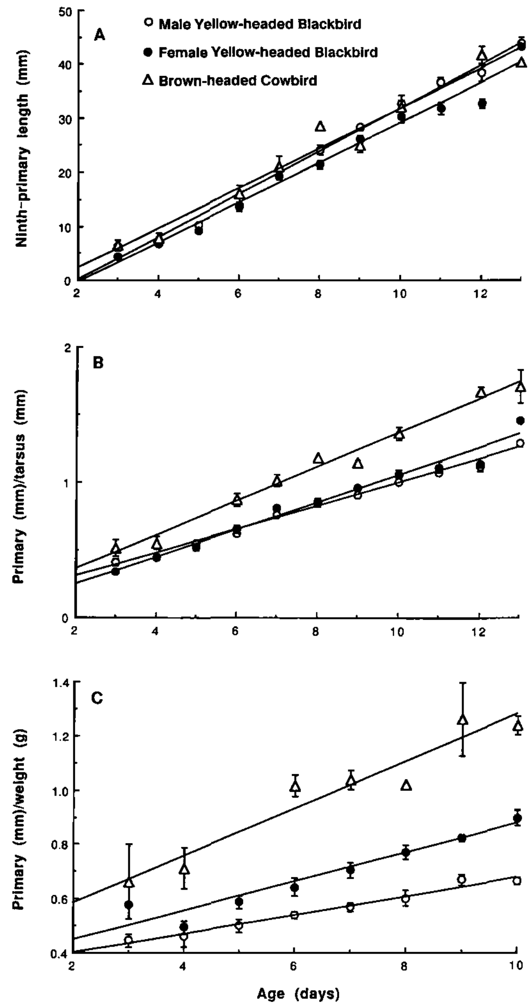

Fig. 2. Changes with age for nestling male and female Yellow-headed Blackbirds, and Brown-headed Cowbirds of: (A) ninth-primary length (mm), with r^2 of 0.9577, 0.9258, and 0.9359, respectively; (B) ratio of ninth-primary length (mm) to tarsus length (mm), with r^2 of 0.9186, 0.9169, and 0.9398; and (C) ratio of ninth-primary length (mm) to weight (g), with r^2 of 0.7849, 0.8524, and 0.8452.

overlap with those of male *obscurus* nestlings. Most *obscurus* nestlings have bright yellow rictal flanges as compared with white of *artemisiae* (Rothstein 1978); however, this may not serve as a dependable character for intermediate forms (S. I. Rothstein, pers. comm.). However, Weatherhead (1989) reported no significant differences between male and female cowbirds by the age of fledging.

Statistical analyses.—The Kolmogorov-Smirnoff test was used to assess normality of all growth measurements (Sokal and Rohlf 1981). All growth data were normally distributed. We used linear regression to test for the significance of growth slopes before using the Student's *t*-test to look for differences between growth slopes (Zar 1984). Nestlings whose primaries had not yet erupted were excluded from all analyses involving primary length. Although linear-regression analyses showed slopes of gape width for all nestlings to be statistically significant, the growth trajectories appeared asymptotic; therefore, for analyses of gape width and weight-to-gape-width ratios, we tested between means on each day of the nesting

TABLE 1. Linear regression equations[a] ($Y = a + bX$) of male and female Yellow-headed Blackbirds, and Brown-headed Cowbirds raised in Yellow-headed Blackbird nests (1-13 days old), Boulder County, Colorado, 1986. Regression equations based on measurements of 36 male and 42 female Yellow-headed Blackbirds, and 11 Brown-headed Cowbirds.

Dependent variable (Y)	Yellow-headed Blackbird: Male	Yellow-headed Blackbird: Female	Brown-headed Cowbird
Weight (g)	$Y = -1.549 + 4.831X$	$Y = -0.045 + 3.403X$	$Y = 1.275 + 2.400X$
Tarsus length (mm)	$Y = 6.153 + 2.601X$	$Y = 6.382 + 2.223X$	$Y = 6.864 + 1.631X$
Culmen length (mm)	$Y = 5.247 + 0.856X$	$Y = 5.220 + 0.762X$	$Y = 4.673 + 0.632X$
Ninth-primary length (mm)	$Y = -7.444 + 3.898X$	$Y = -6.806 + 3.556X$	$Y = -5.706 + 3.740X$
Gape width (mm)	$Y = 10.858 + 0.636X$	$Y = 10.173 + 0.590X$	$Y = 9.548 + 0.411X$
Weight-to-gape-width ratio	$Y = 0.105 + 0.271X$	$Y = 0.147 + 0.208X$	$Y = 0.194 + 0.170X$
Primary-to-weight ratio	$Y = 0.020 + 0.074X$	$Y = -0.104 + 0.105X$	$Y = -0.018 + 0.132X$
Primary-to-tarsus ratio	$Y = 0.120 + 0.117X$	$Y = -0.174 + 0.126X$	$Y = -0.139 + 0.153X$

[a] Slopes of all linear regression equations were significant at $P < 0.0001$; X is age in days.

phase using two-sample t-tests (Zar 1984). Two-sample t-tests also were used to detect differences in mean measurements between adults. Standard-error bars (± 1 SE) are presented in figures of growth, and standard deviations (SD) are provided for all other mean values. A 0.05 probability level was used for statistical significance.

RESULTS

We measured 178 Yellow-headed Blackbird nestlings, and all 11 cowbird nestlings that hatched from the 23 cowbird eggs added. We did not have data for 95 Yellow-headed Blackbirds in follow-up analyses because of predation, starvation, abandonment, or our inability to sex nestlings. We eliminated five additional Yellow-headed Blackbirds from the analyses because either nestling development was abnormal or nestling deformities were present. Therefore, our analysis of nestlings is based on 11 cowbirds, 36 male Yellow-headed Blackbirds, and 42 female Yellow-headed Blackbirds.

Nestling growth.—Slopes of all linear regression equations were significant ($P < 0.0001$; Table 1). During the nestling phase, male Yellow-headed Blackbirds grew at significantly faster rates than female siblings with respect to weight, tarsus length, culmen length, and ninth-primary length (Table 2, Figs. 1 and 2A). Male and female Yellow-headed Blackbirds both grew at significantly faster rates than cowbirds with regards to weight, tarsus length, and culmen length (Table 2, Fig. 1). The growth rate of the ninth primary was significantly higher in male than female Yellow-headed Blackbirds; however, no significant differences were found in

TABLE 2. Statistical differences in growth slopes between: male and female Yellow-headed Blackbirds; male Yellow-headed Blackbirds and Brown-headed Cowbirds; and female Yellow-headed Blackbirds and Brown-headed Cowbirds. Data from Boulder County, Colorado, 1986.[a]

	Male and female Yellow-headed Blackbird			Male Yellow-headed Blackbird and Brown-headed Cowbird			Female Yellow-headed Blackbird and Brown-headed Cowbird		
Variable	t	P	Total df	t	P	Total df	t	P	Total df
Weight (g)	11.63	***	329	13.61	***	208	6.81	***	223
Tarsus length (mm)	5.97	***	329	10.47	***	208	7.10	***	223
Culmen length (mm)	3.23	***	329	6.55	***	208	3.56	***	223
Ninth-primary length (mm)	2.06	*	227	1.28	ns	147	0.15	ns	150
Primary-to-weight ratio	5.12	***	227	6.66	***	147	2.21	*	150
Primary-to-tarsus ratio	2.60	**	227	6.52	***	147	3.64	***	150

*, $P < 0.05$; **, $P < 0.02$; ***, $P < 0.001$; ns, $P > 0.05$. Student's two-tailed t-test.

[a] For weight, tarsus length, and culmen length, df = 157 for male Yellow-headed Blackbirds, 172 for female Yellow-headed Blackbirds, and 51 for Brown-headed Cowbirds. For ninth-primary length, primary-to-weight ratio, and primary-to-tarsus ratio, df = 112 for male Yellow-headed Blackbirds, 115 for female Yellow-headed Blackbirds, and 35 for Brown-headed Cowbirds.

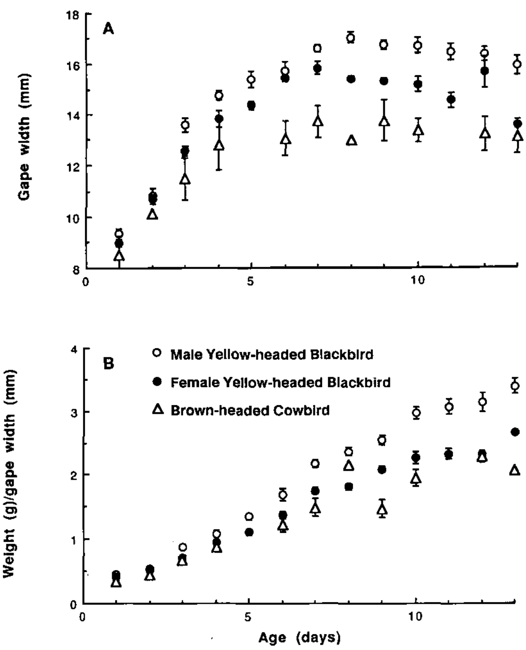

Fig. 3. Changes with age for nestling male and female Yellow-headed Blackbirds, and Brown-headed Cowbirds of: (A) gape width (mm); and (B) ratio of weight (g) to gape width (mm).

the growth rates of the ninth primary between cowbirds and male Yellow-headed Blackbirds, or between cowbirds and female Yellow-headed Blackbirds (Table 2, Fig. 2A).

Significant differences in weight between male and female Yellow-headed Blackbirds, and between male Yellow-headed Blackbirds and cowbirds became apparent by the third day of age (Table 3). Due to the small sample size on day 13, however, the differences between male and female Yellow-headed Blackbirds were not statistically significant. By day 5, differences in weight between female Yellow-headed Blackbirds and cowbirds were statistically significant, but again, due to the small sample size, differences were not significant on day 13 (Table 3). Additionally, male Yellow-headed Blackbirds, for the most part, had significantly wider gape widths than female Yellow-headed Blackbirds and cowbirds (Fig. 3A, Table 3). Both male and female Yellow-headed Blackbirds had significantly wider gape widths than cowbirds by day 3 for males and by day 6 for females (Fig. 3A, Table 3).

Although male Yellow-headed Blackbirds had the largest weight and gape width, they had the smallest gape width relative to their weight, and cowbirds had the largest gape width relative to their weight (Fig. 3B, Table 3). During most of the nestling phase, male Yellow-headed Blackbirds had significantly larger weight-to-gape-width ratios than female Yellow-headed Blackbirds or cowbirds (Fig. 3B, Table 3). Female Yellow-headed Blackbirds tended to have a larger weight-to-gape-width ratio than did cowbirds, but the differences were statistically significant in only 3 of the 11 days that could be tested (Table 3).

Nestling feather development was most rapid in cowbirds and more rapid in female than in male Yellow-headed Blackbirds. The slopes of primary-to-tarsus ratio and primary-to-weight ratio were significantly steeper in cowbirds than male Yellow-headed Blackbirds (Table 2, Figs. 2B and 2C). The same pattern existed between females and cowbirds, and female Yellow-headed Blackbirds had a significantly larger primary-to-tarsus ratio and primary-to-weight ratio than males (Table 2, Figs. 2B and 2C). By the time of fledging, male Yellow-headed Blackbirds attained 55.2% of adult weight, whereas female Yellow-headed Blackbirds were 64.6% of adult weight.

Adults.—Adult male Yellow-headed Blackbirds were significantly larger than adult females in every character measured (Table 4). All Yellow-headed Blackbirds (males and females) also were significantly larger than all cowbirds (males and females) in every character measured except bill width. Female Yellow-headed Blackbirds had the smallest bill widths. With the exception of bill width between female Yellow-headed Blackbirds and cowbirds, male Yellow-headed Blackbirds were significantly larger than male cowbirds, and female Yellow-headed Blackbirds were larger than female cowbirds in every character.

All adults showed a similar primary-to-tarsus ratio, but a larger weight-to-bill width ratio in males relative to females is a characteristic Yellow-headed Blackbirds retained into adulthood. Adult male cowbirds also have a larger weight-to-bill-width ratio than adult female cowbirds (Table 4).

Discussion

Male Yellow-headed Blackbirds were 33% heavier than female Yellow-headed Blackbirds and 45% heavier than cowbirds by fledging age,

TABLE 3. Statistical differences[a] of weight (g), gape width (mm), and weight (g)/gape (mm) between: male and female Yellow-headed Blackbirds; male Yellow-headed Blackbirds and Brown-headed Cowbirds; and female Yellow-headed Blackbirds and Brown-headed Cowbirds. Data from Boulder County, Colorado, 1986.

Age (days)	Male and female Yellow-headed Blackbird			Male Yellow-headed Blackbird and Brown-headed Cowbird			Female Yellow-headed Blackbird and Brown-headed Cowbird		
	P	*t*	df	*P*	*t*	df	*P*	*t*	df
				Weight (g)					
1	0.0021	3.27	42	0.0001	5.66	29	0.0026	3.26	33
2	0.3141	1.03	25	0.2497	1.22	10	0.2913	1.09	15
3	0.0004	3.95	30	0.0020	3.51	22	0.2290	1.24	20
4	0.0228	2.43	25	0.0182	2.65	15	0.3394	0.99	14
5	0.0006	3.91	25	—[b]			—[b]		
6	0.0021	3.46	24	0.0001	5.24	22	0.0100	2.88	18
7	0.0001	6.58	30	0.0001	8.28	22	0.0011	3.86	18
8	0.0001	8.77	25	0.0046	3.89	8	—[c]		
9	0.0001	7.53	34	0.0001	6.81	19	0.0001	6.26	19
10	0.0001	10.66	22	0.0001	12.97	13	0.0018	3.69	17
11	0.0001	9.68	16	—[b]			—[b]		
12	0.0250	2.84	7	0.0001	6.25	10	0.0497	2.58	5
13	0.0600	3.90	2	0.0031	8.79	3	0.1210	5.20	1
				Gape width (mm)					
1	0.1725	1.39	42	0.0154	2.58	29	0.0799	1.81	33
2	0.6069	0.52	25	0.4455	0.79	10	0.4677	0.74	15
3	0.0061	2.95	30	0.0002	4.42	22	0.0057	3.09	20
4	0.0168	2.56	25	0.0011	4.01	15	0.1855	1.39	14
5	0.0043	3.14	25	—[b]			—[b]		
6	0.5362	0.63	24	0.0001	5.23	22	0.0001	9.89	18
7	0.0079	2.85	30	0.0001	10.24	22	0.0001	4.90	18
8	0.0001	7.95	25	0.0002	6.67	8	0.0001	5.13	17
9	0.0001	7.34	34	0.0001	6.82	19	0.0001	5.19	19
10	0.0030	3.34	22	0.0001	7.32	13	0.0044	3.28	17
11	0.0006	4.27	16	—[b]			—[b]		
12	0.0286	1.16	7	0.0001	7.49	10	0.0097	4.07	5
13	0.0804	3.31	2	0.0169	4.83	3	0.6783	0.55	1
				Weight-to-gape-width ratio					
1	0.0048	2.98	42	0.0001	5.43	29	0.0029	3.22	33
2	0.2614	1.15	25	0.1612	1.51	10	0.2879	1.10	15
3	0.0004	3.98	30	0.0084	2.89	22	0.6096	0.52	20
4	0.0434	2.13	25	0.0645	2.00	15	0.4828	0.72	14
5	0.0045	3.12	25	—[b]			—[b]		
6	0.0173	2.56	24	0.0074	2.95	22	0.2291	1.24	18
7	0.0001	5.64	30	0.0001	5.66	22	0.0382	2.24	18
8	0.0001	6.53	25	0.2682	1.19	8	0.1555	1.49	17
9	0.0001	5.38	34	0.0001	5.61	19	0.0001	4.85	19
10	0.0001	5.28	22	0.0001	6.73	13	0.1031	1.73	17
11	0.0001	5.39	16	—[b]			—[b]		
12	0.0224	2.92	7	0.0010	4.60	10	0.8267	0.23	5
13	0.0936	3.03	2	0.0034	8.48	3	0.0014	4.52	1

[a] Two-sample *t*-tests, two-tailed.
[b] No cowbird measurements.
[c] One cowbird and one female blackbird had same weight (i.e. 28 g).

yet females and cowbirds were able to survive and grow well in nests with larger males. Cowbird nestlings grow as rapidly in the nests of Yellow-headed Blackbirds as they do in the nests of Red-winged Blackbirds (Ortega 1991). How smaller females and cowbirds are able to compete with larger male Yellow-headed Blackbirds, particularly when faced with the possibility of hatching a day or two later, is an intriguing question. Female Yellow-headed Blackbirds develop more rapidly than males (i.e. they attain a larger percentage of adult size by fledging; Richter 1983; pers. observ.), and similar accelerated growth patterns probably en-

TABLE 4. Mean (±SD) for measurements of adult Yellow-headed Blackbirds and Brown-headed Cowbirds (subspecies *M. ater artemisiae*). All statistical comparisons[a] made using two-sample *t*-tests, two-tailed.

	Yellow-headed Blackbird		Brown-headed Cowbird	
Variable	Male (n = 20)	Female (n = 18)	Male (n = 14)	Female (n = 16)
Weight (g)	97.74 (±8.48)	55.87 (±5.16)	53.62 (±5.34)	41.26 (±2.68)
Wing chord (mm)	140.89 (±3.42)	114.08 (±3.24)	109.93 (±3.32)	99.57 (±2.70)
Tarsus length (mm)	33.29 (±1.66)	28.26 (±1.44)	25.37 (±2.29)	23.86 (±0.82)
Culmen length (mm)	23.15 (±1.64)	18.95 (±0.82)	16.84 (±1.69)	16.05 (±0.63)
Bill width (mm)	10.03 (±0.38)	8.48 (±0.27)	9.17 (±0.51)	8.56 (±0.29)
Weight-to-bill-width ratio	9.75 (±0.78)	6.60 (±0.64)	5.85 (±0.52)	4.82 (±0.29)
Wing-chord-to-tarsus-length ratio	4.24 (±0.24)	4.05 (±0.21)	4.38 (±0.63)	4.18 (±0.13)
Wing-chord-to-weight ratio	1.45 (±0.13)	2.06 (±0.18)	2.07 (±0.18)	2.42 (±0.14)

[a] For all comparisons between male and female Yellow-headed Blackbirds, $P \leq 0.011$. For all comparisons between male and female cowbirds, $P \leq 0.003$ except culmen length and wing-chord-to-tarsus-length ratio. For all comparisons between Yellow-headed Blackbirds (male and female) and cowbirds (male and female), $P \leq 0.013$, except wing-chord-to-tarsus-length ratio. For all comparisons between male Yellow-headed Blackbirds and male cowbirds, $P \leq 0.001$, except wing-chord-to-tarsus-length ratio. For all comparisons between female Yellow-headed Blackbirds and female cowbirds, $P \leq 0.042$, except bill width.

able the cowbird to survive with the larger Yellow-headed Blackbird foster siblings.

Weight gain and feather development.—Among nestlings, with the exception of gape width, the growth slopes of male Yellow-headed Blackbird nestlings were significantly higher than those of female siblings in every character measured. The growth slopes of both male and female Yellow-headed Blackbird nestlings were higher than those of nestling cowbirds in each character measured except the ninth-primary length. However, a higher proportion of adult weight is attained by female than male Yellow-headed Blackbird nestlings. While male Yellow-headed Blackbird nestlings must spend a greater proportion of their energy on general weight gain, female Yellow-headed Blackbird and cowbird nestlings attain a greater proportion of their adult weight earlier and, therefore, can channel more of their energy into earlier feather development (Richter 1983). Earlier feather development also may enable female Yellow-headed Blackbirds to fledge earlier in some cases (Richter 1983). Faster growth and earlier feather development of the smaller sex has been observed in other sexually dimorphic species, whether the male or the female is larger (Holcomb and Twiest 1971, Bortolotti 1984, Richter 1983, 1984, Delannoy and Cruz 1988).

Richter (1983) suggested that, because of accelerated feather development, female Yellow-headed Blackbirds are likely to begin energetically-expensive thermoregulation earlier than male Yellow-headed Blackbirds. This may require more energy expenditure by the parents in more food deliveries to female nestlings than would be expected if there were no disparity in feather development. Other studies have shown no association between feather development and the onset of homeothermy (see O'Connor 1984), and have shown an association between temperature and weight (Gottie and Kroll 1973). Once homeothermy begins, however, the feathers appear to function mainly in reducing energetic demands (Shilov 1973). Accelerated feather development in cowbirds and female Yellow-headed Blackbirds also suggests that they may indirectly assist their foster siblings and brothers, respectively, with thermoregulation. This phenomenon has been observed in House Wrens (*Troglodytes aedon*; Freed 1981).

Gape width.—Little emphasis has been placed on gape width in studies of asynchronously hatching, sexually-dimorphic birds, yet gape width may be paramount in competition between sexually dimorphic siblings. The mouth is one of the first structures used by nestlings (O'Connor 1984), and gape dimensions influence parental feeding (Quinn 1990). Gaping nestlings elicit feeding responses from their parents (Welty 1982, O'Connor 1984), and the largest nestlings with the largest gape widths may receive the most food. The most important growth characteristic that may enable female Yellow-headed Blackbird nestlings to compete with their male siblings, and cowbird nestlings to compete with larger host siblings is a larger gape width relative to their weight. The larger gape width of female Yellow-headed Blackbirds and cowbirds may allow them to receive more food deliveries than would be expected if their weight-to-gape-width ratios were the same as larger males.

Growth strategy or happenstance?—Accelerated growth of a nestling character may be considered a "growth strategy" if the particular character is not exaggerated in size in adults. However, an accelerated-growth character that is exaggerated in adults may not indicate that the growth of that character was not adapted for nestling existence; other adaptations, such as those associated with aerodynamic requirements and adult foraging needs, also influence adult morphology.

Because the primary-to-tarsus ratios of adult male and female Yellow-headed Blackbirds, and adult male and female cowbirds are similar, the accelerated development of cowbirds and female Yellow-headed Blackbirds, as nestlings, is likely an adaptation for nestling life. Even though the weight-to-bill-width ratio is smaller in adult cowbirds and adult female Yellow-headed Blackbirds than in adult male Yellow-headed Blackbirds, the smaller weight-to-gape-width ratio of nestling cowbirds and nestling female Yellow-headed Blackbirds still may be specifically adapted for nestling life with larger male Yellow-headed Blackbird nestlings. Bill width and gape width, even though they are both measured as the width of bill at loral feathering (Baldwin et al. 1931), are quite different from other measurements in that the width actually decreases with maturity into adulthood. As nestlings age, the width decreases as the fleshy rictal flanges harden. We suggest that the larger gape (relative to weight) of cowbirds and female Yellow-headed Blackbirds, indeed, are an adaptation for nestling existence with larger nest mates.

Although female Yellow-headed Blackbird nestlings are smaller than male siblings, and cowbird nestlings are smaller than both male and female Yellow-headed Blackbird nestlings, by fledging age the cowbirds and female Yellow-headed Blackbirds achieve earlier feather maturation and attain a higher proportion of their adult weight than male Yellow-headed Blackbirds. As indicated, the data from our study demonstrate that cowbird nestlings and female Yellow-headed Blackbird nestlings have larger gape widths relative to their body size than male Yellow-headed Blackbird nestlings; this differential may enable cowbirds and female Yellow-headed Blackbirds to compete effectively with the larger male Yellow-headed Blackbird nestlings and result in sex ratios being female-biased.

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