DEVELOPMENT OF YOUNG BREWER'S BLACKBIRDS

Martha Hatch Balph

Brewer's Blackbirds (*Euphagus cyanocephalus*) are common in much of the western U.S. Several workers have studied aspects of the breeding behavior of this species (LaRivers 1944; Howell and Bartholomew 1952; Williams 1952; Horn 1968, 1970). However, there appears to be little published information on the development of young Brewer's Blackbirds. The objective of this paper is to present some findings on this topic, and where possible to compare Brewer's Blackbird development with that of other passerines, particularly members of the family Icteridae.

METHODS

I observed free-living, young Brewer's Blackbirds in Logan, Utah, during late May and June, 1973 and collected data from 41 nestlings aged 0–13 days at 10 nests. Of these birds, 37 were of known age, and four were of estimated age. The nests were in urban situations, varying from hedgerows bordering lawns to brushy roadside vegetation.

I removed the birds from their nests for about 10–20 min to examine them. I weighed them to the nearest 0.1 g on a triple-beam balance and measured linear growth parameters with calipers to the nearest 0.5 mm; these parameters included the wing, first primary, central rectrix, culmen, commissure, tarsus, and hallux. Notations of plumage development and of the condition and coloration of soft parts were made without the use of a color chart. I also documented behavior at my approach to young in the nest or young away from their nests. I recorded the birds' ages as "day 0" during the first 24 hours after hatching, as "day 1" from 24–48 hours, and so forth. Nestlings were individually marked on the tarsi or feet with a felt-tipped marker or with fingernail polish until they were about 1 week old, when they were banded.

Data were collected between 07:00 and 18:30, 35% in the morning and 65% in the afternoon. I visited individual nests at approximately the same time each day, but was unable to collect data at all active nests on all days. Nest losses, due apparently to predation and flooding, and fledging of young after the age of 9 days caused progressive reductions in sample size. On five occasions, I captured and collected data from banded young 1–2 days after they fledged.

For purposes of comparison, I measured 10 adult Brewer's Blackbirds (five males, five females) captured in Logan in June, 1974.

I obtained supplementary data on behavioral ontogeny from an earlier study of captive young. On 18 June 1967, I collected four Brewer's Blackbird nestlings at the approximate age of 5 days in Laramie, Wyoming. These were hand fed a mixture of hydrated Gerber's high protein pablum, strained beef, ground egg with eggshell, honeybee larvae, small flying insects, and earthworms. When the birds began to feed themselves, I added canned dog food, millet seed, mealworms, and grit to their diet. Water was provided beginning at 15 days.

I kept the birds in their original nest until they fledged. After they fledged, I maintained them in a 56 × 51 × 38 cm cage and released them daily for 1–3 hours into a

TABLE 1

MEASUREMENTS OF ADULT BREWER'S BLACKBIRDS

Measurement	Males (n = 5)		Females (n = 5)		Both Sexes (n = 10)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Weight (g)	69.7	2.91	60.4	6.06	65.1	6.64
Wing Chord (mm)	135.0	4.47	122.2	2.17	128.6	7.52
First Primary (mm)	82.4	3.19	76.5	1.58	79.4	3.91
Central Rectrix (mm)	102.8	3.56	91.4	2.61	97.1	6.69
Exposed Culmen (mm)	21.1	0.55	19.4	1.08	20.2	1.21
Culmen, Nostril to Tip (mm)	14.5	0.87	13.1	0.65	13.8	1.03
Commissure (mm)	12.5	0.61	12.0	0.79	12.2	0.72
Tarsus (mm)	33.3	1.10	32.2	0.98	32.8	1.14
Hallux (mm)	20.7	0.45	20.6	1.02	20.6	0.75

6.1 × 3.7 × 2.4 m room. I monitored behavioral development of four birds (two males, two females) from 5–12 days and three birds (one male, two females) from 13–42 days.

MORPHOLOGICAL DEVELOPMENT

Information on morphological development is from free-living Brewer's Blackbirds. The results are presented and discussed in this section under the broad headings of growth, plumage development, and condition and coloration of soft parts.

Growth.—Ten recently hatched nestlings, weighed while the down was still wet and probably before their first feeding, averaged 3.7 g (SD = 0.32). Of birds in this sample, three were known to be less than 5 min old and likewise averaged 3.7 g (SD = 0.12). The mean weight of newly hatched Brewer's Blackbirds was 6% that of adult females (Table 1), which is in general agreement with findings for other icterids (Holcomb and Twiest 1968).

Nestlings weighed on day 0 after the down was dry averaged 4.4 g (Fig. 1). The birds gained weight rapidly during the first few days of nestling life. Daily weight gains peaked at 5.8 g on day 5, then decreased to less than 3 g during the second half of the nestling period. Percentage daily increases were greatest ($\geqslant$ 48%) up to day 3, then dropped off sharply and were less than 10% from day 8 on. At 10 days, the birds averaged 70% of adult female weight, which agrees with observations for other passerines (Nice 1943).

Individual variability in weight was attributable partly to asynchronous hatching. At seven nests where the hatching times of the first and last eggs were known to be separated by 24–48 hours, first- and last-hatched birds weighed nearly the same on day 0. After day 0, those first hatched

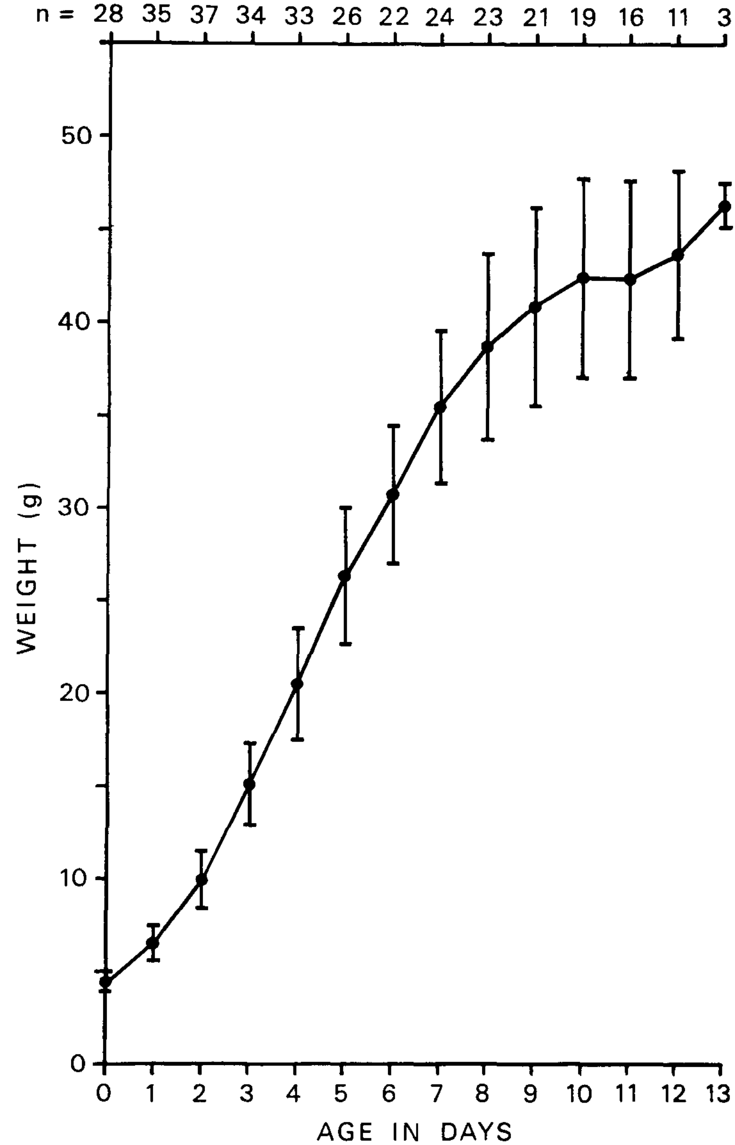

FIG. 1. Relationship between body weight and age in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

weighed more than those last hatched (Fig. 2). The difference was not great, but it was consistent. Presumably, later hatched birds were at a competitive disadvantage during feeding. If food were in short supply, these younger birds might be expected to die. Such brood reduction may be beneficial to

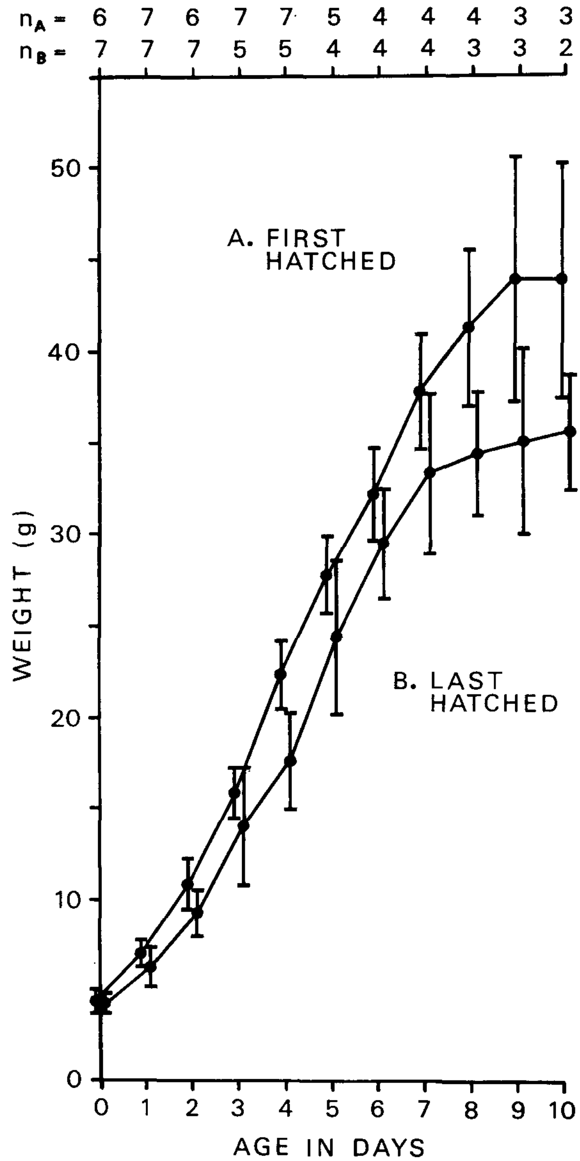

FIG. 2. Relationship between body weight and age in (A) first-hatched and (B) last-hatched Brewer's Blackbirds of asynchronously hatched broods. Dots represent means; brackets indicate mean ± one standard deviation.

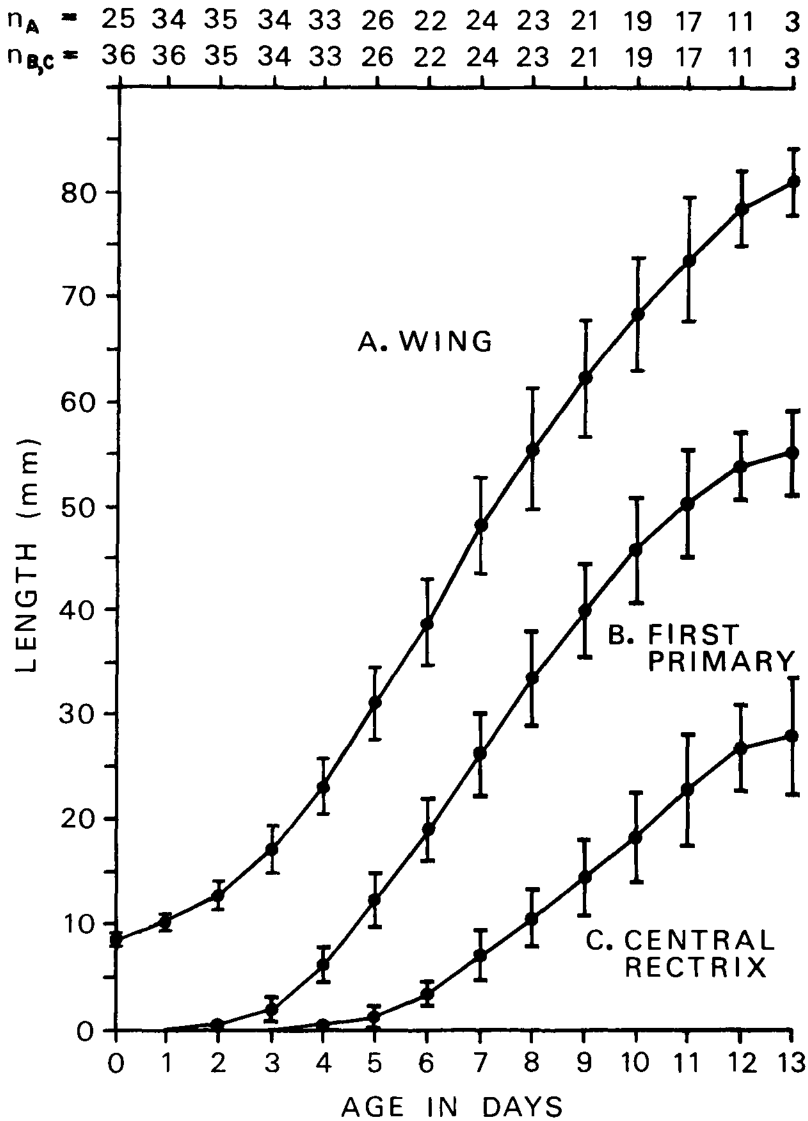

FIG. 3. Relationship between age and (A) wing chord, (B) length of first primary, and (C) length of central rectrix in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

species occupying habitats with unpredictable fluctuations in food availability (Lack 1954, Ricklefs 1965). Some factors besides asynchronous hatching which might have contributed to variation in weight between birds were: (1) sexual dimorphism; (2) differences in brood size, which ranged from 3–6; (3) differences in the spatial distribution of nests affecting the foraging success of adults (Horn 1968); (4) fluctuating weather conditions affecting food availability; (5) differences in the time of day at which birds from different broods were weighed.

The wing, held half open and measured along the chord, followed a sigmoidal growth pattern (Fig. 3). Its daily growth increased during the first half of the nestling period, peaking at 9.2 mm on day 7, then decreased gradually through the second week of nestling life. By day 13, the wing chord was 63% that of adults.

The right innermost primary and rectrix were measured from the point of emergence through the skin to the distal tip. The first primary emerged through the skin on days 2–3 (Fig. 3). Its daily growth was greatest on days 5–9, peaking at 7.4 mm on day 7. The central rectrix emerged 2 days later than the first primary and showed smaller daily increases until very late in nestling life. Then, its daily increment slightly exceeded that of the first primary. By day 13, the first primary had attained 69% of its full growth, whereas the central rectrix was only 28% of adult size.

Three parameters of bill growth were measured: (1) culmen, from the skin of the forehead to the tip of the upper mandible; (2) culmen, from the anterior corner of the nostril to the tip of the upper mandible; (3) commissure, from one commissural point to the other with the bill closed. The exposed culmen increased an average of 0.8 mm daily during the first week of nestling life, lessening to 0.5 mm daily during the second week (Fig. 4). Growth of the culmen from nostril to tip was uniform (about 0.4 mm daily) throughout the nestling period. Daily growth of the commissure exceeded that of the culmen (both measurements) on days 1–4, then dropped below that of the culmen on days 5–7. During the second week, the commissure decreased slightly as the oral flanges became less prominent. These findings are in keeping with those of Holcomb and Twiest (1968) for Red-winged Blackbirds (*Agelaius phoenicius*). Holcomb and Twiest (1968) have pointed out that the development of a large gape early in nestling life provides a good feeding stimulus for the parent, while progress toward a more pointed bill shape later in the nestling period prepares birds for adult foraging.

The tarsus was measured from the point of the joint between the tibia and tarsometatarsus, to the base of the middle toe anteriorly. The hallux was measured dorsally from the point of its articulation with the accessory metatarsal to the tip of the extended claw. Growth of the tarsus and of the hallux (Fig. 5) followed a sigmoidal pattern with the greatest increases on days 3 and 4. Percentage daily increases were greatest (20–29%) during the first 4 days of nestling life and decreased thereafter. The tarsus and the hallux attained 50% of their full growth by days 3–4 and were close to adult size

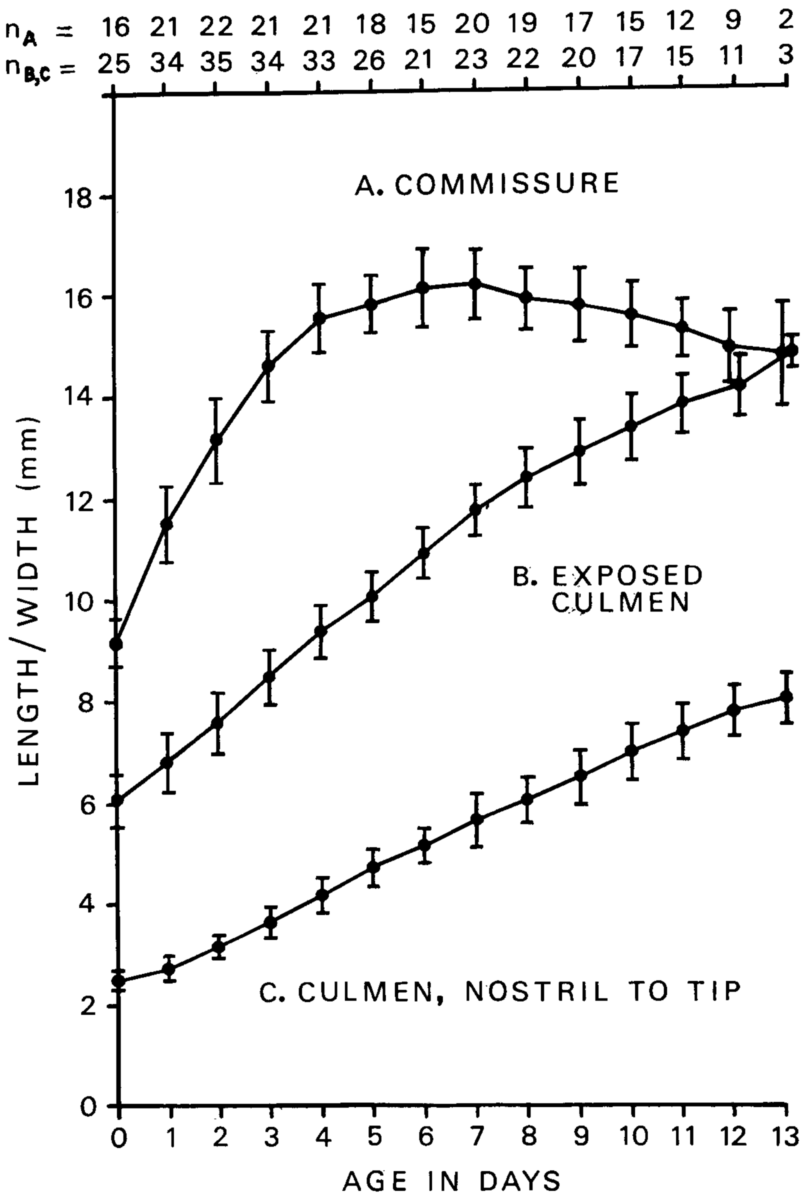

FIG. 4. Relationship between age and (A) width of commissure, (B) length of exposed culmen, and (C) length of culmen, nostril to tip in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

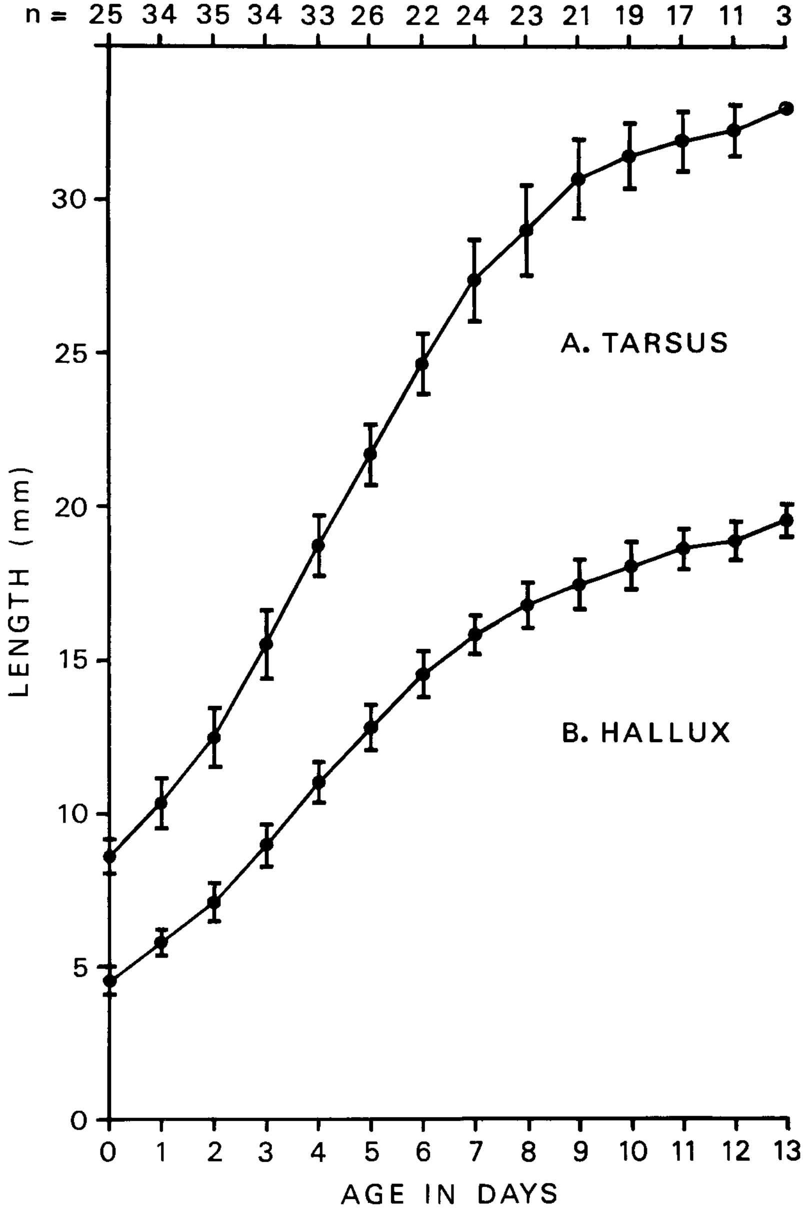

FIG. 5. Relationship between age and length of (A) tarsus and (B) hallux in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

TABLE 2

MAXIMUM LENGTH AND PERCENTAGE OCCURRENCE OF NEOSSOPTILES IN VARIOUS TRACTS OF 23 BREWER'S BLACKBIRDS AGED 0 DAYS

Tract	Region	Maximum Length (mm) $\bar{X}$	Maximum Length (mm) SD	Percentage Occurrence
Capital	Coronal	9.0	1.05	100
Capital	Occipital	8.7	1.15	100
Spinal	Dorsal	10.9	1.35	100
Spinal	Pelvic	7.8	1.41	100
Ventral	Abdominal	1.8	1.33	74
Humeral	—	11.7	1.33	100
Femoral	—	8.8	0.90	100
Crural	—	3.0	0.94	100
Alar	Primaries or Upper Greater Primary Coverts	0.6	0.39	87
Alar	Upper Greater Secondary Coverts	9.7	0.21	100
Alar	Upper Middle Secondary Coverts	9.7	0.21	100
Alar	Alula	0.3	0.41	44
Caudal	Rectrices	2.9	1.36	100

by day 10. Holcomb and Twiest (1968) observed similar, rapid growth of the legs and feet in Red-winged Blackbirds. Development of the legs and feet contributes to a nestling's ability to stretch for food and to grasp and balance (Holcomb and Twiest 1968). In addition, birds reared within the reach of ground predators are under selective pressure to be able to walk from the nest before they can fly (Beason and Franks 1973). Brewer's Blackbirds place their nests in a variety of situations, including on or near the ground where they are subject to heavy predation pressure (LaRivers 1944). Rapid tarsal relative to wing development in this species may have evolved partly in response to this pressure.

Plumage development.—Nestlings were sparsely covered with pale, grayish-white down on day 0. This observation differs from Linsdale (1936), who describes down color in Brewer's Blackbird nestlings in Nevada as "nearly black." Neossoptiles were most abundant in the capital, spinal, humeral, and femoral tracts, and in regions of the future upper greater and middle secondary coverts in the alar tract. Down lengths on day 0, calculated for the longest neossoptile of each tract or region, were greatest in the humeral tract and in the dorsal region of the spinal tract (Table 2). These findings agree generally with those of Wetherbee (1957) for several other icterids.

Neossoptiles were least abundant in, and were sometimes absent from, the abdominal region of the ventral tract and regions of the future primaries, greater primary coverts, and alulae. The presence or absence of natal down in the abdominal region on day 0 tended to be consistent within broods. In four of five broods examined, 75–100% of siblings had neossoptiles in the abdominal region; whereas in the fifth brood, all nestlings lacked down in this region. Saunders (quoted in Wetherbee 1957) observed a similar phenomenon in newly hatched Brewer's Blackbirds. Although I cannot be certain that the lack of abdominal down in some nestlings in the present study was not due to abrasion, the high degree of similarity among siblings suggests that genetic mechanisms may have been responsible for the variation observed.

Down was lost during the nestling period from the extremities and usually from the crural tract and abdominal region, but vestiges remained attached elsewhere through fledging. On day 12, all but one of 10 birds had neossoptiles still attached to the tips of juvenal feathers in the capital, spinal, humeral, and femoral tracts, and to the tips of upper greater and middle secondary coverts.

Development of the juvenal plumage was categorized as follows: (1) dark papillae not yet visible under skin; (2) dark papillae visible but not yet erupted through skin; (3) sheaths emerging through skin (to 1 mm out of skin); (4) sheaths more than 1 mm out of skin but not yet broken; (5) feathers breaking through sheaths; (6) feathers out of sheaths but of lesser length than sheaths; (7) feathers out of sheaths and of greater length than sheaths. If feathers in a particular region were at more than one stage of development, the median stage was recorded. Ten birds were examined in each age group; these represented a total of 28 individuals.

On day 0, papillae of the primaries were marked by dark pigment in all birds (Table 3). Five of 10 birds also showed darkening of papillae of the alulae and secondaries. Papillae in the spinal and ventral tracts were faintly discernible as unpigmented dots. On days 1 and 2, dark papillae became evident in the spinal, ventral, humeral, femoral, and crural tracts; in the caudal tract (rectrices); and in upper regions of the alar tract. Primaries, and in some birds alulae and secondaries, emerged through the skin on day 2. Emergence of secondaries, and usually of primaries (seven of 10 birds), began distally and proceeded proximally.

Days 3–5 marked the emergence of sheaths through the skin in many regions. By day 5, sheaths were prominent in the spinal, ventral, humeral, femoral, and crural tracts; in the alar tract (primaries, alulae, secondaries, and upper coverts); and in the caudal tract (rectrices, developing from outermost to innermost). Dark papillae were evident in remaining regions of the alar and caudal tracts and in the capital tract.

TABLE 3

DEVELOPMENT OF THE JUVENAL PLUMAGE[1] IN BREWER'S BLACKBIRDS FROM 0–12 DAYS (N = 10)

	Age in Days												
Tract/Region	0	1	2	3	4	5	6	7	8	9	10	11	12
Capital													
Frontal	A	Ab	ab	B	B	B	C	Cd	De	dE	E	eF	Fg
Coronal	A	Ab	ab	B	B	Bc	cd	D	De	Ef	Fg	fG	G
Occipital	A	A	aB	B	B	Bc	cd	De	E	F	fG	G	G
Superciliary	A	A	A	Ab	aB	B	Cd	cD	D	De	def	F	Fg
Auricular	A	A	A	A	aB	bC	cd	D	De	dE	E	eF	Fg
Postauricular	A	A	A	Ab	B	B	bC	cD	dE	Ef	F	Fg	G
Interramal	A	A	A	A	ab	B	B	C	cD	De	E	ef	Fg
Malar	A	A	A	A	aB	B	B	Cd	D	De	def	efg	fG
Submalar	A	A	A	Ab	B	B	Bc	cD	D	dEf	eF	fG	G
Spinal													
Cervical	A	B	B	B	bC	Cd	D	dE	ef	F	fg	G	G
Interscapular	A	B	B	Bc	C	D	De	E	F	F	fg	G	G
Dorsal	A	Ab	B	B	bC	D	De	Ef	F	F	fG	G	G
Pelvic	A	Ab	B	B	Bc	cD	D	E	F	F	Fg	fG	G
Ventral													
Cervical	A	Ab	B	B	C	D	De	E	eF	Fg	fG	G	G
Sternal	A	Ab	B	B	Cd	D	dE	eF	F	Fg	fG	G	G
Axillar	A	A	A	B	B	bC	cd	de	E	F	Fg	fG	G
Abdominal	A	A	B	B	C	D	dE	Ef	F	F	Fg	fG	G
Humeral	A	B	B	Bc	Cd	D	dE	Ef	F	Fg	G	G	G
Femoral	A	aB	B	B	Cd	D	dE	Ef	F	Fg	G	G	G
Crural	A	Ab	B	B	bC	cD	dE	E	ef	Fg	fG	G	G
Alar													
Primaries	B	B	C	cD	D	D	E	F	F	F	F	fG	G
Secondaries	ab	B	Bc	cD	D	D	E	F	F	F	F	fG	G
Alula	ab	B	bC	cD	D	De	def	F	F	Fg	fg	G	G
Upper Greater Primary Coverts	A	Ab	Bc	Cd	D	D	De	E	eF	Fg	fG	G	G

TABLE 3—*Continued*

Tract/Region	Age in Days												
	0	1	2	3	4	5	6	7	8	9	10	11	12
Upper Middle Primary Coverts	A	A	aB	B	bC	cD	De	E	eF	fg	G	G	G
Upper Greater Secondary Coverts	A	ab	B	cd	D	D	De	Ef	F	Fg	G	G	G
Upper Middle Secondary Coverts	A	Ab	B	Bc	Cd	D	De	Ef	F	fg	G	G	G
Under Greater Primary Coverts	A	A	A	A	A	A	A	abc	aD	def	adef	dfg	ef
Under Middle Primary Coverts	A	A	A	A	A	A	Bc	bcd	bde	cE	dfg	fg	fG
Under Greater Secondary Coverts	A	A	A	A	Ab	Ab	D	dE	def	F	fG	G	G
Under Middle Secondary Coverts	A	A	A	Ab	aB	bc	cd	cD	dE	E	efg	fg	fG
Under Lesser Secondary Coverts	A	A	A	Ab	aB	aB	bC	cD	De	Eg	fg	G	G
Marginal Coverts	A	Ab	B	Bc	C	cD	De	E	Ef	efg	fG	fG	G
Carpometacarpal Coverts	A	A	Ab	aB	B	bc	Cd	cD	dE	eF	Fg	G	G
Caudal													
Rectrices	A	Ab	B	B	bC	cD	de	E	ef	F	F	F	F
Upper Tail Coverts	A	A	Ab	B	Bc	Cd	De	E	eF	F	F	Fg	G
Under Tail Coverts	A	A	A	aB	B	bc	D	D	Ef	F	F	Fg	G
Postventral	A	A	A	aB	B	bc	cD	de	Ef	F	Fg	fG	G
Anal Circlet	A	A	A	Ab	B	B	bcd	dE	E	eF	fG	G	G

[1] The stages of development of the juvenal plumage are coded as follows: A,a = no dark papillae; B,b = dark papillae visible beneath skin; C,c = sheaths emerging through skin; D,d = sheaths $>$ 1 mm out of skin; E,e = feathers rupturing sheaths; F,f = feathers out of sheaths but of lesser length than sheaths; G,g = feathers out of sheaths and of greater length than sheaths. Capital letters indicate 60-100 percent of birds; small letters indicate 20-50 percent of birds.

TABLE 4

PERCENTAGE OF YOUNG BREWER'S BLACKBIRDS OPENING THEIR EYES TO VARYING DEGREES WITH INCREASING AGE

Age in Days	n	Maximum Parting of Eyelids (mm)					
		0.0	0.5	1.0	2.0	3.0	4.0
0	29	100	0	0	0	0	0
1	34	88	12	0	0	0	0
2	35	51	40	9	0	0	0
3	34	9	50	29	12	0	0
4	33	0	0	67	33	0	0
5	26	0	0	8	81	11	0
6	22	0	0	0	50	50	0
7	24	0	0	0	21	71	8
8	23	0	0	0	0	48	52
9	21	0	0	0	0	5	95
10	19	0	0	0	0	0	100

On day 6, primaries broke through the distal portions of their sheaths. Similar timing of primary rupture has been described in several other passerines, including Red-winged Blackbirds (Holcomb and Twiest 1970), House Sparrows (*Passer domesticus*) (Weaver 1942), and Rufous-sided Towhees (*Pipilo erythrophthalmus*) (Barbour 1950). Rupture of other teleoptiles occurred in the more advanced tracts and regions on days 6–7, and in remaining regions by day 10. Apteria associated with the spinal tract were concealed by teleoptiles by days 7–8. Overlapping of the mid-ventral apterium proceeded more slowly, particularly on the lower abdomen, but was complete by day 12 in most birds. Daily weight gains decreased during this period of rapid feather production, as in many other passerine species (Banks 1959, Holcomb 1968, Holcomb and Twiest 1968, Bateman and Balda 1973).

Condition and coloration of soft parts.—The eyes of all birds were closed on day 0 (Table 4). On days 1–3, nestlings began to open their eyes slightly while gaping. By days 8–9, the birds were alert and kept their eyes open for extended periods in my presence.

The irides of all nestlings were dark brown when the eyes first opened. By days 12–13, four of 11 birds had minutely paler irides than others of the same age and probably were males. A hand-raised male had grayish-white irides by the age of 3 weeks.

The mouth lining was bright pink or red, which is typical in nestling icterids (Ficken 1965). The mouth lining became tinged with grayish near the end of the nestling period, thus changing toward the black color in adults.

The tongue was pale in young nestlings but darkened posteriorly after day 9. The skin was a bright, yellowish pink on day 0, and the abdominal viscera were clearly visible through it. The skin became thicker, more wrinkled, and dull in hue through the course of the nestling period.

The nestlings' bills, tarsi, feet, and claws were pale at hatching and darkened to the black color of adult structures by fledging. The bill was predominantly flesh-colored, grayish near the tip, on days 0–1. The prominent oral flanges and the egg tooth were white. The bill became darker and grayer than body skin, markedly so toward the tip, on days 2–3. The bill continued to darken through the nestling period, until by day 12 it was nearly black. During the latter part of nestling life, the flanges regressed somewhat and became grayish. The egg tooth was inconspicuous after about the first week, but a remnant was still discernible at 13 days.

The tarsi and feet were flesh-colored, and the claws white, on days 0–1. The tarsi and feet became perceptibly darker and grayer than body skin on days 3–4 and were nearly black by days 10–11. Slight proximal darkening of the claws was evident by days 2–3. By day 5, the claws were medium gray proximally and pale gray or white distally; and by days 10–11 they were black.

BEHAVIORAL DEVELOPMENT

The development of activities in free-living Brewer's Blackbirds from 0–13 days, and in captives from 5–42 days, is summarized in Table 5. Behavior is described and discussed in this section within several general categories: responses concerned with nutrition, body maintenance, locomotion and related activities, escape responses, social behavior, and vocalizations.

Responses concerned with nutrition.—Three nestlings observed at hatching first gaped when they were 2–4 min old. During the early part of the nestling period, birds gaped when I gently shook them, touched their nests, or made lip-smacking sounds. Young nestlings always gaped vertically; however, at 7–9 days the birds began to orient their gaping toward siblings or toward a pointed object moved from side to side several cm from their heads. A few days later, they began to flutter their wings while begging. Free-living birds gaped less readily in my presence toward the end of nestling life than they did earlier, probably because of increasing ability to discriminate between reinforcing and non-reinforcing stimuli.

Independent feeding responses developed near the time of fledging. I first saw bill-wiping by a wild bird on day 10 and by hand-raised birds on day 12. Exploratory pecking appeared in hand-raised birds on day 14. The birds initially directed pecks toward various objects which contrasted visually with the background, but by the age of 4–5 weeks they pecked exclusively at edible objects. At 3–4 weeks, the birds were able to catch insect prey and

TABLE 5

ONSET AND DURATION OF ACTIVITIES IN YOUNG BREWER'S BLACKBIRDS, FREE-LIVING (———) OBSERVED FROM DAYS 0–13 AND HAND-RAISED (----------) OBSERVED FROM DAYS 5–42

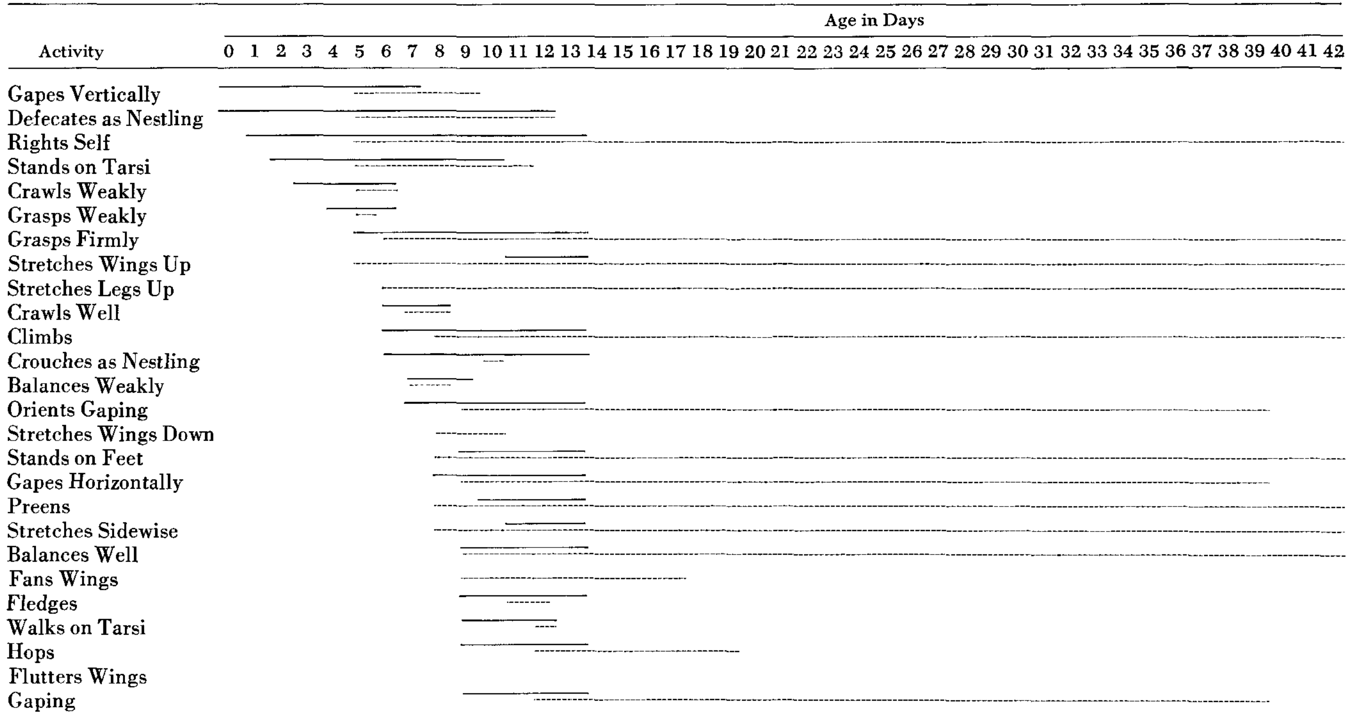

TABLE 5—*Continued*

Activity	Age in Days																																										
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Hop-Walks																																											
Wipes Bill																																											
Defecates as Adult																																											
Shakes Self																																											
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Walks																																											
Flies Horizontally																																											
Pecks Exploratorily																																											
Lands on Siblings																																											
Bathes																																											
Drinks																																											
Watches Prey																																											
Catches Prey																																											
Picks up Food																																											
Shells Seeds																																											
Lands Skilfully																																											
Suns																																											
Fights																																											
Threatens with Opened Bill																																											

to pick up and shell millet seeds; however, they showed these behaviors when they were only slightly hungry. As time since the last hand feeding increased, they reverted to begging. Similar findings have been reported for other altrices beginning to feed independently (Nice 1943). By day 39, hand-raised birds attained complete independence in feeding, which agrees with Williams' (1952) observations of free-living Brewer's Blackbirds.

Defecation by hand-raised nestlings was directed upward but was not typically over the side of the nest. Droppings were in the form of fecal sacs until fledging when the membranous covering was lost. Feeding and handling stimulated defecation in nestlings but not in fledglings.

Free-living and hand-raised birds occasionally regurgitated undigested food in the form of pellets 1–2 cm in length. I observed this phenomenon three times in wild birds aged 11–12 days and nine times in captives aged 6–28 days. Two pellets regurgitated by free-living nestlings contained small pebbles ($\leqslant 3 \times 2$ mm), bits of eggshell and snailshell ($\leqslant 4 \times 2$ mm), undigested hard insect parts ($\leqslant 5 \times 3$ mm), a 3 mm thorn, and strands of fibrous plant material ($\leqslant 26$ mm in length). Regurgitation of pellets has been observed in nestling Common Crows (*Corvus brachyrhynchos*) (Parmalee 1952) and in a 33-day-old Bobolink (*Dolichonyx oryzivorus*) (pers. obs.), as well as in adult corvids (Harlow 1922, and others).

Body maintenance.—My observations of body maintenance activities were primarily on captive birds. However, I did record preening, stretching, and shaking by a few free-living nestlings, beginning on days 10–11.

Hand-raised birds began to preen and to stretch during the middle part of nestling life. Preening commenced on days 8–9, shortly after the rupture of many teleoptiles, and it probably aided in the removal of sheaths during the latter part of the nestling period. Preening was initially directed toward the wing, under the wing, and to the breast, as in Song Sparrows (*Melospiza melodia*) and American Redstarts (*Setophaga ruticilla*) (Nice 1943). Stretching up of both wings was already present on day 5, and other stretching movements appeared on days 6–8. Stretching down of both wings, a temporary movement in passerine development (Nice 1943), occurred only on days 8–10.

The birds scratched their heads from day 12, just after fledging. At first they scratched directly, but soon they began to scratch indirectly as well. On day 16 and thereafter, they invariably used the indirect method. This ontogenetic pattern of direct scratching superseded by indirect scratching has been reported in several other passerines and in a few non-passerines (Ficken and Ficken 1958, Nice and Schantz 1959, Berger 1966).

The birds began to shake themselves shortly after fledging. They slept with their bills tucked into the upper wing coverts from the time of fledging,

TABLE 6

PERCENTAGE OF FREE-LIVING, YOUNG BREWER'S BLACKBIRDS CAPABLE OF GRASPING AND BALANCING WITH INCREASING AGE

Age in Days	n	Behavioral Capacity[1]					
		DNG	G<5	G≧5	B<5P	B≧5F	B>5G
3	15	100	0	0	0	0	0
4	21	71	29	0	0	0	0
5	19	32	47	21	0	0	0
6	14	0	36	64	0	0	0
7	20	0	0	90	10	0	0
8	16	0	0	31	69	0	0
9	15	0	0	20	53	20	7
10	11	0	0	0	0	36	64
11	9	0	0	0	0	0	100

[1] DNG = does not grasp; G < 5 = grasps < 5 sec; G ≧ 5 = grasps ≧ 5 sec; B < 5P = balances < 5 sec, coordination poor; B ≧ 5F = balances ≧ 5 sec, coordination fair; B > 5G = balances > 5 sec, coordination good.

but they did not support themselves on one leg on a perch until days 18–19. They performed bathing movements, always at water, beginning on days 18–23. Occasionally, they adopted a sunning posture near a lamp starting at 25–34 days.

Locomotion and related activities.—The first locomotor activity to develop was righting. Of 12, 0-day-old nestlings placed on their backs on a flat surface, 11 made no attempt to right themselves, and one squirmed slightly but could not turn over. On day 1, four of 10 birds placed on their backs righted themselves, five turned onto their sides, and one made no effort to turn over. On day 2, all of 10 birds righted themselves. Soon afterwards, nestlings began to raise themselves on their tarsi, at first only during gaping. They also began to crawl at this time.

The ability to grasp and balance developed gradually during the nestling period. At 3–5 days, birds began to cling to the nest lining with their toes during removal from their nests. Free-living nestlings failed to grasp a perch, 46 mm in circumference, placed against their feet on day 3 (Table 6). On day 4, six of 21 birds were able to grasp the perch weakly; and by day 6, nine of 14 birds grasped firmly for 5 sec. Most birds were first able to balance unsteadily on the perch on day 8, and to balance with good coordination on day 10.

Nestlings, both free-living and hand-raised, were consistently unable to balance when first able to grasp a perch. A similar phenomenon has been reported in seven species of terrestrial breeding, non-icterine passerines

(Holcomb 1966a). However, Holcomb (1966b) found that nestlings in an upland breeding population of Red-winged Blackbirds were usually able to balance when first able to grasp. He suggested that this early ability to balance was the product of strong selection pressure in an aquatic environment, on a species which has recently spread into terrestrial habitats. If this hypothesis is correct, one would suspect that an icterid historically nesting in terrestrial situations should fit the developmental pattern of terrestrial breeding non-icterids rather than that of the Red-winged Blackbird. My results indicate that the statement holds for Brewer's Blackbirds.

Fledging by free-living young occurred at the earliest between days 9 and 10, and at the latest on day 13. Williams (1952) found the nestling period at undisturbed Brewer's Blackbird nests to be 13 days. Disturbance was a contributing factor to early nest-leaving by some birds in my study. On a few occasions, young of 10–12 days fledged as I approached their nests. Birds from the age of 9 days were generally restless when I returned them to their nests after routinely examining them, but in several cases I was successful in preventing premature fledging by cupping my hands over a nest for several minutes until its occupants became calm.

Locomotion on the ground was initially by hopping, beginning on days 9–11 in free-living young. A variant of hopping was "hop-walking," in which hops were interspersed with walking steps. Both hopping and hop-walking were usually accompanied by fluttering of the wings. Several other passerines which walk as adults, have been reported to hop when they first leave the nest (Nice 1943, 1950; Horwich 1969). Another early form of terrestrial locomotion was walking on the tarsi, used over short distances. Walking in the adult manner appeared on day 13 at the earliest, and it entirely replaced other gaits in hand-raised birds by day 20.

Flying was preceded by fanning of the wings, beginning on day 9 in hand-raised nestlings. Free-living birds were capable of short (< 1 m) descending flights on days 10–11, at which time the wing chord was about 55% that of adults. One free-living, 13-day-old fledgling flew horizontally for approximately 5 m. Red-winged Blackbirds and Brown-headed Cowbirds (*Molothrus ater*) are also capable of some flight at the time of fledging (Nice 1950), but Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) are unable to fly for the first 4–5 days after they leave the nest (Fautin 1941). Hand-raised Brewer's Blackbirds did not begin to fly until several days after fledging; however, I believe that this was at least partly due to insufficient motivation, since flight by free-living birds generally occurred during attempts to escape from me. Coordination upon landing was at first poor to fair in both free-living and hand-raised birds. Captives were able to land skilfully by day 23.

Escape responses.—Free-living young crouched when I approached their nests, beginning usually on days 7–8 when their eyes had opened to about 3 mm (16 of 20 birds). Of four hand-raised nestlings, only one gave this response to me, at 10 days. Schaller and Emlen (1961) found that free-living, nestling Common Grackles (*Quiscalus quiscula*) opened their eyes to 3 mm by 200 hours and began to crouch to a visual stimulus at 200–220 hours (days 8–9). These workers additionally demonstrated that pattern vision was acquired as early as 150 hours (day 6), and that visual experience was necessary for the normal development of discrimination between parent birds and other stimuli appearing at the nest rim. Further study might be expected to yield similar results for Brewer's Blackbirds.

Free-living nestlings aged 10 days or older occasionally hopped or fluttered from their nests at my approach. Fledglings aged 11–13 days typically crouched motionless until I touched or almost touched them, when they attempted to escape. Such responses to me were rare or absent in hand-raised birds up to the age of about 5 weeks. However, as the captive birds attained independence in feeding, they began to escape when I approached them.

Social behavior.—Hand-raised birds began to peck or nibble at one another's bill, toes, tail, and body feathers shortly after fledging. Such pecking evoked no discernible responses by recipients during the first several days out of the nest. Birds at this age occasionally begged to, and landed upon, one another.

Mutual pecking, followed by the retreat of one bird, occurred on day 25 and thereafter. Pecking encounters were usually precipitated when two birds attempted to gain possession of a single food item, such as an insect. On day 27, a bird at a feed dish faced an arriving bird and opened its bill, whereupon the newcomer retreated. This threat posture was assumed on many later occasions, usually in the presence of food. A threatened bird sometimes responded by assuming a similar posture; if neither bird retreated, the encounter either ended in a standoff or resulted in a fight. The largest bird, a male, was dominant to both females.

Vocalizations.—Free-living birds gave four calls which appeared in the following order: (1) peeping sounds, (2) "tutz-utz-utz," (3) the squawk, and (4) the location note (terminology after Williams 1952). Ten recently hatched nestlings gaped without vocalizing. However, day 0 nestlings older than 2-3 hours gave peeping sounds while gaping (Fig. 6). The call was produced in series and appeared to be associated with hunger. At 6–9 days, birds began to give a second, similarly motivated call of lower frequency, "tutz-utz-utz." This call appeared initially as a single note interspersed with peeps, but by days 10–12 it had replaced peeping sounds and was given in series.

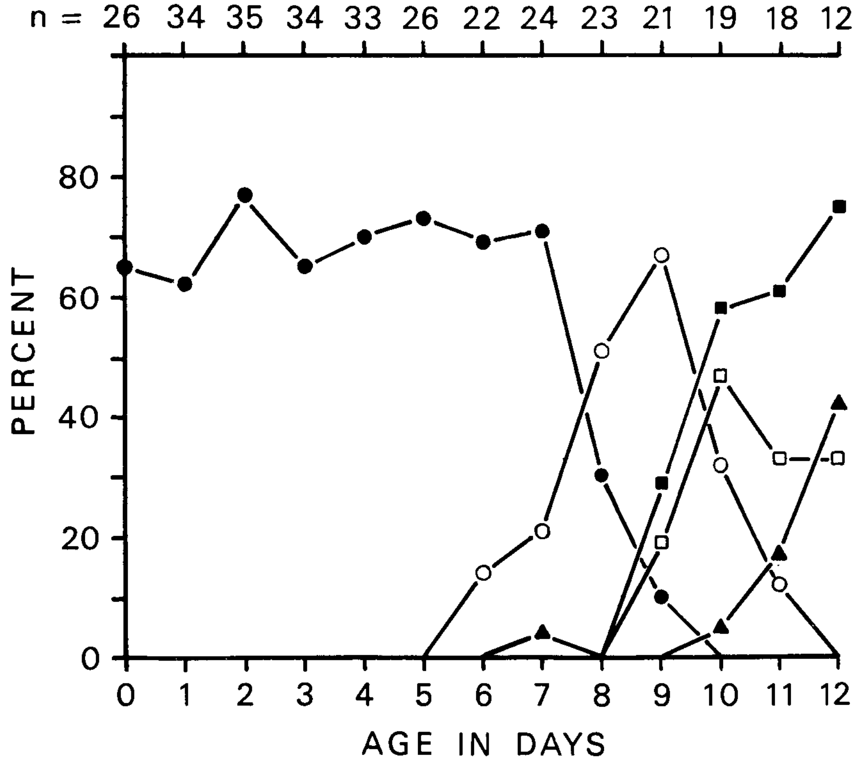

FIG. 6. Percentage of free-living, young Brewer's Blackbirds giving several calls with increasing age: (●) peeping sounds; (○) mixture of peeping sounds and "tutz-utz-utz;" (□) "tutz-utz-utz;" (▲) squawk; (■) "chup."

A third call, the squawk, was a single, harsh note of approximately 0.2 sec duration. Stimuli which evoked this call were capture of birds by me and sudden movement in the birds' immediate environment. I first heard the squawk on day 7, the age at which crouching appeared. A fourth call was a single, short, low frequency "chup," Williams' (1952) "location" note. Birds gave this call from the age of 9–10 days while standing or hopping on the ground, either as fledglings or as nestlings temporarily removed from their nests by me. "Chup" calls by one bird evoked similar calls from nearby siblings.

Hand-raised birds gave each of the above calls, in a sequence similar to that in free-living birds. The captive birds continued to give occasional peeping sounds for about a week after fledging, at times when they were partly satiated with food. The "peep" call in these fledglings appeared to function as a low intensity begging vocalization, to be replaced by the louder, more conspicuous "tutz-utz-utz" as time since the last feeding increased. At 5–6 weeks, hand-raised birds sometimes gave squawks when subordinated during agonistic encounters. Williams (1952) reported squawks from adults under similar circumstances.

A hand-raised male gave subsong beginning at 28 days. A female produced subsong on one occasion, at 35 days. These observations of subsong are consistent with findings for other young passerines (Lanyon 1960).

SUMMARY

The purpose of this study was to describe the development of young Brewer's Blackbirds. Observations were made of morphology and behavior in 41 free-living nestlings aged 0–13 days, and of behavior in four hand-raised birds aged 5–42 days.

Recently hatched nestlings averaged 3.7 g or 6% of the weight of adult females. Daily weight gains increased until day 5, then decreased. By day 10, the birds averaged 70% of adult female weight. Within asynchronously hatched broods, last-hatched birds made smaller daily gains than did first-hatched birds.

The wing, the tarsus, and the hallux followed a sigmoidal growth pattern. By day 10, the tarsus was almost fully grown, whereas the wing chord was slightly over half of adult size. Growth of the commissure exceeded that of the culmen on days 1–4, then dropped below that of the culmen.

The nestlings were sparsely covered with whitish down at hatching. Sheaths of primaries emerged through the skin on day 2 and ruptured on day 6. Sheaths of teleoptiles in other regions emerged on days 3–7 and ruptured on days 6–10.

The nestlings' eyes began to open on days 1–3 and were fully open by days 8–9. Sexual dimorphism in eye color was faintly discernible at 12–13 days and was obvious in hand-raised young by 3 weeks. The nestlings had red mouth linings. Their bills, tarsi, feet, and claws were pale at hatching and were nearly black by the time of fledging.

The nestlings first gaped shortly after hatching. They began to orient their gaping at 7–9 days and to show independent feeding responses near the time of fledging. Hand-raised birds attained complete independence in feeding by 39 days. Nestlings and fledglings occasionally regurgitated pellets.

The birds began to preen and to stretch in the middle part of the nestling period. Hand-raised young scratched their heads from the age of 12 days, at first directly, later indirectly.

Nestlings were first able to right themselves on days 1–2. Most birds were able to grasp a perch for 5 sec on day 6, to balance unsteadily on day 8, and to balance with good coordination on day 10. They fledged on days 9–13, and they hopped before they walked. Free-living birds were capable of short (< 1 m) flights on days 10–11 and of longer flights by day 13.

Free-living nestlings began to crouch at my approach at 7–8 days. Hand-raised birds showed agonistic behavior, including pecking encounters and an open-billed threat posture, starting at 25–27 days. Birds aged 0–13 days gave two begging calls, a squawk, and a "location" note; and hand-raised young produced subsong beginning at 4–5 weeks.

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LITERATURE CITED

BANKS, R. C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor 61:96–109.

BARBOUR, R. W. 1950. Growth and feather development of towhee nestlings. Am. Midl. Nat. 44:742–749.

BATEMAN, G. C., AND R. P. BALDA. 1973. Growth, development, and food habits of young Piñon Jays. Auk 90:39–61.

BEASON, R. C., AND E. C. FRANKS. 1973. Development of young Horned Larks. Auk 90:359–363.

BERGER, A. J. 1966. Head-scratching behavior of some hand-raised birds. Wilson Bull. 78:469.

FAUTIN, R. W. 1941. Development of nestling Yellow-headed Blackbirds. Auk 58: 215–232.

FICKEN, M. S. 1965. Mouth color of nestling passerines and its use in taxonomy. Wilson Bull. 77:71–75.

FICKEN, R. W., AND M. S. FICKEN. 1958. Head-scratching in *Seiurus* (Parulidae) and other passerines. Ibis 100:277–278.

HARLOW, R. C. 1922. The breeding habits of the Northern Raven in Pennsylvania. Auk 39:399–410.

HOLCOMB, L. C. 1966a. The development of grasping and balancing coordination in nestlings of seven species of altricial birds. Wilson Bull. 78:57–63.

———. 1966b. Red-winged Blackbird nestling development. Wilson Bull. 78:283–288.

———. 1968. Growth of nestling goldfinches compared to adult size and differential development rate of structures in relation to their function. Nebr. Bird Rev. 36:22–32.

——— AND G. TWIEST. 1968. Red-winged Blackbird nestling growth compared to adult size and differential development of structures. Ohio J. Sci. 68:277–284.

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

HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49:682–694.

———. 1970. Social behavior of nesting Brewer's Blackbirds. Condor 72:15–23.

HORWICH, R. H. 1969. Behavioral ontogeny of the Mockingbird. Wilson Bull. 81:87–93.

HOWELL, T. R., AND G. A. BARTHOLOMEW, JR. 1952. Experiments on the mating behavior of the Brewer Blackbird. Condor 54:140–151.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

LANYON, W. E. 1960. The ontogeny of vocalizations in birds. Pp. 321–347. *In* Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, eds.). Publ. No. 7, Am. Inst. Biol. Sci., Washington, D.C.

LARIVERS, I. 1944. Observations on the nesting mortality of the Brewer Blackbird, *Euphagus cyanocephalus*. Am. Midl. Nat. 32:417–437.

LINSDALE, J. M. 1936. Coloration of downy young birds and of nest linings. Condor 38:111–117.

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

———. 1950. Development of a Redwing (*Agelaius phoeniceus*). Wilson Bull. 62: 87–93.

——— AND W. E. SCHANTZ. 1959. Head-scratching movements in birds. Auk 76: 339–342.

PARMALEE, P. W. 1952. Growth and development of the nestling crow. Am. Midl. Nat. 47:183–201.

RICKLEFS, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505–510.

SCHALLER, G. B., AND J. T. EMLEN, JR. 1961. The development of visual discrimination in the crouching reactions of nestling grackles. Auk 78:125–137.

WEAVER, R. L. 1942. Growth and development of English Sparrows. Wilson Bull. 54:183–191.

WETHERBEE, D. K. 1957. Natal plumages and downy pteryloses of passerine birds of North America. Bull. Am. Mus. Nat. Hist. 113:341–436.

WILLIAMS, L. 1952. Breeding behavior of the Brewer Blackbird. Condor 54:3–47.

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REQUEST FOR ASSISTANCE

Wood Storks.—As part of an intensive investigation of the biology of Wood Storks, nestling birds in several Florida rookeries are being color-marked. In 1974, red nasal saddles were placed on juvenile storks in south Florida, while in 1975 red patagial disks were used in south Florida rookeries, and blue patagial disks in central Florida. Any sightings of these color-marked storks, or anyone having knowledge of the location of recent Wood Stork nesting, please contact John C. Ogden, National Audubon Research Department, 115 Indian Mound Trail, Tavernier, FL 33070.