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SKELETAL DEVELOPMENT AT THE TIME OF FLEDGING IN HOUSE WRENS[1]

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Abstract. We examined skeletal development at the time of first flight in House Wrens (*Troglodytes aedon*) as one step in assessing whether calcium availability limits nestling growth in this species. Young wrens begin flying with about 49 mg of calcium in their skeletons, 30% less calcium than is found in adult skeletons. Degree of calcification varies greatly from bone to bone at first flight which suggests that, during development, growing nestlings selectively allocate more calcium to certain skeletal components than to others. The coracoids, which directly resist contractions of the large flight muscles, are the most calcified bones in the fledgling body. Unexpectedly, long bones of the wing are not highly calcified at nest-leaving and are less calcified than leg bones. Strong leg bones may reflect the fact that young use legs extensively when competing for food within nests, and that legs probably bear the brunt of hard, awkward landings which young birds experience before flight is perfected.

Key words: calcium, growth, House Wren, skeleton, Troglodytes aedon.

In many bird species, selection should favor individuals who, as young, most rapidly develop the ability to fly because flight usually provides young with several survival advantages including increased access to food and an increased ability to escape predators (Sul-

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livan 1989, Pomeroy 1990). As noted by Barclay (1994), however, prior to being able to fly, young, growing birds presumably must assimilate substantial amounts of calcium. Young in most species do not fly until they are nearly as large as adults, suggesting that a relatively large skeleton is a requirement of flight. The production of full-sized wing bones may be especially important; in several avian taxa, those species with relatively long wings show the greatest time delay between hatching and first flight (Carrier and Auriemma 1992). In addition to producing a relatively large skeleton, Barclay (1994) also suggested that, before flight can occur, some parts of the skeleton, especially the wing bones, may have to be fully calcified to withstand the strong torsion and shear forces placed on bones during flight.

Given this apparent pressure to assimilate large amounts of calcium quickly, young in many bird species—particularly species which consume primarily insects, seeds or fruit—face a problem in that these foods generally contain very little calcium (Turner 1982, Studier and Sevick 1993, Graveland and Van Gijzen 1994). To compensate, parents often supplement diets of dependent young with calcium-rich bits of bone, mollusk shells, or limestone (Maclean 1974, St. Louis and Breebaart 1991, Graveland et al. 1994). Nevertheless, Barclay (1994) argued that the availability of calcium, as much or more than the availability of energy, may still limit clutch sizes, nestling growth rates, and overall reproductive output in some populations of birds.

That young birds require a large, sturdy skeleton before flight can occur seems reasonable. However, at present we have very little information on the extent and pattern of skeletal development at the time of first flight in any bird species. Some preliminary data suggest that young may fledge with substantially less calcium in their skeletons than is found in adult skeletons. We examined skeletal development at the time of first flight in the House Wren (*Troglodytes aedon*), an insectivorous passerine. Our study goes further than previous studies in examining relative development of individual bones in newly fledged young. Thus we could assess not only how much calcium young assimilate into skeletons before first flights but also where in the skeleton that calcium is allocated.

METHODS

House Wrens are small (9–12 g), sexually monomorphic, cavity-nesting songbirds. Females lay 4–8 eggs per clutch. Hatchlings weigh approximately 1 g and are fully altricial. In addition to insects, spiders, and other small invertebrates, parents feed nestlings calcareous grit, including small mollusk shells (Mayoh and Zach 1983; L. S. Johnson, pers. observ.). Young usually remain in nests until first-hatched young are 15–17 days old. At fledging, young weigh as much or more than adults, growth of primary feather 10 is about 84% complete, whereas growth of the outermost tail feather (rectrix 6) is about 37% complete (Zach 1982). Newly fledged young are weak flyers, usually flying only short distances (< 15 m) at one time for at least several days after nest-leaving. Fledglings are fed by one or both parents for about 13 days before reaching independence.

We collected nine adult and nine juvenile male House Wrens (all from different nests) in northern Wyoming. We collected nestlings 15–17 days after hatching began, within hours of when fledging would have (or could have) occurred. Hereafter we refer to juveniles as "fledglings." We chose fledglings haphazardly from each nest with the restriction that we did not take obvious runts.

Various skeletal components were dissected out of each specimen, stripped of as much soft tissue as possible, and then dried at room temperature for 1 month. We then measured length and, in some cases, width, of bones to the nearest 0.01 mm. Lengths of all long bones are maximum lengths, whereas widths are minimum widths. A few bones were broken during dissection and were not measured.

Some bone measurements require clarification (terminology follows Baumel et al. 1993): *Length of cranium* is the straight-line distance from the prominentia cerebellaris at the back of the skull forward to the zona flexoria craniofacialis, the joint at the base of the culmen. *Length of culmen,* or "bill," is the straight-line distance from this same joint to the tip of the premaxillary bone. *Length of sternum* is the straight-line distance from the midpoint of the caudal margin of the sternum to the base of the rostrum sterni (measured on the ventral side), whereas *breadth of sternum* is the distance between the most cranial points of the right and left incisura lateralis (= the sternal notches).

We did not (or could not) separate and examine individual bones of some skeletal components. *Manus* refers to the carpal bones, metacarpal bones, and associated phalanges. *Pes* refers to the four digits of the foot, comprised of from 2–5 phalanges each. *Presacral spine and ribs* refers to the cervical and thoracic vertebrae with attached vertebral and sternal ribs. *Pelvis/caudal vertebrae complex* refers to the two os coxae or hip bones, the synsacrum, and the free caudal vertebrae, including the pygostyle.

ASH AND CALCIUM CONTENT

We chose six adult and six fledglings at random and heated their bones to 600°C for 15 hr in quartz glass crucibles to destroy any organic matter and convert calcium to the soluble oxide. The weight of ash remaining was determined to the nearest 0.01 mg. Small parts of some bones were missing for some specimens, having been broken off during dissection. Broken bones were not ashed. We report final sample sizes with results below.

We expected that relative ash content of fledgling and adult bones would reliably indicate the relative calcium content of those same bones. To confirm this, we determined the amount of calcium in the ash remaining from several of the larger bones examined. We dissolved ash using 1 ml of 1 M HCl and diluted the resulting solution volumetrically to 50 ml with distilled water. The total mg of calcium in each of four 10 ml aliquots taken from this solution was determined by titration with ethylenediaminetetraacetic acid (EDTA), using Eriochrome Black T as an indicator (Koltoff et al. 1969). We used the mean of the four

TABLE 1. Linear measurements (mm), ash weights (mg), and estimated calcium content (mg) of bones and bone groups from adult and fledgling House Wrens. Shown are means with range and sample size in parentheses. Also shown is the degree to which mean value for fledglings approaches mean value for adults for each measurement (fledgling value as a percent of adult value). Mean values for linear measurements and ash weights (but not calcium content—see text) were compared using one-tailed *t*-tests or Wilcoxon rank sum tests. Test results are shown next to "Percent of adult value" number (ns = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

	Adults	Fledglings	Percent of adult value
Skull			
Cranium length	16.5 (16.1–17.5, 9)	15.4 (14.2–16.0, 9)	93***
Cranium width	13.3 (13.0–13.7, 9)	12.6 (12.3–12.9, 9)	95***
Culmen length	15.3 (14.6–16.4, 9)	10.9 (10.3–12.3, 8)	71***
mg ash	66.56 (59.35–84.81, 6)	36.09 (31.03–47.67, 6)	54***
est. mg Ca	20.95 (19.44–23.01, 6)	10.92 (9.46–12.70, 6)	52
Hyoid			
mg ash	1.75 (1.17–2.54, 6)	1.31 (1.10–1.68, 6)	75^{ns}
Presacral spine and ribs			
mg ash	35.78 (31.98–41.95, 6)	28.14 (24.58–39.57, 6)	78*
mg Ca (est.)	12.02 (11.10–13.17, 6)	8.92 (8.21–10.63, 6)	74
Sternum			
Length	11.4 (11.2–11.7, 9)	8.9 (7.9–9.6, 9)	78***
Breadth	6.4 (5.9–6.8, 9)	5.7 (5.3–6.3, 9)	89***
Carina height	4.3 (4.0–4.5, 9)	2.2 (1.8–2.8, 9)	52***
mg ash	10.40 (8.74–12.72, 4)	6.56 (5.67–7.30, 6)	63*
est. mg Ca	3.85 (3.21–4.77, 4)	2.36 (2.07–2.57, 6)	61
Coracoid			
mg ash	3.78 (2.24–4.44, 6)	3.45 (2.44–4.74, 6)	91^{ns}
est. mg Ca	1.43 (0.96–1.76, 6)	1.29 (0.97–1.74, 6)	90
Scapula			
mg ash	2.65 (2.15–3.13, 6)	1.64 (1.24–2.19, 6)	62***
Furcula			
mg ash	1.51 (1.32–1.62, 3)	0.81 (0.68–0.89, 3)	54**
Humerus			
Length	13.5 (13.0–13.8, 9)	12.8 (12.1–13.2, 9)	95***
Width	1.11 (1.03–1.17, 9)	0.94 (0.85–1.04, 9)	85***
mg ash	9.53 (8.09–10.80, 6)	6.81 (5.87–8.05, 6)	71***
est. mg Ca	3.46 (2.81–3.95, 6)	2.50 (2.17–2.89, 6)	72
Radius/ulna			
Length	14.4 (13.8–15.0, 9)	14.1 (13.3–14.6, 9)	98^{ns}
Width	0.87 (0.77–0.91, 9)	0.72 (0.55–0.79, 9)	84***
mg ash	8.02 (7.36–8.80, 6)	5.84 (4.98–6.62, 6)	73***
est. mg Ca	2.96 (2.59–3.26, 6)	2.14 (1.91–2.43, 6)	72
Manus			
mg ash	4.92 (4.35–5.60, 6)	3.06 (2.48–3.76, 6)	62***
est. mg Ca	1.83 (1.65–2.03, 6)	1.15 (1.02–1.28, 6)	63
Pelvis/caudal vertebrae complex			
mg ash	18.7 (16.8–21.7, 6)	14.6 (13.6–15.9, 6)	78***
est. mg Ca	6.48 (5.92–7.58, 6)	4.90 (4.69–5.23, 6)	76
Femur			
Length	14.2 (13.8–14.6, 9)	13.7 (11.6–14.2, 8)	96*
Width	1.01 (0.89–1.10, 9)	0.85 (0.80–0.91, 9)	84***
mg ash	7.02 (6.04–7.84, 6)	5.52 (4.20–6.04, 6)	79**
est. mg Ca	2.58 (2.31–2.94, 6)	2.03 (1.58–2.37, 6)	78

TABLE 1. Continued.

	Adults	Fledglings	Percent of adult value
Tibia			
Length	23.1 (22.4–24.1, 9)	22.8 (21.1–23.5, 8)	99^{ns}
Width	1.10 (0.82–1.33, 9)	0.98 (0.87–1.07, 9)	89*
mg ash	12.82 (11.92–14.59, 6)	11.20 (10.35–12.00, 6)	87**
est. mg Ca	4.77 (4.47–5.54, 6)	4.06 (3.73–4.46, 6)	85
Tarsus			
Length	17.2 (15.9–18.2, 9)	16.0 (15.1–16.3, 9)	93**
Width	1.15 (1.03–1.25, 9)	1.04 (0.87–1.15, 9)	90*
mg ash	8.88 (7.37–10.27, 5)	7.22 (6.97–7.58, 6)	81*
Pes			
mg ash	6.28 (6.02–6.89, 5)	4.18 (3.00–5.57, 6)	67***
Total mg ash	198.57	136.40	69

"mg calcium" values obtained in all subsequent numerical analyses. An error analysis showed that for skeletal components with ash weights of about 3 mg, the uncertainty in our estimate of mg calcium was approximately ± 5% (for larger bones, the error would be proportionately less). We therefore restricted analyses to those skeletal components which, in fledglings, had a mean ash weight of > 3 mg.

For calcium concentrations encountered in our analyses, titration with EDTA provides an accurate estimate of calcium content (typically ± 3‰ relative error) relative to spectroscopic methods. A minor drawback of the procedure is that EDTA simultaneously detects both calcium and the very small amount of magnesium in bone ash. Taylor et al. (1971) estimated that ash of chicken bones is about 37.3% calcium and 0.55% magnesium by weight, i.e., for every 1 mg of calcium in the ash, there is about 0.015 mg of magnesium. We assumed the relative amounts of calcium and magnesium in wren bones would be similar and reduced each estimate of total mg of calcium obtained by titration by 1.5% (1.015/1.000 = 0.985) to obtain a more realistic estimate of the amount of calcium in the various bones.

To estimate the total amount of calcium that wrens assimilate before fledging, we collected four nestlings within a few hours of hatching and, following procedures above, ashed these hatchlings (in their entirety, including digestive tract) and determined the amount of calcium in the ash that remained.

TABLE 2. Mean (± SE, *n*) percent of ash estimated to be calcium, by weight (estimated mg Ca/mg ash × 100).

	Adults	Fledglings
Skull	31.8 ± 1.4 (6)	30.7 ± 1.3 (6)
Spine/ribs	33.8 ± 1.0 (6)	32.1 ± 1.1 (6)
Pelvis	34.7 ± 0.7 (6)	33.7 ± 0.4 (6)
Tibia	37.2 ± 0.6 (6)	36.3 ± 0.4 (6)
Sternum	37.0 ± 0.2 (4)	36.0 ± 0.5 (6)
Humerus	36.4 ± 1.2 (6)	36.8 ± 0.3 (6)
Radius/ulna	37.2 ± 1.2 (4)	36.8 ± 1.0 (6)
Femur	36.8 ± 1.1 (6)	36.7 ± 0.8 (6)
Manus	37.3 ± 1.2 (6)	38.1 ± 1.5 (6)
Coracoid	38.4 ± 1.6 (6)	37.4 ± 1.3 (6)

Results of two-way ANOVA examining effects of bird age on percent of bone ash equal to calcium, controlling for effect of bone type: $F_{1,98} = 1.74$, $P > 0.05$.

STATISTICAL ANALYSIS

Means are reported ± 1 SE, except where noted. We compared means using *t*-tests or, when appropriate, Wilcoxon rank sum tests. Reported probability values are one-tailed because we specifically asked whether fledgling bones were smaller or less calcified than adult bones. Significance level was set at $P < 0.05$.

RESULTS

LINEAR MEASUREMENTS

Linear measurements appear in Table 1. Crania of fledglings were nearly as long (93%) and as wide (95%) as the crania of adults. Fledgling bills, however, were only 71% as long as adult bills. Fledgling sterna were visibly smaller than adult sterna, especially in length (78%) and in the height of the carina, or sternal "keel;" fledgling carinas were only about half the size of adult carinas.

The length of long bones in fledglings ranged from 93% (tarsus) to 99% (tibia) of the length in adults, whereas widths of fledgling long bones ranged from 84% (radius) to 90% (tarsus) of adult widths.

ASH AND CALCIUM CONTENT OF FLEDGLING AND ADULT BONES

The relative amount of ash obtained from the bones of fledglings and adults reliably predicted the relative amount of calcium in those same bones (Table 1). This results from the fact that for any given bone, the percent of ash that was calcium did not differ between fledglings and adults (Table 2). Because we did not measure the calcium content of all bones directly, we use relative ash weights of fledgling and adult bones (which we have for all bones) as our primary indicator of the relative calcium content of fledgling and adult bones.

As indicated by relative ash weights, the amount of calcium in fledgling bones as compared to those of adults varied greatly from bone to bone, ranging from 54–91% (Table 1), and showed no consistent relationship with bone size (e.g., relative ash weights for similarly sized scapula and coracoid: 62% and 91%, respectively). The largest skeletal component, the skull, contained only about half as much calcium in fledglings as it did in adults, primarily because frontal bones of fledgling crania are incompletely ossified and because fledgling bills are short. The furcula, scapulae, and sternum of fledglings also contained little calcium compared to the same bones in adults (relative ash weights: 54%, 62%, and 63%, respectively).

Unexpectedly, long bones of the fledgling wing, the humerus and radius/ulna, did not contain large amounts of calcium (relative ash weights: 71% and 73%, respectively). In fact, long bones of the leg, the femur, tibia, and tibiotarsus appeared to be more calcified in fledglings than long bones of the wing (relative ash weights: 79%, 87%, and 81%, respectively).

Collectively, bones of fledglings produced 136.40 mg of ash on average, about 69% as much ash as bones of adults produced. Assuming bone ash is about 36% calcium (= grand mean of values in Table 2), we estimate that fledgling skeletons contain about 49 mg of calcium.

The bodies of four hatchlings contained a mean of 6.08 ± 1.15 mg (SD) of calcium.

DISCUSSION

At first flight, skeletons of young House Wrens contain about 49 mg of calcium, approximately 30% less calcium than is found in skeletons of adults. Bodies of hatchlings contain only about 6 mg of calcium, so before leaving nests young must assimilate approximately 43 mg of calcium from food and calcareous grit fed to them by parents during the nestling stage. These data, in conjunction with additional data on calcium assimilation efficiency and diet, should assist in determining whether growth of nestlings in our population is limited more by the availability of energy or calcium.

Our results are consistent with the few other data available on the extent of skeletal development at time of first flight in birds. Young Cactus Wrens (*Campylorhynchus brunneicapillus*) and Marsh Wrens (*Cistothorus palustris*) begin flying with about 67–68% as much calcium in their skeletons as in the skeletons of adults (Kale 1965, Ricklefs 1975: his Fig. 10). In contrast, young Rufous-winged Sparrows (*Aimophila carpalis*) apparently begin flying (weakly) with only about half as much calcium in their skeletons as is found in adults (based upon comparison of one juvenile and two adults; Austin and Ricklefs 1977). The Rufous-winged Sparrow has a markedly shorter nestling period than the three wren species and therefore young sparrows likely leave nests at an earlier stage of development than young wrens.

To our knowledge, ours is the first study to examine the developmental state of individual bones at the time of first flight in any wild bird species. Our results indicate that growing House Wrens selectively allocate more calcium to some parts of their skeleton than to other parts. Selective allocation of calcium to certain "critical" bones may help young minimize the time to which they can begin flying, thereby enhancing survival prospects.

Much of the difference in the calcium content of fledgling and adult skeletons results from fledglings having less calcium than adults in two large skeletal components, the skull and sternum. In adults, the skull accounts for about one-third of all calcium in the skeleton, and fledgling skulls contain only about 50% as much calcium as adult skulls. Fledgling cranial bones are quite thin; presumably their strength is rarely tested during the first weeks out of the nest. Fledgling bills also are small. Young may not require full-length, strong bills at fledging because parents feed young for about two weeks after nest-leaving.

Fledgling sterna are noticeably shorter and narrower than adult sterna and the carina is only about half-developed when young begin flying. The carina serves as the site of origin for the supracoracoideus muscles which are largely responsible for the rapid upstroke of the wing, especially during take-off and landing. The large pectoralis muscles also originate, in part, on the carina. A small carina suggests that flight muscles are somewhat underdeveloped at fledging. This could help explain why newly fledged wrens are weak flyers.

We expected that those bones experiencing significant force during flight would be among the most fully calcified bones in fledgling bodies. Consistent with this, the coracoids are most highly calcified in fledglings, containing about 91% as much calcium as in adults. The coracoids function as struts, holding the shoulder and the sternum a set distance apart, and preventing the upper thoracic area from collapsing during contractions of the powerful wing muscles.

Contrary to expectation, long bones of the wing did not appear to be highly calcified at the time of first flight; the fledgling humerus and radius/ulna contained only 71% and 73% as much calcium, respectively, as the same bones in adults. However, we caution that this does not necessarily mean that fledgling wing bones are 25–30% weaker than adult wing bones. Bone strength is not exclusively a function of mineral content. Moreover, we note that all long bones in fledglings are to some degree shorter and narrower than the same bones of adults and for this reason alone we would expect fledgling bones to contain somewhat less calcium. If we assume that long bones approximate the structure of a cylindrical tube, and tube walls (cortices) are equally thick in fledglings and adults, then based upon measurements of length and width, fledgling humeri and radii would have volumes approximately 77% and 76% that of adults, respectively. Thus, long bones of the fledgling wing actually do contain less calcium per unit volume than long bones of the adult wing.

The same is not true of fledgling leg bones. Estimating bone volume as we did above, we would predict the femur, tibia, and tarsus of fledglings to have approximately 77%, 86%, and 82% as much calcium, respectively, as adult bones if the amount of calcium per unit bone volume was the same. This is almost exactly what we found (corresponding values for relative amounts of ash: 78%, 85%, and 81%). That legs are well calcified in young wrens when compared with adults probably reflects the fact that, from an early age, nestlings use legs extensively when competing for food (e.g., standing tall, jockeying for advantageous positions, etc.; Ricklefs 1975). In addition, newly fledged wrens can run very quickly through downed brush when pursued by predators. Having strong leg bones presumably facilitates this activity. Finally, the presence of relatively strong leg bones may reflect the fact that newly fledged wrens are weak, imperfect flyers. One of the more difficult aspects of flight is making slow, controlled landings on the slim branches of shrubs and trees, something young wrens frequently try to do. Such landings require rapid, powerful upstrokes and downstrokes of the wing to generate lift, and wings must be precisely angled with each stroke to position the bird's center of mass directly "through" the center of the branch (see Caple et al. 1983). Until young wrens have perfected such maneuvering, they may be prone to hard, awkward landings in which leg bones are subject to considerable force.

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