Growth and development of nestling Downy Woodpeckers

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Of all the fields within biology, the one to which non-professionals have contributed the most information is undoubtedly Ornithology. This is in part because birds are relatively easy to identify and study with equipment no more sophisticated than binoculars, note pad and pencil; also, birds are conspicuous, charming and found close to human habitations.

In addition, Ornithology was the first branch of biology to develop standardized common names thereby easing the communication between professional and layman, and it may be the only one where amateurs are encouraged to participate in research projects of national and international scope such as the Audubon Christmas Counts and Breeding Bird Censuses as well as the studies of longevity and of movement patterns revealed through banding. These opportunities to make important contributions to the field of avian biology, as one increases in personal knowledge, will hopefully lead to increasing interest in Ornithology and bird banding in years to come.

Unfortunately, many banders that I have met seem to be myopic in their ornithological interest, limiting their activity to trapping, banding, indentifying, and life listing when they could easily learn about — and contribute to — other areas as well. Such skills as careful bird identification, sexing, handling, and measurement prepare the bander to contribute to the knowledge of avian ecology, behavior, and development as well as to the more usual areas of migration patterns and longevity.

The identification of a bird as a distinct individual by means of a unique band combination on its leg permits the bander to learn more about changes in anatomy with age, individual variation in behavior, as well as such ecological parameters as territory size, mate and territory fidelity, survival rate, and seasonal changes in habitat usage and foraging patterns. Since band return rates are so poor (see for instance Memorandum MTAB-30, 15 July 1976), the bander might be able to contribute more to the knowledge of Ornithology in the areas of ecology than in those usually thought to be his domain. In this paper I will present the results of a study of nestling Downy Woodpecker *(Picoides pubescens)* development and relate it to the highly evolved nesting strategy of this species.

Many banders have the opportunity, permits, and minimal required equipment to conduct similar studies. Hopefully, more consideration will be given to such potential studies in addition to the more familiar banding pursuits.

The study of nestling development as part of an overall adaptive nesting strategy is currently receiving much interest (see Ricklefs, 1968 and 1974 for extensive bibliographies), and enough information has accumulated to permit comparisons between orders, families and genera in the way various groups have responded to selection pressure shaping growth and development (Ricklefs 1968).

The problems of studying the hole-nesting woodpeckers seem to have discouraged students of development, however. Hoyt's (1944) study of Pileated Woodpeckers *(Dryocopus pileatus)* is the only study of woodpecker development cited in Ricklef's (1968) extensive review. This is unfortunate because their small eggs, short incubation periods, and long nestling stages relative to open-nesting passerines of similar size (Lack 1968) suggest a quite different adaptive strategy from that of the passerines whose development has been extensively studied.

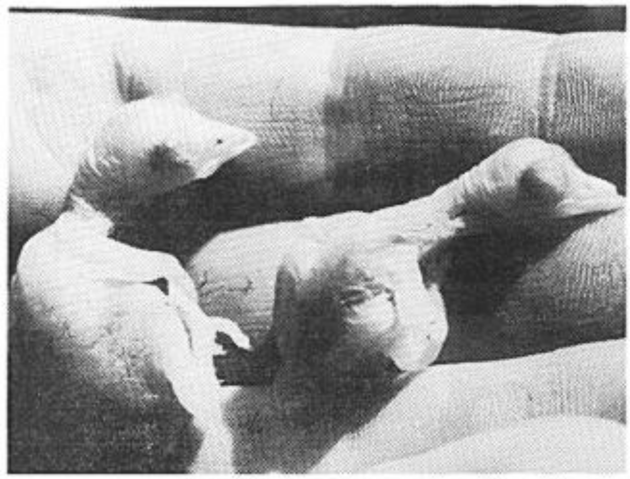
In June 1975, I took advantage of an unusually low Downy Woodpecker nest located in a dead aspen *(Populus tremuloides)* to conduct this study. Although the total variation in growth rates of Downy Woodpeckers cannot be revealed in a study of this scope, I suspect that a greater sample size would alter little the overall picture presented here.

Study area and methods

I found the nest in a small grove of aspens in the Perins Peak Wildlife area 7.7 miles west of Durango, La Plata County, Colorado. This site is at the lower altitudinal limits (about 7,000 feet) for aspens which occur here in isolated "islands" where there is enough moisture on north-facing slopes for their growth. Vegetation surrounding the aspen islands consists of ponderosa pines *(Pinus ponderosa)* and associated shrubs of which scrub oak *(Quercus gambelii)* mountain mahogany *(Cercocarpus montanus)*, serviceberry *(Amelanchior spp.)*, antelope bitterbrush *(Purshia tridentatum)*, and snowberry *(Symphoricarpos oreophilus)* are conspicuous elements. Various woodpeckers seem to prefer aspens as nesting trees (Kilham 1971, Crockett and Hadow 1975, Inouye 1976) and one pair each of Downy Woodpeckers, Common Flickers *(Colaptes auratus)* and "Red-naped" Sapsuckers *(Sphyrapicus [varius] nuchalis)* have nested within 25 to 50 m of each other in this grove for the past three years with no apparent conflict.

Before beginning my study I had to gain access to the hole in a way that would protect its occupants while permitting their removal for measurement at frequent intervals. A series of large nails were driven into the aspen so as to construct a ladder for climbing the tree. The nest hole was then opened by sawing 6-inch cuts diagonally downward from the hole to right and left and connecting the base of these cuts with a third. The resulting triangular "door" was hinged to the tree below, and held closed with four pieces of white adhesive tape: two covering the diagonal cuts, and two more surrounding the tree at the top and bottom of the diagonal tapes. The four-sided "bandage" that resulted protected the nestlings from light, draft, and rain, and was easily removed and replaced when I checked the nest before hatching, or measured the nestlings afterward. The parents were little bothered by this procedure: they hesitated only briefly before returning to the tree after I opened the hole, and they continued incubating within 5 minutes from the time I left the tree.

For about 2 weeks I checked the hole daily, before the nestlings hatched and I could begin measuring them. Each nestling was identified by painting its tail with waterproof laundry markers. This was redone as necessary until the nestlings were 16 days old; then I banded them and no further painting was necessary. Measuring was done at 2-day intervals until fledging, starting at 07:30 each time, and the following measurements were made: body weight (using an Ohaus triple beam balance);



Day 0. No sign of feathers.

overall length along the back from tip of beak to end of longest rectrix; culmen from skin of forehead to tip of upper mandible; wing chord; ulna; tibiotarsus; tarsometatarsus from base of hallux to joint with tibiotarsus; hallux along its ventral surface; central right rectrix; 1st and 3rd distal primaries and distal secondary of the right wing. Descriptions of the feather development in the various tracts; the color and state of development of beak, eyes, ears, feet and claws; and the behavior of the nestlings before and during measurement were also recorded. Finally, I tested the ability of the nestlings to perch on finger, pencil, and the vertical surface of an aspen, and photographed the nestlings before replacing them in the hole. Care was taken to orient the bird the same way each time a particular measurement was made, since errors of 1 or 2 mm could easily occur from different degrees of leg or wing flexion. To minimize stress on the adults, I removed nestlings only when both parents were out of sight, and I removed only two nestlings at a time for measurement. The parents continued to feed and sanitize the nest at the same rate while I was measuring their offspring, and they gave no vocalizations which would indicate distress. I have no reason to think that the procedures used were harmful in any way to the birds, or that they had an impact on the nestling's rate of growth.

To obtain comparative measurements from adult birds, I measured 13 male and 10 female skins at the Denver Museum of Natural History, 1 male and 6 females at the University of Colorado, and 2 male specimens in the Fort Lewis College Collection. All specimens were of the subspecies *P. p. leucurus*, the only subspecies that Bailey and

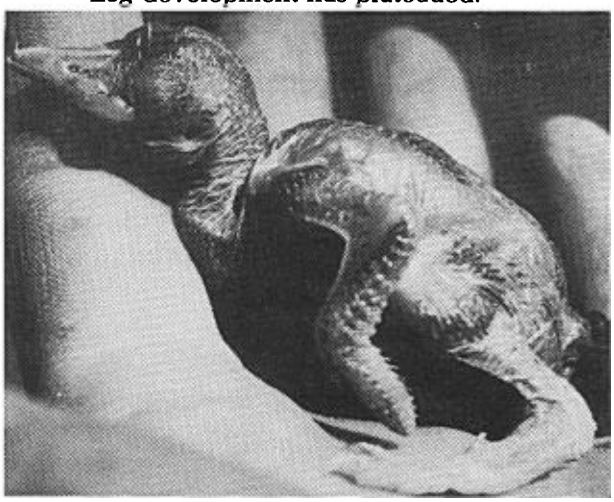
Niedrach (1965) list for western Colorado, and I measured only those birds taken between 1 January and 31 May to insure that they were fully grown when taken. Since two of the most important measurements, overall length and weight, could not be obtained from study skins, I had to rely on the tags for these, resulting in sample sizes of 9 and 2 respectively. Otherwise the data from all 32 adults are included in computations of adult measurements (Table 5).

Hatching data

After checking the nest for about 2 weeks, I found that 2 of the 6 eggs had hatched on the evening of 20 June, and 2 more eggs had hatched by the next morning. This indicated that the youngest nestling was 12 hours or more younger than the oldest. The remaining two eggs never hatched. The younger birds were smaller in all measurements than were the older two, but the individual nestlings grew at about the same rate which led to the last nestling to hatch remaining retarded in growth by about the equivalent of 2 days throughout the nesting stage. Despite this difference, all four nestlings fledged within 3 or 4 hours time 18 days after the last nestling hatched.

Like the Pileated Woodpeckers described by Hoyt (1944), the nestling Downys appeared to be unusually retarded in development at hatching. They were completely naked with feather papilla visible as faint dots only in the posterior part of the ventral tract, and in the greater primary and secondary coverts of the most advanced nestlings. The last nestling to hatch had no papilla visible in any feather tract. Their thin skin revealed their digestive organs and blood vessels inside, eyes and ears showed no cracks, bill and claws were white, the tip of the tongue was white, toes were flesh colored, and the upper mandible with its white egg tooth was 1 mm. shorter than the lower. Despite the appearance of physical underdevelopment, however, only the smallest nestling failed to right itself when placed on its back, and all four nestlings raised their heads and gaped with accompanying begging notes when handled.

Day 6. Alar tract sheaths have come through skin. Upper mandible still shorter than lower. Leg development has plateaued.

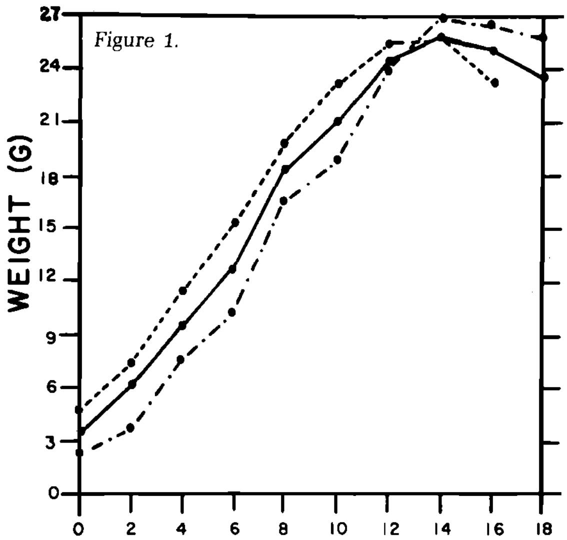


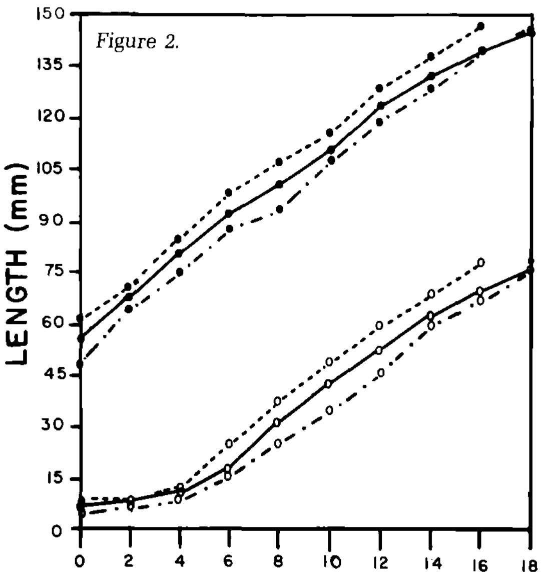
Morphological development

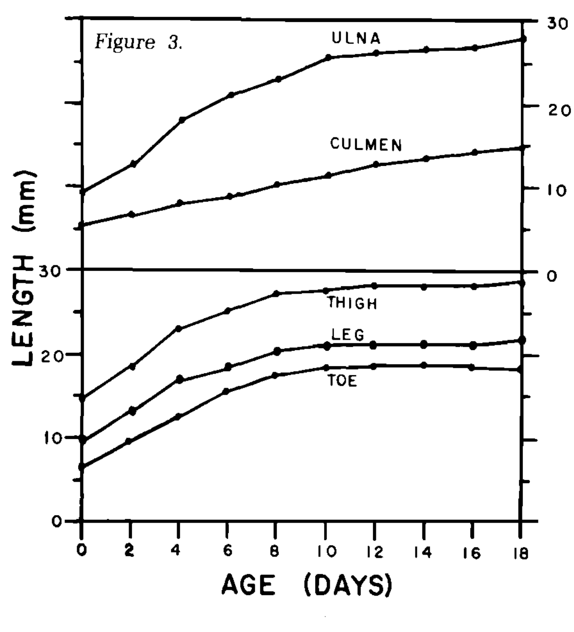
The rate of weight gain, development of overall length, wing chord, ulna, culmen, tibiotarsus, tarsometatarsus, hallux, and tail are presented in Figures 1 through 4, and the degree of their development relative to that of adult Downy Woodpeckers is given in Figure 5 and Table 4. These show that the overall length, and the length of wings, culmen, tail, and the various remiges continued to increase throughout nestling life and had not reached adult proportions at fledging. Leg parts, on the other hand, completed growth by halfway through nestling life and weight had peaked and started to decline in some nestlings as early as 4 days before fledging. The ulna followed a similar pattern of development to that of the leg parts and its slight apparent growth after day 8 (Figure 3) may be due to measuring error rather than to actual growth. Several patterns of development are shown by the various body parts; early, rapid growth and plateau in leg parts and weight; continuous, constant rate in length and culmen; and slow early, rapid later in the remiges. These varied in the same manner in the degree of development at hatching (Figure 5).

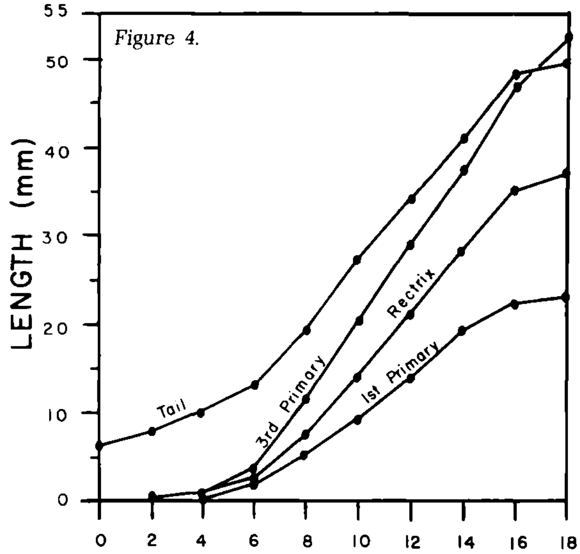
The development of the soft parts is summarized in Table 1. Bills and feet darkened from white or pink to dark grey. In the claws the greying progressed from base to tip, while in the bill it was reversed. The inner back toe was retarded both in the length of time it took to grey and in its development of clasping. There were conspicuous rictal flanges in the corner of the mandibles which began to atrophy soon after the middle of the nestling period, and the egg tooth disappeared by the 4th day. The eyes had a milky blue appearance immediately after opening, but they became bright black by the 12th day.

The developmental rate of the various feather tracts is summarized in Table 2, and that of the remiges is shown in Figure 4. The direction of feather development was from posterior to anterior in the capital, ventral and spinal tracts;









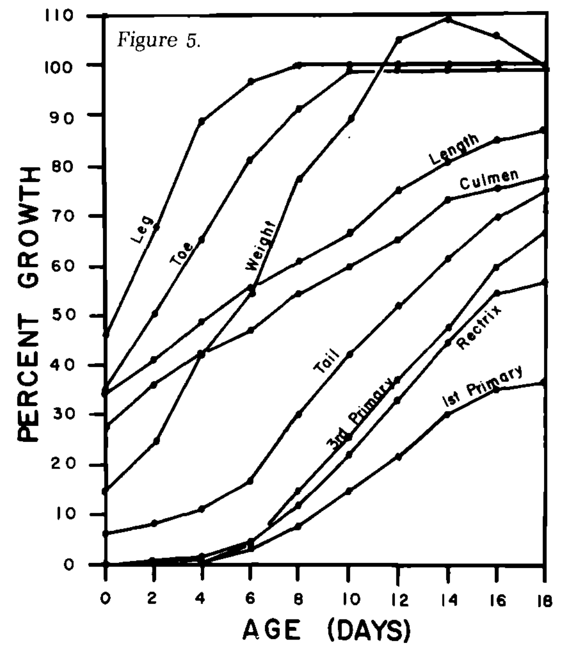


Figure 1. Weight gain of nestling Downy Woodpeckers from hatching (day 0) to fledging. The weight gain of the most advanced bird is indicated by the dashed line, the mean of all four nestlings by the solid line, and that of the most retarded bird by the dot-dash line.

Figure 2. Development of Downy Woodpecker overall length (solid circles above) and wing chord (open circles below) from hatching to fledging. Dashed line marks the development of the most advanced, the dot-dash line marks the development of the most retarded, and the solid line plots the mean measures for all four nestlings.

Figure 3. Mean developmental rates of the leg parts thigh (tibiotarsus), leg (tarsometatarsus), and toe (hallux) below; culmen and ulna above of 4 nestling Downy Woodpeckers.

Figure 4. Mean developmental rate of the tail, right central rectrix, and the 1st and 3rd primaries of the right wing of 4 Downy Woodpecker nestlings.

Figure 5. Relative growth rates of some Downy Woodpecker body parts expressed as percent of adult measurements. See text for details. Leg and toe are tarsometatarsus and hallux

Table 1. Timing of some conspicuous events in the development of nestling Downy Woodpecker anatomy.

Part	Appearance, hatching	Appearance, Comp.	Date[1]
Beak	White, conspicuous egg tooth, upper mandible 1 mm. shorter than lower.	Egg tooth gone.	4
		Uniform length.	8
		Dark grey.	10
		Rictal flange reduced.	12
Tongue	White tip.	Grey tip.	4
Toes	Claws white, toes pink.	Anterior claws grey.	4
		Posterior claws grey.	8
		Feet grey.	10
		Feet greenish-grey.	16
Eyes	Closed, no hint of crack.	Open a crack	4
		Open 2 mm.	6
		Completely open.	8
		Black irides.	12
Ears	Closed, no hint of crack.	Open a crack.	4
		Completely open.	8
Sexual dichromatism obvious.		Red crown, male.	8

[1]Number of days after the last nestling hatched when the most developed nestlings had reached the stage of development listed. Most retarded nestling was 2 days behind in most events.

from distal to proximal on the under wings; from trailing edge to leading edge in the dorsal wing coverts; and from medial to lateral in humeral and crural tracts. There was some hint of medial to laterial sequencing in the ventral tract also. Feather development was noticeably retarded under the wings, around the eyes, and at the base of the beak. These filled out just before fledging.

Feather development was so complete at fledging that only the remiges, rectrices, and greater remige coverts on the underwing still had sheaths on their bases. All of the dorsal apteria were covered several days before fledging in the most advanced nestlings, and at fledging in the most retarded. The conspicuous "white moustache" feathers fluffed out just before the nestlings left.. Newly fledged birds appeared short-tailed but otherwise completely feathered when seen in the woods.

Behavioral development

To the observer outside the nest, vocalizations are the first hint that the nestlings have hatched, and changes in the pattern of vocalizing provide a barometer of the growth taking place inside. As Lawrence suggested (1967: 125) but did not actually observe, nestling Downy Woodpeckers can be heard giving pip-pip-pip calls plus a longer, rasping note almost immediately after hatching. The soft pip was given almost continuously by one or more birds between feedings; the rasp was done while gaping. The shift from pip to rasp occurred when the parent appeared in the nest hole but could also be elicited when I climbed the tree, darkened the hole with my hand, or removed the tape holding the trap door shut. On the 16th day I first heard the nestlings give the only adult vocalization that I heard from them — the "whinney" (Short 1971). It appeared to be given spontaneously during breaks in pip calls rather than in response to any particular stimulus. Lawrence (1967) also noted that Downy nestlings give the "adult location call" which is most likely this same note. During the last days before fledging, the nestlings were silent for longer and longer time periods, seemingly in preparation for post-fledging silence. Then they were silent except for rasp notes given just before and while the parents fed them.

The nestlings were able to right themselves and gape soon after hatching. Gaping occurred during handling when the nestlings were jostled, or when I touched the sides of the upper mandible with a pencil during the early days of measuring them. Although I could not see them at times other than when the nest hole was open, I assume that the same stimuli that elicited rasping also elicited gaping since the two behaviors occurred simultaneously. When gaping during the first days of life, the nestlings teetered on their large abdomens using their tarsi as supports and their wings for balance while stretching the neck upward with wide open beak and rasping. Their necks were not strong enough to hold up the head for more than a second or two on the first day. By the second day they could hold their necks erect for several seconds, and by the 4th day they could not only hold their heads erect for longer periods of time but they could also elevate their abdomens from the ground by pushing upward from the tarsi. This increased the distance that they could reach.

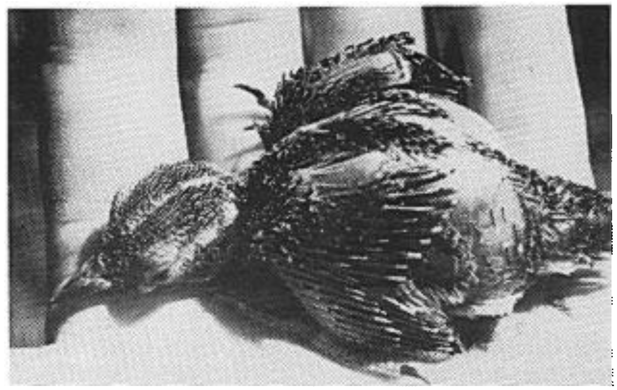
Righting was done in one of two ways depending upon how old the nestlings were when doing it. When they fell backwards or were placed on their backs during the first day of life, they righted themselves by pushing laterally with one wing and the outstretched head so that they rolled over one side and onto their abdomens. By four days of age they righted by reaching over their abdomens posteriorly with their heads at the same time as they pushed anteriorly with both wings, thus flipping over their tail and onto their feet. I term these two types of righting "lateral" and "anterio-posterior" respec-

Table 2. Development of nestling Downy Woodpecker plumage in the various feather tracts. Numbers indicate the number of days after hatching that these events occurred.

Tract/location	P. V.[1]	P. T.	S. S.	F. S.	Complete[2]
Capital					
Posterior	2-4	4	6	8-10	16
Anterior	6	8	10	12-14	18
Spinal					
Cervical	4	6	8	10	16
Interscapular	2	2	6	8-10	16
Dorsal	2	2	6	8-10	16
Pelvic	2	4	6	8-10	16
Humeral	2	2-4	6	8-10	16
Femoral	2	2-4	6	8-10	16
Crural	2	4	6	8	16
Ventral					
Anterior	6	8	10	12-14	18
Posterior	0	2-4	6	8-10	16
Caudal					
Rectrices	0	0-2	0-2	8-10	?
Alar					
Primaries	2	2	4-6	8-10	?
Secondaries	2	2	4-6	8-10	?
Greater primary coverts	0-2	2	4-6	8-10	16
Secondary coverts	—	—	4-6	8	16
Eye coverts	—	—	10-12	14	16

[1]Abbreviations are as follows: P. V. equals papilla visible under skin, P. T. equals papilla thickened, S. S. equals papilla through skin, F. S. equals feathers out of sheath.

[2]Based on estimation rather than measurement. Development was considered complete when the apterium was completely covered by the feather tract and sheaths had broken from base of feather.



Day 10. Feathers barely penetrating sheaths.

tively in Table 3. The most retarded nestling could gape but could not right himself before the second day after hatching, and the shift to anterio-posterior righting was proportionately retarded.

The development of grasping and clinging progressed rather rapidly and may provide insight into the comparative rates of development of the muscles that flex and extend the toes. Two-day-old nestlings could hyperextend their toes slightly, but could not flex them. The degree to which they could hyperextend increased by day 4, and by day 6 they could also flex their toes to about 2/3 closed. The most retarded nestling could barely flex his toes at this time. By day 8 the most advanced birds could hang for several seconds underneath my finger, using only their outer anterior toes, and by the 12th day they were suspending from my finger with all four toes clasped.

At this time they could also perch vertically on the rough bark of an aspen using their tails for support, but they could only suspend for several seconds from a pencil. The most advanced nestlings could suspend for several minutes from the pencil, could perch vertically (chin themselves) from my finger on the 14th day, and by the 16th day they could hitch upward on rough aspen bark by hopping from one knot (formed by the shelf fungus *Fomes* spp.) to the next. They were never able to cling to smooth aspen bark vertically during these tests, and I have seen fledglings slip and slide on smooth aspen bark several days after fledging. Thus adult birds may move across aspen bark, by hitching from one roughened spot to another rather than by clinging to smooth bark, a suggestion supported by Kilham's (1971) observations with Yellow-bellied Sapsuckers *(Sphyrapicus varius)*.

As the sensory systems of the nestlings matured, they became more selective in their response to my activities and to other stimuli. This selectivity can be seen in three sources of data: 1) Greater selectivity in the stimuli that would elicit gaping and rasping; 2) The development of an alert appearance when handled; 3) Escape and attack attempts during measurement. These all became apparent after the ears opened on day 8 and the eyes brightened on the 12th day after hatching.

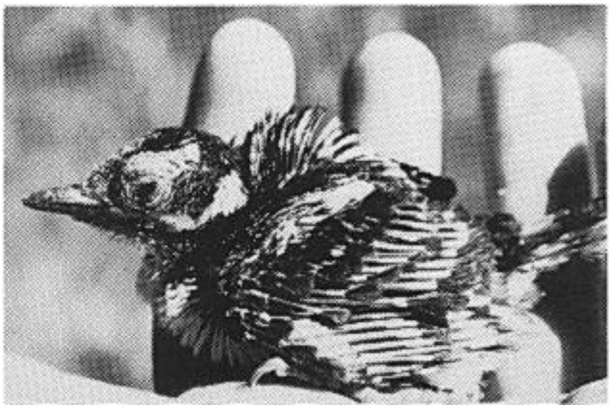
Through the 8th day the nestlings rasped when the tree was being climbed and the nest hole opened, but this changed from day 10 until fledging. On days 10 through 12 the rasp ceased when the door was actually open, and the nestlings gave the pip note but did not rasp when they were handled. They began to rasp once again when the hole was taped shut and I was climbing down the tree. This pattern was the same on the 14th day except that 3 of 4 nestlings were silent during measurement, and the least developed bird gave only soft pips. All were silent when measured on the 16th and 18th days. They hunched down when the hole was opened and became progressively harder to extract beginning on the 12th day.

The most advanced of the 14-day-old birds appeared more alert than any had appeared previously, all nestlings appearing alert on the 16th day. The change in the bird's posture and manner was striking at this time. The eyes were kept open as the bird was handled, the head and body were held erect, and jerky head movements from side to side and to the front reminded me of an adult bird making flight-intention movements. The plumage was sleeked, and the little birds had the appearance of being much more mature than they had been on previous days.

Sixteen-day-old nestlings first attempted to escape while being handled, both by flying away from me, and by hiding under vegetation. Although they first attempted to fly at 14 days, these flights were no longer than 1 to 2 feet, and their goal appeared to be movement from a horizontal to a vertical surface rather than escape. The nestlings frequently jumped from the scale's pan to the sides of the pan, or from the hand or lap to the front of my shirt. There was no movement away from me, and there was no attempt to hide under vegetation. On the 16th day, however, flights of up to 4 m from the scale ended with the little birds crawling under grass or bushes. The most advanced male flew almost 10 m when the nest was opened, and landed in a bush, clutching it with both feet. The little birds hitched up an aspen when they were placed there for photos, and a 6 m flight by one bird from this tree led to a 20 minute search before it was found and replaced in the nest.

Table 3. Summary of events in the behavorial development of Downy Woodpeckers and the age of first occurrence.

Behavorial pattern	Age of first occurrence
Pips and rasps.	0
Gaping response, head extended.	0
Hyperextension of toes.	0
Rights self laterally.	0-2
Anterio-posterior righting.	2-4
Partial flexion of toes.	4
Suspends from under finger, anterior toes.	8
Suspends from finger, pencil, bark, all toes.	12
Preens abdominal feathers.	12
Eyes held open throughout handling.	12
First flight, 1-2 feet long.	14
First flight of 10 m or more.	16
Hitches up tree.	16
Tries to escape, hides under vegetation.	16
Adult-like "whinney" call.	16
Pecks at observer.	18
Fledge.	18



Day 12. Conspicuous tufts of feathers.

Although the nestlings remained in the nest when replaced on the 16th day, they were obviously quite mature both behaviorally and anatomically — almost ready to fledge. The most advanced bird had already fledged when the nest was visited on the 18th day, and the remaining three nestlings fledged soon thereafter. I continued to visit the aspen grove during the week after fledging and on several occasions saw fledglings fly silently in pursuit of an adult, rasping after landing until the parent fed it. The family group thus stayed together for at least a week outside of the nest, but the silence, crypsis (hiding ability), and increasing mobility of the fledglings made it impossible to follow them after one week.

Downy Woodpecker development in evolutionary perspective

This brings us to the question, "Why is it adaptive for Downy Woodpeckers to have a long nestling period when compared with passerine birds of similar size"?

Lack observed (1968) that relative to open nesting passerines, woodpeckers had small eggs, short incubation periods, and long nestling stages. This suggested that woodpeckers had evolved their

Table 4. Percent development of some Downy Woodpecker parameters at hatching (1st no.) and fledging (2nd no.) compared with some other birds.

Parameter	Downy Woodpecker[1]		Brewer's B. B.[2]		Pinyon Jay[3]		Horned Lark[4]	
Weight	14.8	100.0	5.7	70.7	6.1	75.51	7.1	—
Overall length	34.0	87.6	—	—	—	—	—	—
Wing chord	6.8	74.6	6.6	63.0	—	—	6.9	53.3
Culmen	28.2	78.2	30.2	73.3	—	—	35.6	64.4
Tarsometatarsus	46.1	100.00+	25.9	100.6	—	—	—	—
Hallux	35.6	98.4	21.8	94.7	—	—	25.3	87.3
1st Primary	0.0	36.4	—	—	0.0	62.7	0.0	57.1
3rd Primary	0.0	67.0	0.0	69.0	—	—	—	—
Central rectrix	0.0	57.3	0.0	28.0	0.0	23.6	0.0	18.8

[1]This study. See Table 5 for adult measurements on which the calculation is based.
[2]Calculated from data in Balph 1975.
[3]Calculated from data in Bateman and Balda 1973.
[4]Calculated from data in Beason and Franks 1973.

pattern of development because food was more abundant when nestlings were being raised than when eggs were being formed. By this hypothesis, woodpeckers with reduced resources during egg formation lay eggs with little yolk, which leads to the hatching of less developed nestlings. These nestlings then require a longer nestling period to reach the stage of development equivalent to that of passerines. By comparing the degree of Downy Woodpecker development at hatching and fledging with that of some passerine birds (Table 4) we can test this hypothesis. For it to be correct, Downys should be underdeveloped at hatching, should have a long nestling period, and should fledge at the same level of development as similar-sized passerines.

The nestling period is long, since most open-nesting passerines fledge at between 7 and 12 days of age. But are nestling Downys underdeveloped at hatching? Table 4 shows that the answer depends upon which parameter one is comparing. While nestling Downys appear to be underdeveloped in feathers, they are similarly developed to Brewer's Blackbirds and Horned Larks in wing chord, and much better developed in weight and in the development of the various leg parts than are any of the three passerines. They are also stronger, since they can right themselves and gape on day 0 in all but the least developed case, while gaping occurs later in Pinyon Jays (Bateson and Balda 1973) and also in the Cactus Wren (*Campylorhynchus brunneicapillus*, Anderson and Anderson 1961), and righting ability developed later in Brewer's Blackbirds (Balph 1975) in addition to these other two species.

Fledgling Downys appeared to be at least equally developed in all parameters except 1st primary when compared to the three passerine species (Table 4) and strikingly more developed in weight and rectrices. Indeed, they had reached the same degree of development at days 8 and 10 in those last two parameters as had Brewer's Blackbirds and Horned Larks when they fledged at similar age. Downy fledglings were also more completely developed in wing chord, culmen, and hallux than were Horned Larks and Brewer's Blackbirds. Although Holcomb (1966) and I did not collect our data in exactly the same way, the development of toe flexion and suspension between days 4 and 12 in Downys is not very different from the development of grasping and balancing ability in 7 passerine species between 5 and 9, suggesting that Downys may be more mature behaviorally at fledging than are some passerines. Nestling Downys also can fly very well at fledging (and can fly to some degree 2 days before), while some passerines cannot fly at all for several days after fledging (e.g. Fitch and Fitch 1955; Maher 1964). The relatively complete feather development in Downys, especially in rectrices (Table 4) and body feathers (text) contrasts with that of at least some passerines (e.g. Bateman and Balda 1973).

Instead of supporting Lack's (1968) hypothesis, these data support the following conclusions. 1. At hatching Downy nestlings are more developed in leg parts and behavioral patterns related to reaching upward for food (righting and gaping) and less advanced in feather development than are some passerine nestlings. 2. Nestling Downy Woodpeckers develop first those behaviors and parts related to increasing their reach upward, then develop feathers and sense organs. 3. Fledgling Downy Woodpeckers are as well developed in almost all measured parameters as are those passerines to which they were compared, and they are more completely developed in rectrices, wing chord, hallux, flight, and grasping. These characteristics must have adaptive value to woodpeckers.

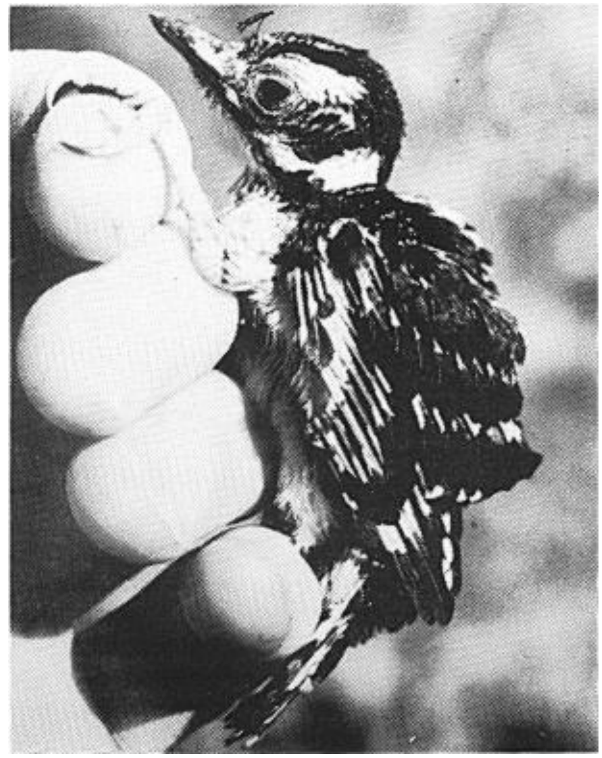
Internestling competition for food could cause selective pressure for the comparative overdevelopment at hatching — and rapid post-hatching development — of those features that facilitate reaching upward. Unlike the situation in those open-nesting birds I have observed where the parent birds land at the edge of the nest, reach over and feed the young, parent woodpeckers squeeze through a hole well above their nestlings and climb down head first, feeding them while hanging vertically from the wall of the nest cavity. In the darkness of the nest hole food is delivered to those nestling beaks that reach the parent first. Since food comes from above, nestlings that can not reach as high as their siblings would get less food and thus be selected against, especially in times of food shortage.

On the other hand, feathers are relatively less important to the nestling woodpeckers because the nest cavity is better insulated than is an open nest, and I have observed that parent woodpeckers continue to brood for at least the first week after hatching. Sense organs need not develop quickly because the nest cavity is safe from those predators that cannot enter, and enemies that could enter the nest hole would trap the youngsters even if they sensed danger. The quick development of leg parts, strength, and balance would thus be favored at the expense of feathers and sense organs, leading to the pattern of development observed from hatching through early nestling life.

Table 5. Adult Downy Woodpecker measurements.[1]

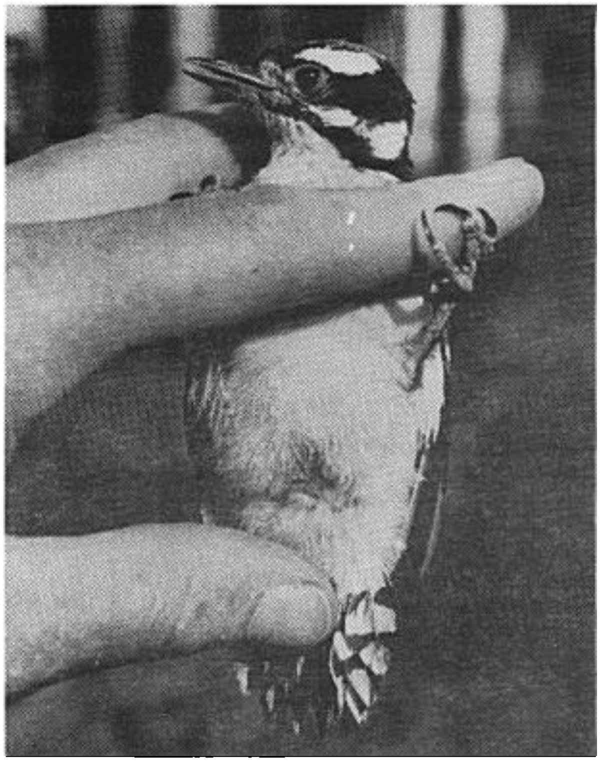
Structure	Mean ± 1 S.D.		N[1]
Weight	23.7		2
Overall length	165.5	33.7	9
Culmen	18.8	0.6	32
Wing chord	101.9	2.6	32
Tarsometatarsus	19.1	1.1	32
Hallux	19.1	1.1	32
Rectrix	64.6	2.8	32
1st Primary	63.2	2.4	32
3rd Primary	78.7	2.5	32

[1]Number of birds on which this mean is based. Standard deviations were not calculated for weight because of the small sample size, see text for details. Units are grams for weight, mm. for length.



Day 12. Advanced nestling. Note tail position.

The ability to fly and to grasp well after fledging are obviously important to woodpeckers. Whereas the fledging perching bird can move from the nest by hopping from branch to branch (e.g. Fitch and Fitch 1955) or across the ground (Maher 1964, Beason and Franks 1973) fledging Downys must crawl through a vertical hole and then grasp vertical bark while perching or moving about in search of food. Working over vertical surfaces requires greater strength than perching on a horizontal surface since gravity must continually be overcome. The ability to grasp is favored before fledging through internestling competition because, as the nestlings become able to cling to the vertical surface of the nest cavity, they receive food closer and closer to the nest hole (Lawrence 1967). Nestlings that did not develop the ability to grasp as rapidly as their siblings did would thus receive less food. The proportionately greater development of rectrices is adaptive since they are needed as supports when perching vertically, and as shock absorbers when landing. Greater development of body feathers would be adaptive if they provided better insulation and thus more efficient use of calories. Fledglings that can fly to parents arriving with food instead of perching conspicuously and calling to them probably benefit both by being fed more often and by attracting less predation. Thus the long nestling period of Downy Woodpeckers appears to be the result of two evolutionary forces. 1. Since nest holes are relatively safe from predation there is little selection pressure to get away from the nest early. 2. In the absence of selection for early fledging, selection has favored a long nestling period and overdevelopment of features which lead to greater success after fledging.



Day 16. All apteria covered. The most advanced birds can fly 10 m or more at this age.

This study not only demonstrates that the nestling strategy of Downy Woodpeckers differs from that of the perching birds that have been studied, but also shows that more parameters of development than just the rate of weight gain must be studied if the breeding biology of an avian species is to be understood evolutionarily. While there have been many studies of weight gain, there have been few studies that measure enough parameters to give a complete picture of developmental biology. I hope that this paper will stimulate more studies of woodpecker development, as well as more complete studies of the development of other birds.

Literature cited

Anderson, A.H. and A. Anderson. 1961. Life history of the Cactus Wren Part IV: development of nestlings. *Condor* 63:87-94.

Bailey, A.M. and R.J. Niedrach. 1965. Birds of Colorado, Vol. I. Denver Museum of Nat. Hist., Denver. 454 pp.

Balph, M.H. 1975. Development of young Brewer's Blackbirds. *Wilson Bulletin* 87: 207-230

Bateman, G.C. and R.P. Balda. 1973. Growth, development, and food habits of young Pinyon Jays. *Auk* 90:39-61.

Beason, R.C. and E.C. Franks. 1973. Development of young Horned Larks. *Auk* 90:359-363.

Crockett, A.B. and H.H. Hadow. 1975. Nest site selection by Williamson and Red-naped Sapsuckers. *Condor* 77:365-368.

Fitch, H.S. and V.R. Fitch. 1955. Observations on the Summer Tanager in northeastern Kansas. *Wilson Bulletin* 67:45-54.

Holcomb, L.C. 1966. The development of grasping and balancing coordination in nestlings of seven species of altricial birds.

Hoyt, J.S.Y. 1944. Preliminary notes on the development of nestling Pileated Woodpeckers. *Auk* 61:376-384.

Inouye, D.W. 1976. Nonrandom orientation of entrance holes to woodpecker nests in aspen trees. *Condor* 78:101-102.

Kilham, L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers I. Preference for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, racoons, and other animals. *Wilson Bulletin* 83:159-171.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London. 409 pp.

Lawrence, L.D.K. 1967. A comparative life-history study of four species of woodpeckers. Ornithological Monographs #, A.O.U. 156 pp.

Maher, W.J. 1964. Growth rate and development of endothermy in the Snow Bunting *(Plectrophenax nivalis)* and Lapland Longspur *(Calcarius lapponicus)* at Barrow, Alaska. *Ecology* 45:520-528.

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis* 110:419-451.

Ricklefs, R.E. 1974. Energetics of growth in birds, pp 152-297. *Inn* Avian Energetics. Publ. Nuttal Ornith. Club, 15 (R.A. Paynter, Editor). 334 pp.

Short, L.L. 1971. Systematics and behavior of some North American woodpeckers, Genus *Picoides* (Aves). Bull. Am. Mus. Nat. Hist. 145:1-118.

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