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MORPHOLOGICAL GROWTH, BEHAVIORAL DEVELOPMENT, AND PARENTAL CARE OF BROAD-WINGED HAWKS

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Abstract.—Patterns in morphological growth, behavioral development, and parental care of Broad-winged Hawks (*Buteo platypterus*) are described and compared with other birds. Rapid body growth preceded feather growth and development of stand, walk, and self-feeding in nestling hawks. During rapid body growth, nestlings slept most of the time, and were fed and brooded by female parents. Successful performance of walk and self-feeding occurred only after body weight and bill and tarsus lengths were 80 to 90 percent of adult sizes. Nestling development and parental care of hawks resembled altricial development except that chicks hatched with open eyes and were covered with down. Prepennae down could provide insulation for development of homeothermy. A thermoregulatory function for down may be important only when female parents must leave nests for long periods to hunt during food shortages. Nestling hawks took an active role in parental feeding bouts compared with young of some altricial species and visual perception appeared important in coordinating their feeding behavior. Early development of vision, together with constraints in bill structure, may have contributed to the evolution of active nestling feeding behavior.

CRECIMIENTO, DESAROLLO DE PATRONES DE CONDUCTA Y CUIDADO PARENTAL EN *BUTEO PLATYPTERUS*

Sinopsis.—En este trabajo se describe y se compara con otras especies de aves el crecimiento de pichones, desarrollo de patrones de conducta y el cuidado parental en *Buteo platypterus*. El rápido crecimiento corporal, precede al desarrollo del plumaje, desarrollo de la postura, el caminar y el poder los pichones alimentarse por si solos. Los pichones duermen la mayor parte del tiempo durante el periodo de crecimiento rápido, y en este tiempo son cobijados y alimentados por la hembra. Caminan adecuadamente y se alimentan por si solos, sólo despues que su peso y el largo del pico y tarso, han alcanzado del 80 al 90% del peso y tamaño de los adultos, respectivamente. El desarrollo de los polluelos y el cuidado parental de los adultos se asemeja al de especies altriciales, con la excepción de que los pichones *B. platypterus* nacen cubierto de plumón y con los ojos abiertos. El plumón en estas aves puede proveer aislamiento térmico, para el desarrollo de la homotermia. Por lo general las hembras pasan mucho tiempo en el nido cubriendo y cobijando a los polluelos. Es probable que la función termoreguladora del plumón sea particularmente importante sólo en periodos de escasez de alimentos, cuando para cazar las hembras se ven obligadas a permanecer fuera del nido por periodos prolongados de tiempo. Contrario a otras especies altriciales en donde la alimentación es pasiva, los polluelos de este halcón juegan un rol muy activo en los encuentros alimentarios con sus progenitores. La percepción visual parece ser muy importante en la coordinación alimentaria. El temprano desarrollo de la visión, unido a las limitaciones impuestas por la particular estructura del pico de estas aves, puede haber contribuído al desarrollo evolutivo de este activo patrón de conducta alimentaria.

Morphological and behavioral development can be species typical in that similar patterns occur in most members of a species given a normal

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range of environmental conditions (Miller 1981, Oyama 1982, Ricklefs 1983). The diversity of developmental pathways along which avian species progress from hatching to adulthood is considerable. Nice (1962) used five criteria of hatchlings to classify birds into eight categories along a precocial-altricial spectrum; eyes (open or closed), down (present or absent), mobility (ambulatory or nest-bound), provider of nourishment (self or parent), and parental care including defense, brooding, and food showing (present or absent). Ricklefs (1973) examined relationships between rates of body growth and maturation of function in 81 avian species. Young of most precocial species have mature homeothermic, pedal locomotor, and self-feeding capabilities shortly after hatching and grow three to four times slower than altricial chicks, which acquire these functions only after body growth is nearly completed. In this paper we describe developmental patterns of Broad-winged Hawks using traits Nice (1962) and Ricklefs (1973) used in their comparative studies of avian development. By comparing patterns in morphological growth, behavioral development, and parental care of Broad-winged Hawks with other birds, we consider the functional utility of some aspects of postnatal development in hawks.

METHODS

Subjects and study sites.—Thirty-three nestlings from 15 nests and 10 parents from five of these nests served as subjects during the 1980, 1981, and 1982 breeding seasons. Titus and Mosher (1981) provided detailed descriptions of study sites in Garrett and Allegany counties, Maryland. We designated the first day posthatch as day 1. We knew hatch dates (±24 h) for 25 nestlings and collected growth data from 22 of these birds at 10 nests. We estimated ages of 8 nestlings with a model based on wing length (Lyons and Mosher 1983). These 8 nestlings and 3 known-age nestlings served as subjects for behavioral observations.

To minimize effects of human disturbance on nestling and parental behavior, we did not collect extensive growth data from nestlings monitored for behavioral development. We marked all nestlings and some adults with indelible dyes for individual recognition. Nestlings could not be sexed because of insufficient sexual dimorphism in external morphology (Lyons and Mosher 1983) and behavior. Gender specific differences in developmental rates observed in other Falconiformes (Bartolotti 1984, Moss 1979, Newton, 1977, Scharf and Balfour 1971) probably contributed to variability in our developmental data.

We distinguished individuals of three mated pairs by blue dye placed on breast feathers or by naturally occurring plumage differences. We sexed adults by comparing parental behavior to that described by Matray (1974) who correlated behavior with the presence (female) or absence (male) of a brood patch on trapped adults. Males never brooded chicks and their nest visits were brief. Females fed and brooded chicks, and delivered sticks and green sprigs to nests for several weeks posthatch

(Lyons et al. 1986). These gender specific differences in behavior are widespread among Accipitridae.

Growth of feathers and body parts.—We recorded length of the tarsus, bill (without cere), flattened wing, 4th and 6th primaries, central and outer rectrices, and body weight during visits at 2–5 d intervals. We measured tarsus and bill lengths with calipers, wing and feather lengths with a steel rule, and body weights with a portable electronic balance. We tethered 2 nestlings to elevated platforms at the base of 2 nest trees (see Petersen and Keir 1976) from 27–38 and 29–46 d posthatch. Each night wire cages were secured to platforms to protect tethered nestlings from nocturnal predators. We obtained extended growth records from tethered individuals by delaying departure. All growth data from 35–46 d were from these birds.

For each morphological variable we fitted mixed-longitudinal growth data with a logistic equation:

$$W(t) = A/(1 - \exp[\{2.2/t_{50\text{-}90}\} \times \{t_{50} - t\}])$$

where $W(t)$ is the predicted size at age t (d), A is the asymptote of the growth curve, $t_{50\text{-}90}$ is the time (d) required to grow from 50 to 90 percent of asymptotic size, and t_{50} is the age at which rate of growth is maximal (the inflection point of the logistic curve). We added t_{50} and $t_{50\text{-}90}$ to determine the age at which 90 percent of asymptotic size was reached. In this model $(2.2/t_{50\text{-}90})$ is equivalent to Ricklefs' (1967) logistic growth rate constant describing the rate at which the asymptote is achieved. Since all data were fitted by the same logistic model all growth rate constants are directly comparable. We fitted logistic equations to growth data using nonlinear least squares regression (Jennrich 1983) with age assigned the independent variable. Initial estimates of the parameters of each logistic equation are required by this computer program and we calculated these using Ricklefs' (1967) graphical curve fitting method.

Behavioral development and parental care.—We spent over 225 h watching 11 nestlings and their 10 parents at 5 nests. We used a 15–60× spotting scope and made observations from blinds suspended in trees or placed on the ground 32–60 m from nest trees. To reduce chances of nest desertion by parents, we constructed blinds over a 3–4 d period after hatching. Earliest records of behavior began 4 d posthatch.

We collected quantitative data on nestling and parental behavior at 3 nests containing 2, 2, and 3 nestlings. We randomly prescheduled 30 observation periods of 4.6 h duration between 06:00 and 21:00 from 4–31 d posthatch. Observations began 15–20 min after entering a blind and each period consisted of eight 30 min recording sessions separated by five min rest intervals. We used an instantaneous scan sampling method (Altmann 1974) and recorded parental and nestling postures and activities every 30 s during each 30 min session. We scanned individuals at a nest in the same order and for the same brief time period.

Recorded parental behavior included attendance, brooding, and feeding of nestlings. Recorded nestling postures and behavior patterns included lie, sit, stand, one-leg-stand, head-droop-sleep, head-tuck-sleep, walk, and self-feeding. These postures and behavior patterns were essentially identical in form to those described in Golden Eagles (*Aguila chrysaetos*) (Ellis 1979).

Individual nestlings or adults served as the focus for observations when we recorded postures and nonfeeding activities. We observed an entire brood of nestlings when recording parental feeding or self-feeding by nestlings. In each scan, we recorded feeding whenever at least 1 nestling was eating. We transformed behavioral data by dividing the number of scan samples when a posture or activity occurred by the total number of samples (488) recorded for an individual in each 4.6 h observation period. Changes in behavior over time were evaluated statistically with linear least squares regression.

RESULTS

Chicks hatched with open eyes and were covered with a thick prepennae down (Fig. 1). From hatching to day 10 chicks remained downy and morphological development was characterized by rapid body growth. Growth rates for the bill, tarsus, and body weight increased and reached respective maxima at 1.5, 7.8, and 10.6 d (Table 1, Fig. 2). After day 11 growth rates for these body parts declined as nestlings approached adult sizes.

Primaries of the alar tract were the first contour feathers to emerge on the body at 9 d posthatch. Wing length and 4th and 6th primary lengths reached maximum growth rates at 19–22 d, at which time the bill, tarsus, and body weight attained 90 percent of asymptotic sizes (Table 1, Fig. 2). Rectrices emerged 2–4 d after primaries and attained maximum growth rates on day 25.

During the first 9 d nestlings spent 97 percent of the time in the lie posture (Table 2), and head-droop-sleep and parental feeding were predominant activities (Table 3). Hawk chicks took an active role in parental feeding compared to some altricial species in which adults directly place food into the gaping mouths of begging nestlings. Hawk chicks oriented toward the parent's food-laden bill, reached forward and actively grabbed food morsels. They appeared to rely on vision to coordinate their feeding behavior.

Prior to day 10 all sleep occurred in the head-droop-sleep posture. Head-tuck-sleep first appeared at 10–15 d (Table 3) and accounted for an increasing proportion of sleep time ($F = 6.8$; df = 1,73; $P < 0.01$) as nestlings matured and overall time spent sleeping declined ($F = 284.9$; df = 1,73; $P < 0.001$). Coinciding with appearance and development of head-tuck-sleep was the emergence and growth of contour feathers on the dorsal surface of the body and wings. Feathers may have supported the head in the head-tuck-sleep posture.

From 10–31 d stand and one-leg-stand were first performed and gradually replaced lie as predominant postures (Table 2). When stand and one-leg-stand became primary postures at 28–31 d, nestling body growth

FIGURE 1. A one-day-old Broad-winged Hawk chick sits on top of a hatching egg. Siblings hatch asychronously over a 1–4 d period.

was nearly completed (Table 1, Fig. 2). The developmental trend in walk paralleled that for stand. Walk was first performed at 8–10 d and was poorly coordinated. The wings were often flapped or drooped to the nest, aiding in support and balance. By 18–20 d walk was well coordinated and wings were usually held close to the body.

Nestling self-feeding appeared on day 20 and increased in frequency ($F = 7.6$; df = 1,11; $P < 0.05$) until observations ended (Table 3). Tearing meat from prey provided by parents required strength and coordination. Successful performance of self-feeding occurred only after body growth was nearly completed (Table 1, Fig. 2).

Female parents spent a lot of time at the nest, brooding and feeding nestlings (Table 3). As nestlings matured, females devoted less time to attending ($F = 106.9$; df = 1,28; $P < 0.001$), brooding ($F = 73.2$; df = 1,28; $P < 0.001$), and feeding nestlings ($F = 9.7$; df = 1,28; $P < 0.01$), and presumably spent more time hunting for food. Females removed uneaten parts of prey from nests and frequently appeared to retrieve these for subsequent feeding bouts. Caching during the breeding season has been reported in many Falconiformes (Lyons and Mosher 1982).

Male parents never brooded nestlings and spent very little time at nests. Their visits ($N = 35$) never exceeded 3 min. One male fed nestlings on 2 occasions at 15–17 and 22–24 d posthatch. The sequence of events for each of these 2.5 min feeding bouts was similar. The male delivered a

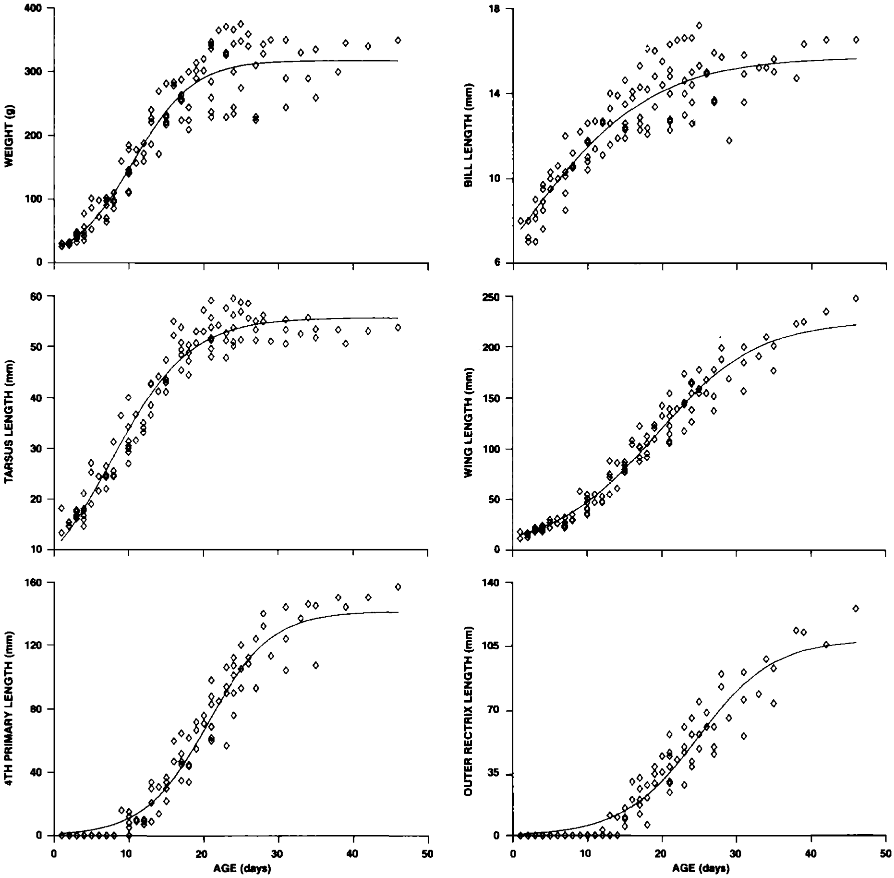

FIGURE 2. Broad-winged Hawk growth data and logistic growth curves for body parts and feathers. Each plot contains 110 measurements of 22 nestlings from 10 nests.

small mammal to the nest, tore off a piece of meat, and fed it to a nestling. After vocalizing several "dismissal" calls (see Matray 1974) from a perch 5–7 m above the nest, the female flew onto and supplanted the male from the nest rim. She then continued the feeding bout. These observations are unusual in that Matray (1974) never saw a male feed nestlings in 110 food deliveries.

Nestlings first left nests at 29–31 d. From days 30 to 46 morphological development consisted of contour feather growth, particularly in long flight feathers of the wings and tail, and slow growth of the body (Table 1, Fig. 2). Few observations of nestling or parental behavior were made after nestlings first left nests because of difficulty in locating birds in dense overstory canopy. Young hawks spent much of this time perched on

TABLE 1. Descriptive growth parameters (± asymptotic standard deviation) from logistic equations fitted to hawk growth data by nonlinear least squares regression.

Morphological variable	Age (d) at maximum growth rate	Time (d) to grow from 50 to 90% of asymptote	Logistic growth rate constant
Bill length	1.5 ± 0.7	18.6 ± 1.5	0.118
Tarsus length	7.8 ± 0.3	11.4 ± 0.6	0.193
Body weight	10.6 ± 0.4	8.7 ± 0.6	0.252
Wing length	19.1 ± 0.5	15.1 ± 0.7	0.146
4th primary	20.5 ± 0.4	9.3 ± 0.6	0.235
6th primary	21.7 ± 0.4	10.4 ± 0.6	0.212
Central rectrix	24.7 ± 0.5	10.9 ± 0.3	0.202
Outer rectrix	24.8 ± 0.6	11.1 ± 0.8	0.197

branches close to their nest and often returned for food delivered by parents during brief nest visits.

DISCUSSION

Ricklefs (1968, 1973) calculated growth parameters for over 100 bird species and numerous comparisons can be made with Broad-winged Hawks. Based on Ricklefs' (1968) equation correlating growth rate with adult body size for 52 altricial and semi-altricial species, Broad-winged Hawks have an expected growth rate constant of 0.224. The observed growth rate constant for body weight (0.252, Table 1) is slightly higher than predicted and is three to four times greater than that for similar sized precocial species (see Ricklefs 1973).

A second useful measure for comparing growth rates of similar sized species is the time required to grow from 10 to 90 percent of the asymptote, $t_{10\text{-}90}$ (Ricklefs 1967). This growth parameter can be derived from data in Table 1 by multiplying $t_{50\text{-}90}$ by two. Hungarian Partridge

TABLE 2. The percentage of scan samples nestling hawks spent in each of four postures. Each entry is based on 2928 to 3904 samples collected over 24 to 32 nestling-hours of observation.

Age (d)	Postures			
	Lie	Sit	Stand	One-leg-stand
4–6	99	1	0	0
7–9	97	3	0	0
10–12	83	17	1	0
13–15	81	18	1	0
16–18	78	18	3	0
19–21	58	25	17	0
22–24	51	18	32	1
25–27	43	17	39	2
28–31	17	8	55	21

TABLE 3. The percentage of scan samples female parents and nestling hawks spent in 6 behavioral states. Entries for sleep postures are based on 2928 to 3904 samples of nestling behavior and remaining entries are based on 488 to 2440 samples of brood or parental behavior.

Nestling age (d)	Parental nest attendance	Brooding	Parent feeding nestlings	Nestling self-feeding	Head droop sleep	Head tuck sleep
4–6	97	86	12	0	88	0
7–9	91	65	17	0	82	0
10–12	78	56	15	0	52	1
13–15	58	45	7	0	49	1
16–18	41	34	5	0	44	4
19–21	32	13	9	3	20	5
22–24	16	6	9	6	16	7
25–27	8	0	8	3	11	4
28–31	3	0	3	13	4	2

(*Perdix perdix*) are precocial birds similar to Broad-winged Hawks in adult body size. Estimates of $t_{10\text{-}90}$ for Hungarian Partridge (Ricklefs 1973) are 45–57 d greater than Broad-winged Hawks. In 17 days hawk chicks grow from 10 to 90 percent of asymptotic body weight (Table 1, Fig. 2). This represents an average daily weight gain of 16 g and concurs with growth data Fitch (1974) collected from two Broad-winged Hawks.

Rapid body growth of Broad-winged Hawks precedes feather growth (Table 1, Fig. 2) and development of stand, walk, and self-feeding (Tables 2 and 3). During the period of rapid body growth nestlings spend most of the time sleeping, and being fed and brooded by female parents. Successful performance of stand, walk, and self-feeding occur only after the bill, tarsus, and body weight are 80–90 percent of adult sizes. Coinciding with nestling developmental adjustments are changes in parental behavior. The general trend is from greater to lesser dependence on parents.

Rapid body growth of nest-bound chicks, delayed development of mature feeding and pedal locomotory behavior, and dependence on parental feeding and brooding are altricial traits in avian development (Nice 1962, Ricklefs 1983). These characteristics are evident in developmental patterns of other semi-altricial Falconiformes (Bartolotti 1984, Ellis 1979, Moss 1979, Newton 1977, Scharf and Balfour 1971), semi-altricial Ciconiformes (Jenni 1969; Kahl 1962, 1966; Milstein et al. 1970; Telfair 1983; Werschkul 1979) and altricial Passeriformes (Banks 1959, Kuhlman 1909, Ricklefs 1979a). Of 27 taxonomic orders of Aves considered by Nice (1962), 19 occupy a fairly uniform position on a precocial-altricial spectrum. This conservative phylogenetic pattern suggests that avian developmental pathways are evolutionarily inflexible, or that development is constrained by inflexible attributes of adult morphology or ecology (see Ricklefs 1979a,b, 1983).

Nice's (1962) classification emphasizes that nestling condition varies principally on a single axis from independence to dependence on parental care. Nest-bound altricial and semi-altricial chicks are generally fed items that are difficult or impossible for inexperienced birds to secure on their own. Hunting and feeding behavior of Broad-winged Hawks, for example, requires strength, coordination, and skills that take time to develop. Rapid body growth supported by intensive parental care shortens the period when these dependent chicks are vulnerable to predators (Werschkul 1979). In contrast, self-feeding precocial chicks consume foods that are readily accessible to non-flying, unpracticed birds. Mobility reduces risks of predation and homeothermic capabilities free parents from brooding precocial chicks. Early development of homeothermic, ambulatory, and self-feeding capabilities removes limitations on brood size imposed by parental care, enabling adults to rear more precocial offspring. If species specific ecological conditions permit chicks to feed themselves, early maturity of function is favored by natural selection, but precocity of development places constraints on rates of body growth (Ricklefs 1973, 1979a,b, 1983).

Broad-winged Hawks exhibit two traits that distinguish semi-altricial from altricial patterns of avian development: chicks hatch with open eyes and are covered with down (Fig. 1). Prepennae down could provide insulation for homeothermy in nestling hawks; however, the great amount of time female Broad-winged Hawks spend brooding downy chicks (Table 3) suggests that a thermoregulatory function for down is not always needed and may be important only when females must leave nests for long periods. During times of food shortage females share hunting responsibilities with adult males and survival of chicks may depend on their ability to maintain their own body temperatures.

Newton (1978) and Moss (1979) compared behavior of Sparrowhawks (*Accipiter nisus*) nesting along forest edges where prey was abundant with those nesting farther from good feeding areas. Along forest edges male parents provided most of the prey required by the brood and females supplemented food deliveries by hunting near the nest. Females were observed on most visits to nests along forest edges and spent much time brooding and attending nestlings. At nests deep in the forest, males alone could not provide enough food. Females hunted at considerable distances from the nest, spent less time brooding and attending nestlings, and were seen less often during nest visits.

Early visual development is useful to Broad-winged Hawk chicks during parental feeding bouts in which chicks orient toward the parent's food-laden bill, reach forward and actively grab food morsels. Blind altricial passerine chicks adopt a more passive role in early feeding behavior as parents directly place food into their gaping mouths (Kuhlman 1909). The bills of hawk chicks at hatching are the same shape as their parents and are relatively large. Body weight, wing, tarsus and bill lengths are, respectively, 7, 6, 19 and 40 percent of adult sizes at hatching (Fig. 2). The hooked bill structure of nestling and parent hawks may preclude gaping behavior as an efficient form of feeding nestlings (Newton 1977). In support of the hypothesis that hooked bill structures place constraints on forms of nestling feeding behavior, neither Strigiformes nor Psittaciformes young exhibit gaping behavior to the extent seen in Passeriformes and chicks from all three taxonomic orders are blind at hatching. Budgerigar (*Melopsittacus undulatus*) parental feeding consists of head bobbing movements, bill grasping in which bills are fitted together at longitudinal right angles, and regurgitation of food (Brockway 1964). Barn owl (*Tyto alba*) chicks appear to rely on tactile cues, taking food from their parent when strips of meat brush against the bristles around the base of their bills (Bunn and Warburton 1977). Hooked bills of Falconiformes and Strigiformes are thought to have evolved as a morphological adaptation for dismembering animal and insect prey. Constraints induced by this adaptation in bill structure, together with early development of visual sensory function, may have contributed to the evolution of the particular feeding behavior observed in nestling Broad-winged Hawks.

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