EARLY GROWTH AND DEVELOPMENT OF THE COMMON BARN-OWL'S FACIAL RUFF

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ABSTRACT.—The ability of the Common Barn-Owl (*Tyto alba*) to localize sounds produced by potential prey can be explained on the basis of sensitivity to differences in interaural time and intensity. The size of the owl's head is a prime determinant of interaural time differences, whereas the facial ruff is the prime determinant of interaural intensity differences. During the 60 days following hatching, the physical structures that establish these binaural cues undergo massive growth. Barn-owl chicks are altricial and scantily feathered when they hatch. Growth of the head and ruff feathers occur at separate times during early maturation. Between 11 and 30 days after hatching, the diameter of the head approximately doubles. Between 35 and 60 days, facial ruff feathers emerge and grow to nearly adult length (ca. 20 mm). During the first 60 days of life, the barn-owl auditory system would be subject to widely varying binaural cues which eventually stabilize. *Received 5 April 1988, Accepted 25 May 1988.*

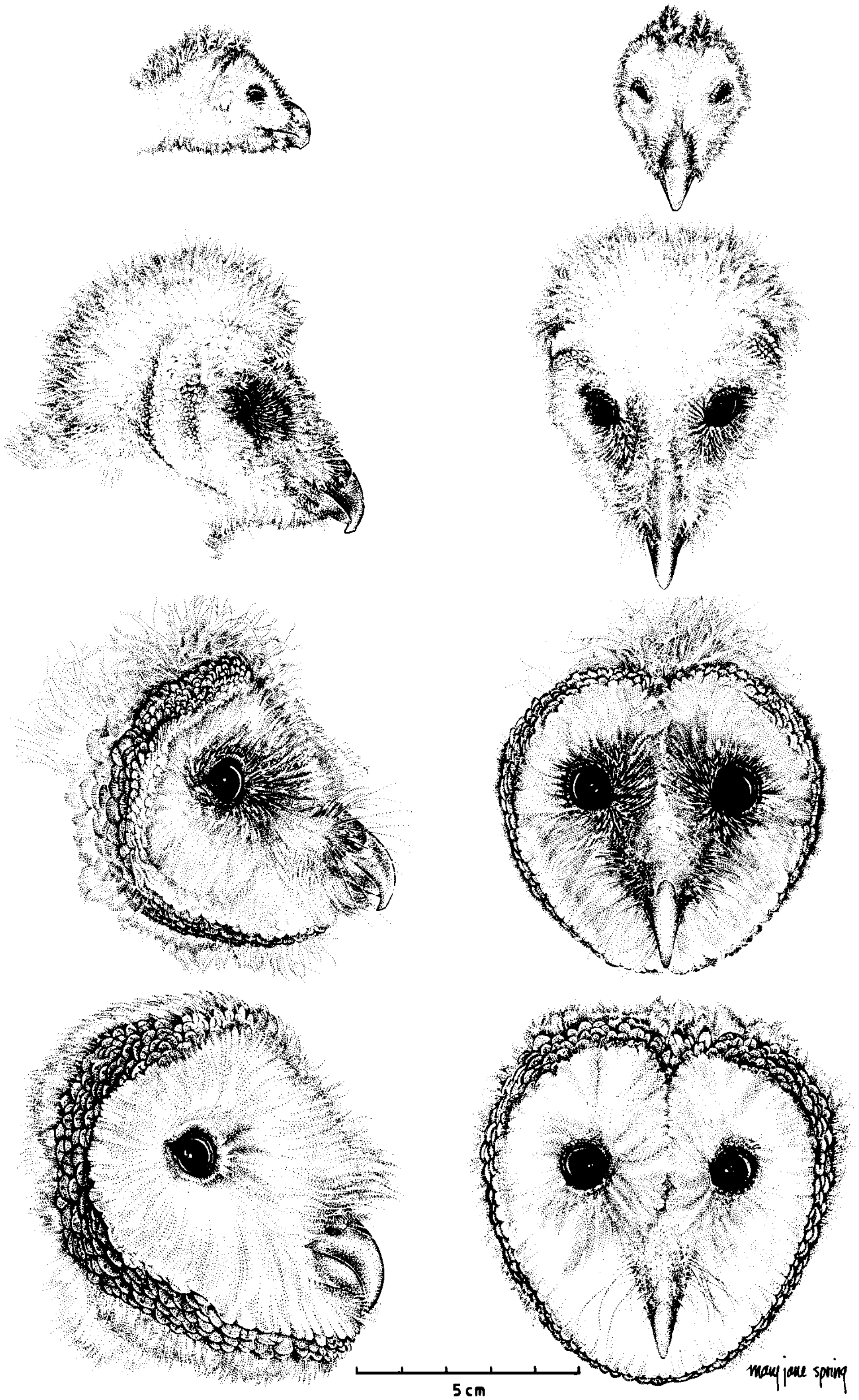
BARN-OWLS are noted for their ability to localize sounds produced by prey (Payne 1971). In part, the auditory capabilities depend on the gross morphology of the external ear and related structures (Payne 1970, Knudsen 1980, Kühne and Lewis 1985). Because variations in these structures alter the way owls hear, these variations should affect the development and function of the auditory system (Knudsen et al. 1984). Binaural auditory cues, especially interaural time and intensity differences, provide sufficient information for barn-owls to accurately localize sound (Moiseff in press [b]). These cues originate from the distance between the ears and from the acoustical properties of the facial ruff (Payne 1970, Knudsen 1980, Kühne and Lewis 1985, Moiseff in press [a]).

Interaural time differences result from the path-length that sounds take to reach each ear (Blauert 1983). Path-length is determined by a combination of the distance between the ears and the angle from which the sound originates. Additional factors such as presence of feathers and head shape further influence the time difference.

The auricular feathers comprising an owl's facial disk hide the feathers of the facial ruff. The ruff forms a curved wall around the periphery of the face to give the face its characteristic heart-shaped appearance (Payne 1971). Curved ruff feathers grow in a densely packed hexagonal array of 8 parallel rows. They form a roughly parabolic dish on each side of the head. Species-specific differences in the degree of asymmetry between the two sides of the facial ruff can be observed. The ruffs of diurnal species such as the Burrowing Owl (*Athene cunicularia*), have largely symmetrical sides, whereas nocturnal species such as the Boreal Owl (*Aegolius funereus*), Screech Owl (*Otus* spp.), and Common Barn-Owl (*Tyto alba*) have markedly asymmetric ruffs (Kühne and Lewis 1985, Norberg 1978).

The broad, densely packed feathers of the ruff act as efficient acoustical reflectors for sound frequencies above approximately 4 kHz. These are sounds with wavelengths less than approximately 7.5 cm (Payne 1970, Knudsen 1980, Kühne and Lewis 1985, Moiseff in press [a]). The feathers increase the area over which sound is collected from about 1 cm^2 (i.e. area of the auditory canal) to approximately 35 cm^2. This increased area alone can increase the bird's sensitivity to sound by about 20 dB (Payne 1971). Asymmetry of the ruff results in each ear being maximally sensitive to sound that originates from disparate spatial locations. The ruff on the left ear is directed below the visual horizon; the ruff that surrounds the right ear is directed above this plane. This arrangement creates intensity differences between the ears. The differences vary as a function of sound location (Moiseff in press [a]).

Owl chicks hatch after an average incubation time of 30 days (Bunn et al. 1982). At hatching, the chicks are altricial, and largely featherless,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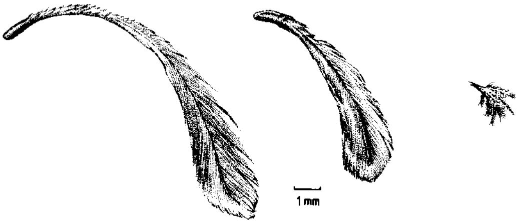

Fig. 2. Facial ruff feather development. Left to right: 50 days, 40 days, and 21 days.

with the exception of small amounts of natal down that grow in strips at specific regions of the body. During maturation, the animal's size increases dramatically and the body is eventually covered with mature plumage. Growth and maturation of the skull and facial ruff should affect the binaural auditory cues available to the owl.

Methods

Barn-owl chicks were hatched by their captive parents. Three chicks from one clutch and 2 chicks from a different clutch were removed from their nest 1 week after the youngest bird hatched. This delay allowed the chicks to receive full parental care during this critical time. Early survival depends on adequate temperature regulation and feeding. When the chicks were first removed from their nests they could be identified easily by differences in size. Each chick was fit with a permanent, numbered, aluminum leg band (1 cm diameter, Gey Band Co.) and housed communally in a single enclosure. They were fed small mouse and rat parts every 4 h or upon demand, until satiation. As the birds matured, appropriate changes were made in their feeding schedules to ensure that all birds had unrestricted access to food.

Body mass was measured with a top-loading balance (Sartorius 1413). Lineal measurements were taken with calipers. Head diameter was measured by placing the jaws of the calipers on the skin surrounding the ear canals. The caliper jaws were closed until they exerted slight pressure on the skin; care was taken to minimize any deformation of the soft tissue during measurements. The diameter of the left ear opening was also measured with calipers designed for inside measurements. The shape of the ear opening changed with age. The youngest birds had circular openings; in older birds, the openings were "D" shaped. We measured the maximum dimension. In the case of circular openings, the diameter was measured. The "D" shaped openings were measured along the longest axis. Photographs of the head were taken daily in standardized planes (frontal, lateral, and horizontal). Two or three feathers were plucked carefully from the facial ruff daily, and saved in individually labeled vials for subsequent measurement and photographing. Two of the birds had ruff feathers cut as part of a separate investigation and feather measurements were not made. All ages referred to the number of days after hatch.

Results

During the first 60 days after hatching, both the size of the head and the presence and form of the facial feathers changed dramatically (Fig. 1). During the first 3 weeks the predominant change was an increase in head diameter. This was followed by a 3-week period of ruff feather growth. The tips of the facial ruff feathers were darker than surrounding feathers, and formed a clearly visible ring around the face (Fig. 1, third from top). The body of the ruff feathers were obscured by fine, pennate, uniformly colored pin-feathers: the facial disk. Together, the facial ruff and facial disk give the characteristic heart-shaped face. The facial ruff feathers developed during the first 2 months (Fig. 2). Initially, the feather was down-like (Fig. 2, right). As the feather emerged it took its characteristic shape (Fig. 2, middle and left). Feathers were broadest near the tip and curved perpendicularly to the flat surface of the feather. The curvature was greatest near the base of the mature feather.

Frequent measurements enabled us to follow the growth of specific structures during early development. Weight was used as a general indicator of growth. The owl chicks weighed from 80–150 g when first removed from their nest. The mass of each of the chicks increased linearly until age 31 days and then leveled off at between 500 and 575 g for the next 20 days (Fig. 3). This was followed by a period during which their mass decreased to the nominal adult mass of approximately 470 g.

Head diameter increased in a nearly linear

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Fig. 1. Lateral and frontal views of the barn-owl's head during development. The diameter of the skull in the lower two frontal views was approximate by measuring the distance between the lateral edges of the eyes. Top to bottom: 10 days, 21 days, 40 days and 50 days.

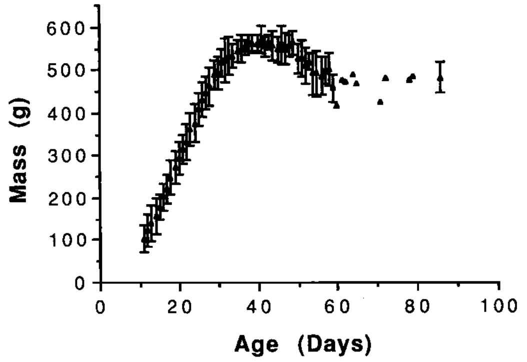

Fig. 3. Relationship between body mass and age. Mean and standard deviation from 5 individuals. Measurements between day 60 and 82 were from one individual.

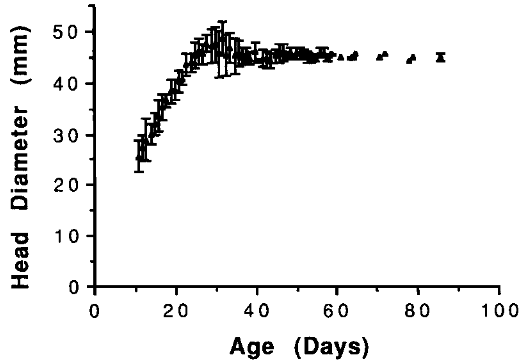

Fig. 4. Average head diameter vs. age. Mean and standard deviation from 5 individuals. Measurements between day 60 and 82 were from one individual.

fashion over the first 30 days (Figs. 1 and 4). When the head growth stabilized, at about 37 days, the average head diameter was 45 mm. The apparent peak and subsequent decrease in the head diameter (at about 28 days) was a measurement artifact and not statistically significant. At this time, the facial-ruff feathers were particularly stiff and hard to deflect without distorting the underlying soft tissue. This made it difficult to measure the head diameter and resulted in small measurement errors. The problem disappeared after a few days, when the larger feathers could be more easily displaced.

The ear canals are located on the sides of the head, roughly behind the eyes. Our measurements were confined to the left ear canal due to the way we restrained the owls during measurement. Cursory inspection of the right ear canal did not reveal any major size differences between the two sides, but the canals were not compared quantitatively. The external ear canal diameter increased continuously during the first 2 months (Fig. 5). At 10 days, the average diameter was 2.0 mm, and increased to 6.2 mm at day 30. Ear canal diameter continued to increase through day 60, to an average diameter of 11.0 mm. Assuming that the ear canal was circular, the area of the ear opening varied from 2.5 mm^2 at 12 days to 95 mm^2 at 60 days, a 38-fold increase.

Facial and ruff feathers changed dramatically during the first 2 months (Figs. 1 and 2). The down feathers in the region that eventually contained the ruff were noticeably different from down feathers located in other areas of the head. Ruff-region down was significantly shorter (1–2 mm) than down from other areas of the head (average 10 mm), although the shapes of the down were similar.

At about 1 month, the down feathers were replaced by the tips of the developing, differentiated, ruff feathers. For 3 or 4 days, the sheathed stalks remained intact. After this time, the sheath began to flake away, and revealed the curled tip of the emerging feather. In 2–3 days, the feather was unfurled and took its natural, adult-like shape. The length and width of the feathers that developed into the facial ruff were first measured at 36 days, when the surrounding sheath flaked off. Feather width was 3.0 mm, and remained nearly constant during maturation. The tip of the ruff feather is its

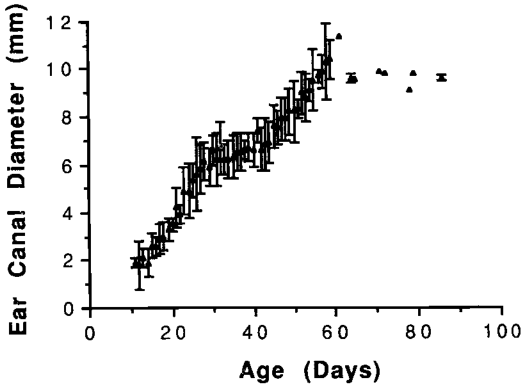

Fig. 5. Average diameter of left ear canal vs. age. Mean and standard deviation from 5 individuals. Measurements between day 60 and 82 were from one individual.

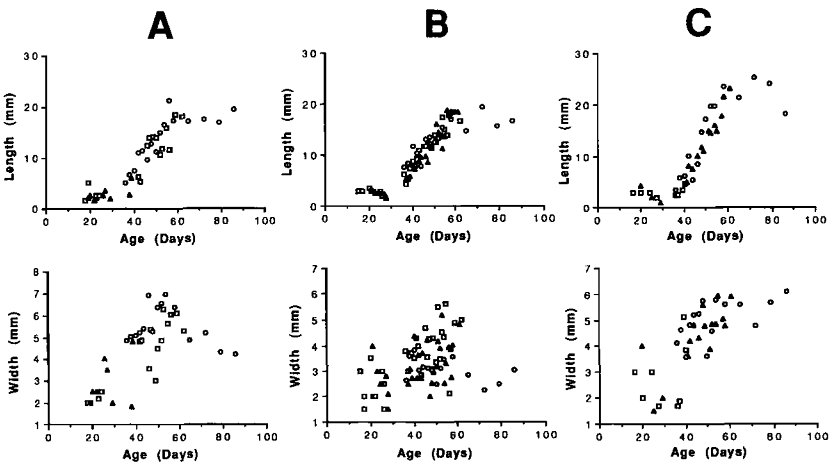

Fig. 6. Growth of ruff feathers. Lengths (Top) and Widths (Bottom) of ruff feathers from three locations on the owl's head. A: Above the ear canal; B: Adjacent to ear canal; C: Below ear canal. Results from three individuals are superimposed on each graph.

widest point, and is also the first to develop. All the ruff feathers reach approximate adult length at about 60 days. The adult length of the ruff feathers varied depending on the region of the face (Fig. 6). Ruff feathers from above the ear reached a maximum length of about 18 mm, whereas those from the extreme lower region of the face had a maximum length of 25 mm. Over the next several months the ruff feathers differentiated, with a gradual increase in both width and length from the inner to the outer rows of the ruff.

Discussion

Knudsen et al. (1984) showed that the barn-owl ear canal, skull, and facial ruff grew rapidly during the first 2 months after hatching. Their simple measurement of facial ruff diameter obscured the fact that the feathers comprising the ruff undergo massive morphological changes during this period. Our data concentrated on the growth of the specialized facial ruff feathers in the context of the other growth that occurred at this time.

Head diameter and ruff-feather growth occurred during separate periods. The head diameter increased through the first month, whereas the facial ruff emerged and grew during the second month (Fig. 7). The diameter of the head (measured ear to ear) increased twofold from day 14 to day 36 post hatch. During the first month the body mass increased linearly. This was followed by a period during which there was no further increase in mass, and then a slight decrease in mass that stabilized at the adult weight. The final weight decrease was similar to that observed by Wilson et al. (1987), and was associated with a decreased food intake after growth stabilized. The greatest amount of head growth occurred during the first month. Throughout the entire 2-month period, the ear canal diameter increased by almost 40 times. Ear canal and ruff feather growth did not stabilize until approximately 60–65 days after hatching. Knudsen et al. (1984) reported that facial ruff diameter stabilized at approximately 42 days. The differences between these findings may be attributed to the curved shape of the maturing feather. Increased length of these

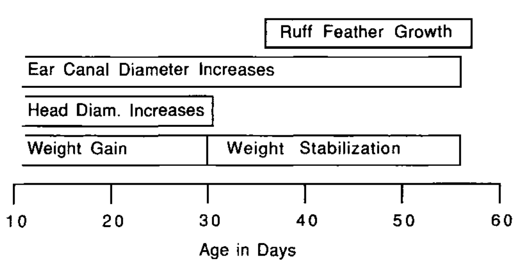

Fig. 7. Temporal organization of development of external acoustic apparatus. Each box indicates the time during which the specified growth occurs. The open left side of some boxes indicate that earlier measurements were not made.

curved feathers may not be immediately evident as an increase in ruff diameter.

The growth pattern over the first 60 days has several implications with respect to binaural cues during this period of growth. Head diameter and facial-ruff feather size directly affect the binaural cues available to both immature and mature barn-owls. The head diameter sets a lower limit for the range of interaural time differences that the bird experience as a function of spatial location of the sound. To a first order approximation, the relationship between interaural time difference (ITD) and angular position of a sound source (x radians) is proportional to the distance between the two ears (estimated by the head radius, r) and can be described by:

$$\text{ITD} = \frac{r}{v}(x + \sin x),$$

where v = speed of sound (Woodworth 1938). Over the range of $-90°$ to $+90°$ this function is nearly linear. A similar relationship has been experimentally measured for the adult barn-owl (Moiseff and Konishi 1981). From this relationship we can obtain an approximation of the maximum interaural time delays (i.e. sound presented 90° to one side of the head) that would result at each age. Over a period of day 10 to day 60, based solely on head diameter, the maximum interaural time difference would nearly double. Because this approximation excludes effects of the growing feathers, it probably underestimates the change in maximum interaural time differences.

Structures act as sound barriers and reflectors only at those frequencies whose wavelengths are smaller than the size of the structure (Blauert 1983). The facial ruff functions as a frequency-dependent directional acoustical receiver (Payne 1970, Knudsen 1980, Kühne and Lewis 1985, Moiseff in press [a]) that is most effective for frequencies above 4 kHz. For frequencies greater than 4 kHz the feathers of the ruff impart directionality to each ear and increase the sensitivity of each ear by about 20 dB. Thus, during the initial 60 days post hatch, the intensity of the environmental sounds vary greatly. The immature chick should be less sensitive than adults to high frequency sounds. Localization accuracy will also be reduced until ruff growth is complete.

The acoustic capabilities of immature owls, which include their ability to localize sounds, are largely unknown. In part, this results from the difficulties in eliciting reliable acoustically mediated behaviors from extremely young owls (Moiseff and Haresign unpublished data). It is difficult to establish the manner in which the owl's auditory system is matched to the individual's auditory environment. Knudsen et al. (1984) have shown that a barn-owl's auditory system will adjust to the particular range of binaural cues experienced during a critical period of development. This period is less than 120 days post-hatch and encompasses the growth of the facial disk. Growth stabilized at about 60 days, after which most metrics attained mature values. By remaining physiologically plastic beyond this point of growth stabilization, barn-owl auditory systems adapt to morphological variations.

The final size of an owl may depend on endogenous factors such as sex, and on exogenous factors such as nutrition. Because sound localization and acoustic abilities are important for detection, localization and ultimately prey capture, it is of paramount importance to survival that the auditory systems be capable of adapting to such size variations.

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