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GROWTH AND PLUMAGE DEVELOPMENT OF NESTLING LONG-EARED OWLS

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Abstract. We report the growth rates and plumage development of Long-eared Owls (*Asio otus*) in two developmental stages from hatching to fledging, the nestling period (1–22 days) and prefledging period (23–37 days). We used the logistic growth equation to model nestling mass gain. Mass gain was most rapid during the nestling period. Average mass gain per day was highest between seven and 13 days of age. At 16 days of age nestlings displayed defined facial disks and complete second down. Nestlings left the nest at 22 days of age. Mass gain slowed considerably after nest departure and continued to slow up to fledging. Appearance of defensive and concealment behaviors occurred nearly simultaneously with departure from the nest. To our knowledge this is the first detailed report of nestling growth rates and plumage development for Long-eared Owls in North America.

Key words: Asio otus, *concealment, down development, growth rate, logistic growth function, postnatal growth, prefledging period.*

Crecimiento y Desarrollo del Plumaje de Pichones de *Asio otus*

Resumen. Presentamos las tasas de crecimiento y el desarrollo del plumaje de *Asio otus* en dos etapas de desarrollo desde el momento de eclosión hasta el de emplumamiento: el período de pichón (1–22 días) y el período previo al emplumamiento (23–37 días). Usamos la ecuación de crecimiento logístico para modelar el aumento de la masa del pichón. El incremento de la masa fue máximo durante el período de pichón. El incremento de masa promedio por día fue máximo entre los 7 y 13 días de edad. A los 16 días de edad, los pichones mostraron discos faciales definidos y el segundo plumón completo. Los pichones dejaron el nido a los 22 días de edad. El incremento en la masa disminuyó considerablemente luego del abandono del nido y continuó disminuyendo hasta el emplumamiento. La aparición de los comportamientos defensivos y de ocultación ocurrió casi simultáneamente con la partida del nido. A nuestro entender, este es el primer informe detallado sobre las tasas de crecimiento de los pichones y el desarrollo del plumaje para *A. otus* en América del Norte.

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The Long-eared Owl (*Asio otus*) is widely distributed in the Northern Hemisphere. It is most often found in groups of trees, hedgerows, small woodlands, wooded draws, and forest edges in open landscapes from sea level to timberline (Marks et al. 1994, Holt 1997, Holt et al. 1999). Due to its wide distribution, the Long-eared Owl has been extensively studied in North America and Europe. Although much is known about nesting biology (Marks et al. 1994), little information exists about the growth and development of young after hatching. Wijnandts (1984) described growth rates and plumage development for Long-eared Owls in the Netherlands, but we could find no comparable data for Long-eared Owls in North America. Here, we describe growth rates and plumage development of wild nestling Long-eared Owls from Montana, USA.

METHODS

STUDY AREAS

Our study areas were located approximately 65 km apart in the Mission (47°38′N, 114°92′W) and Missoula (46°58′N, 114°52′W) valleys of west-central Montana. Annual precipitation ranges from 30–36 cm and mean summer daytime temperature is 15°C, although midsummer temperatures can easily exceed 30°C.

Native grasslands, introduced domestic grasses, and agricultural fields in both valleys support a limited diversity of small mammals, numerically dominated by voles (*Microtus* spp.) and deer mice (*Peromyscus maniculatus*). Seasonal creeks, wooded draws, and planted shelterbelts provide roosting and nesting habitat for Long-eared Owls.

NEST SEARCHES

We monitored Long-eared Owl communal roost sites weekly from October to March, increasing the frequency of visits as the roosts began to disband in late February and March. Beginning in late March, we inspected all stick nests in areas adjacent to communal roosts and all suitable habitat within our study area.

We climbed to occupied nests to record clutch size and estimate egg-laying date. If nestlings were present we weighed them and estimated their ages based on prior experience with known-age chicks. We avoided flushing females from their clutches again until the approximate hatching date of the first egg. We considered hatch day as day 1 of nestling age.

DESCRIPTIVE OBSERVATIONS

After the first egg hatched we visited the nest every three days, except in cases of inclement weather, to record the body mass of all nestlings. We weighed nestlings using 30, 100, 200, and 500 g capacity Pesola scales with 1.0, 2.0, 5.0, and 10.0 g increments, respectively. During each visit we described and recorded nestling plumage and development. We recorded when the eyes opened, eye color, when the egg tooth was lost, stages of down development, at what age the quills of the primary, secondary, and tail feathers emerged, and development of the facial disk and ear tufts. We also described distinctive nestling behaviors such as defensive and concealment posturing. We photographed two nestlings, each from different nests, on every visit to chronicle nestling growth and development from hatching to fledging. We used the photographs to support our general observations of nestling behaviors. We could not determine the sex of nestlings.

We classified stage of down development on a continuum scale beginning with the protoptile (first) down and ending when the mesoptile (second) down was completely emerged. We defined three stages of mesoptile down development: (1) when the mesoptile was subcutaneous, (2) when the mesoptile emerged through the skin surface, and (3) when the mesoptile down had completely emerged and replaced the protoptile down.

Long-eared Owl eggs hatch asynchronously and we had little problem recognizing individuals by mass and plumage development during the first two weeks of growth. Between 14 and 16 days of age, we banded nestlings with U.S. Fish and Wildlife Service aluminum bands to continue to identify individuals. Long-eared Owl nestlings leave the nest before they can fly. After flightless nestlings departed from their nests we located them by searching the tree canopy within a 100 m radius of the nest. We recorded distance from the nest and height in the tree canopy for each owl. We continued to search for the chicks until they had fledged or could not be found during several consecutive nest visits. We defined fledging (albeit subjectively) as sustained, self-controlled flight between two points with agile take-off, midair agility, and controlled landings. We verified fledging by recapturing young after their first flight.

STATISTICAL ANALYSES

We used our measurements of mass to construct graphs of mass gain over time. To describe overall growth we pooled all the data points and plotted them on one graph. We also constructed graphs of mass gain for individual nestlings. To model postnatal growth of Long-eared Owls, we fit a logistic growth curve to the pooled mass gain data and to data points for individual nestlings. Although the Gompertz and von Bertalanffy's models were considered, the logistic model was chosen because it fit the data well and is frequently used for birds, in particular owls (Ricklefs 1968, Winjandts 1984, Wilson et al. 1987, Holt et al. 1992, Nagarajan et al. 2002). We used the form of the logistic equation

$$y_i = \alpha/\left(1 + ye^{-\beta x_i}\right) + \varepsilon_i,$$

where y_i is the log of the mass of nestling i, α is a parameter related to the asymptote of the growth curve, y is a parameter related to time of origin, β is a parameter related to growth, x_i is the age of nestling i (in days), and ε_i is random error.

To meet the assumption of independence, the random effect of individual nestlings had to be accounted for. To determine which coefficients should be considered random, we calculated individual model fits for each chick and looked at confidence intervals to see if any of the coefficients could remain fixed. Additionally, to meet the assumption of constant variance for nonlinear regression methods, we used the log of the mass to fit the models. We examined diagnostic (QQNorm) and residual plots to assess whether model assumptions had been met. The mixed-effects logistic model gave us an average growth rate from our sample of nestlings and also allowed us to analyze variability in growth rate among individual chicks.

We compared our graphs of observed mass gain with the models to assess how well the models fit. We also used model parameters to calculate absolute body mass gain over three-, five-, and seven-day intervals. We chose these intervals to investigate relationships between mass gain and timing of departure from the nest. We used the coefficient of determination to measure correlations between nestling age and height in the canopy and distance from the nest. We calculated summary statistics for the descriptive observations that we recorded. Values are given as means ± SD.

RESULTS

In 175 nest visits, we monitored 52 nestlings in 15 nests: 26 nestlings in 8 nests in the Missoula valley and 26 in 7 nests in Mission valley. For nests with complete data, mean clutch size was 5.0 ± 0.8 (range = 4–6, n = 11). Mean number of young hatched per nest was 3.8 ± 1.7 (range = 1–6, n = 10) and mean number of young known to have fledged per nest was 2.2 ± 1.2 (range = 1–5, n = 11). It was impossible to locate all chicks after they left the nest during every visit; as a result, our mean number of young fledged per nest is likely underestimated.

NESTLING PERIOD: 1–22 DAYS

Growth and plumage development. Nestlings hatched wet with eyes closed and an egg tooth present. By the end of day 1, nestlings had dried and were covered in white, fluffy protoptile down. Mean weight at hatching was 18.4 ± 2.0 g (range = 15–23 g, n =

13). Eyes opened fully at 6.4 ± 1.4 days of age (range = 4–10 days, $n = 30$). Generally, initial eye color was a dull green or gray and the eyes appeared opaque or unclear for several days. Eye color developed through a progression of yellowish hues attaining a clear, bright yellow color by 32 days of age. The egg tooth was lost at 6.4 ± 1.2 days of age (range = 4–12 days, $n = 9$).

The second, mesoptile down replaced the protoptile down in several stages. The mesoptile down was visible subcutaneously along the capital and humeral feather tracts at 6.2 ± 1.4 days of age (range = 4–9 days, $n = 26$). At 9.4 ± 1.0 days of age (range = 7–11 days, $n = 23$), the mesoptile down emerged through the skin and began replacing the protoptile down. Mesoptile down had completely replaced the protoptile down by 14.0 ± 2.7 days of age (range = 7–19 days, $n = 43$).

The quills of the primary remiges emerged at 11.1 ± 3.8 days of age (range = 5–22 days, $n = 51$). The quills of the secondary remiges emerged at 11.4 ± 4.3 days of age (range = 5–26 days, $n = 51$), although a detailed inspection of the nestling was needed to make this assessment. Retrix quills appeared at 12.5 ± 4.9 days of age (range = 5–30 days, $n = 51$). By 13 days of age, the primary and secondary quills were clearly visible. Generally, the primary and secondary remiges began to erupt from their quills at 16 days of age and the retrices at about 19 days of age.

Facial disk development. At 14 days of age, the facial disk began a rapid development, darkening near the bill and eyes and expanding outward. At 16 days of age, the facial disk had changed to a dark gray-black color and was easily recognizable on most nestlings. By day 19, the structure of the modified filoplume facial feathers became apparent, markedly contrasting with the mesoptile down on the rest of the head and body. A brown border outlined the facial disk by 22 days of age.

Development of the ear tufts coincided with the development of the facial disk. At 19 days of age, ear tufts were distinct and comprised of mesoptile down, but owls did not appear to have the ability to change the position of the tufts.

Nestling defensive behavior. We observed feather fluffing and bill-clacking in a small number of nestlings at 16 days of age. Defensive behavior began a pronounced development when the nestlings were 19–22 days of age and coincided with departure from the nest.

PREFLEDGING PERIOD: 23–37 DAYS

Flightless nestlings left their nests at 22.1 ± 2.8 days of age (range = 16–28 days, $n = 52$). Mean weight at time of nest departure was 248 ± 20 g (range = 213–308 g, $n = 33$). A weak correlation was found between nestling age and distance from the nest ($r^2 = 0.22$, $n = 117$). No correlation was found between chick age and height in the canopy ($r^2 = 0.001$, $n = 117$). We did not observe members of any brood returning to the nest structure after leaving the nest, nor did we observe mixed groups of chicks from different nests.

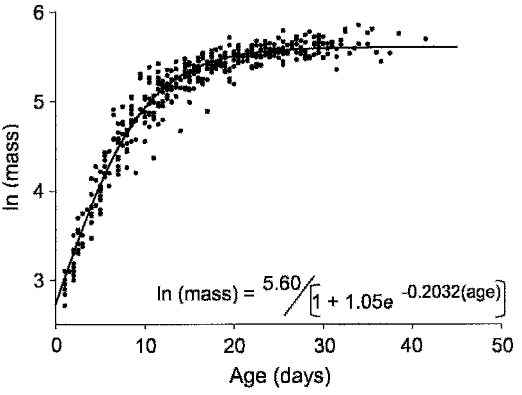

FIGURE 1. Fitted logistic equation and growth curve for body mass gain in nestling Long-eared Owls in Montana, from hatching to fledging.

Facial disk development. A chestnut-brown color developed below the eyes and expanded up and outwards on the facial disk after 25 days of age. At 33 days of age the facial ruff was fully formed, and by 36 days of age the disk was almost entirely brown with a buff fringe developing along the outer edges of the ruff. At this point, facial disk characteristics resembled adult features, but were a bit richer in overall color.

Concealment behavior. After leaving the nest, nestlings developed concealment behaviors and by 25 days of age the concealment posture was distinct. By four weeks of age cryptic plumage patterns and behavior made the young owls increasingly difficult to locate.

Fledging. Young fledged at 34.6 ± 3.1 days of age (range = 29–41 days, $n = 20$). Mean weight at fledging was 270 ± 26 g (range = 230–320 g, $n = 10$). Most initial flights were short but controlled. We could not consistently recapture fledglings; consequently, information regarding the timing and acquisition of juvenal plumage is incomplete.

POSTNATAL MASS GAIN

Long-eared Owl nestlings grew most rapidly between one and 19 days of age (Fig. 1). According to the logistic growth models, mass gain per day increased until 13 days of age, then began to slow gradually up to 19 days of age. Mass gain slowed considerably after 19 days of age and was minimal by fledging (Fig. 2). Mass gain per day did not change significantly when we performed calculations for five- and seven-day intervals.

DISCUSSION

LONG-EARED OWL GROWTH AND DEVELOPMENT

Overall growth rate, mass gain increments, and intra- and interspecific variation in growth can be compared among organisms using the logistic, Gompertz, and von Bertalanffy growth functions (Starck and Ricklefs 1998a). Our logistic growth constant ($k = 0.203$) is similar to that reported by Wijnandts (1984)

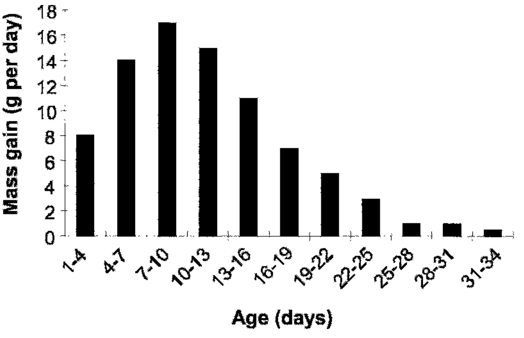

FIGURE 2. Absolute mass gain for Long-eared Owls in Montana over three-day intervals from hatching to fledging calculated using the fitted logistic equation (Fig. 1).

for the Long-eared Owl in Europe (k = 0.225), suggesting that this species may grow at similar rates throughout its range. Plumage development and the timing and acquisition of nestling behaviors reported by Wijnandts (1984) are also similar to those reported here.

Starck and Ricklefs (1998b) provided avian growth rate data for many species, including growth functions calculated from 13 studies involving owls. Of the seven studies that used the logistic model, three reported growth constants higher than ours. All seven of these studies involved tree-nesting owl species. Ricklefs (1968) observed that the ground-nesting Snowy Owl (*Nyctea scandiaca*) grows relatively more quickly than the Barn Owl (*Tyto alba*) and Great Horned Owl (*Bubo virginianus*), both of which nest above the ground, suggesting that Snowy Owls are subject to greater predation pressure than owls that nest above the ground. Holt et al. (1992) argued that selective pressure favors rapid growth and development in ground-nesting Short-eared Owls (*Asio flammeus*) as an antipredator adaptation because: (1) it minimizes the time predators have available to locate nests, and (2) asynchronous dispersal can increase chances of reproductive success should a predator locate the nest in the latter stages of the brooding period. In addition, both Short-eared and Snowy Owls experience the greatest mass gain per day five to seven days prior to leaving the nest (Holt et al. 1992; J. Petersen and DWH, unpubl. data). In our study, mass gain per day was greatest nearly two weeks before nestlings left the nest.

Our data support the observation that tree-nesting owl species may grow less rapidly than ground-nesting species. However, more information is needed to determine whether physiological factors have constrained the growth rate of Long-eared Owls, or if slower growth has been largely influenced by a release from predation resulting from nesting above the ground.

NESTLING BEHAVIORS

Long-eared Owls leave their nests about two weeks before they can fly and hide in the surrounding vegetation. In all nestlings, defensive behaviors were acquired rapidly prior to nest departure, while the appearance of the concealment posture occurred within the first several days after leaving the nest. The rapid acquisition of these behaviors prior to and following nest departure suggests that development of these behaviors is innate.

When in concealment posture, all young and adult Long-eared Owls had (1) open eyes, (2) erected white feathers around the bill and eyebrows, (3) erected ear tufts, and (4) compressed body feathers giving the appearance of a thin, upright posture. Bondrup-Nielson (1983) argued that three features of the concealment poses of Long-eared Owls (*Asio otus*), Elf Owls (*Micrathene whitneyi*), Great Gray Owls (*Strix nebulosa*), Saw-whet Owls (*Aegolius acadicus*), and Boreal Owls (*Aegolius funereus*) do not support the notion that the function of the pose is to conceal the owl. These three features include: (1) open eyes, (2) increased exposure of white feathers around the eyes, and (3) the abrupt manner in which the pose is adopted, especially in Northern Saw-whet and Elf Owls. Most often we found Long-eared Owls in the concealment posture, indicating that this response was induced at some distance from us, similar to the response of the Northern Saw-whet Owl (Catling 1972). All Long-eared Owls appeared inconspicuous while watching us. Consequently, we believe that open eyes are advantageous. If the threat is lethal, closed eyes may result in serious injury or death. In our opinion, the white markings in the facial region provided disruptive coloration and effectively drew attention away from the more subtle features of the owl. The tufts of Long-eared Owls may also aid in concealment by resembling vegetation such as twigs or small branches and disrupting the outline of the owl ("broken off stub effect"; Sparks and Soper 1970). Finally, because Long-eared Owls remain relatively motionless in concealment pose, their cryptic plumage coloration and patterning appears, to our eyes, to be effective camouflage. We believe the pose adopted by Long-eared Owls fits the concealment posture criteria outlined by Holt et al. (1990). The pose also provides a "protective" function as described by Bent (1938).

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