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Nestling growth rates of Short-eared Owls.—The Short-eared Owl (*Asio flammeus*) is a widely distributed ground-nesting species (Burton 1973). Nests are difficult to locate, and consequently few data are available concerning the owl's breeding biology (Clark 1975, Cramp 1985). Clark (1975) reported nestling growth for three captive Short-eared Owls from Manitoba, Canada. Hagen (1952) provided growth data for two nestling Short-eared Owls from Norway. Wijnandts (1984) reported growth models for Hagen's data and perhaps from some unpublished data. Unfortunately, it is unclear if the unpublished data were for masses or some other category; the numbers were not stated. Here we describe growth rates of wild nestling Short-eared Owls. To our knowledge, this is the first report of such data for North America.

Study area.—Nantucket Island is located approximately 32 km south of Cape Cod, Massachusetts. The island (130 km^2) consists of moraines and out-wash plains from Pleistocene glaciation (Woodsworth and Wigglesworth 1934), and is unique in its composition of maritime heaths and "moorlands" (Tiffney and Eveleigh 1985). There are no native mammalian predators, but feral and domestic dogs and cats do occur.

Methods.—Nine nests were located during April and May 1985. We located nests by searching the grassland area where male Short-eared Owl courtship flights took place. We weighed nestlings at four nests every other morning until they dispersed from their nests, using 100-, 300-, and 500-g capacity Pesola scales with increments of 1.0, 2.0, and 5.0 g, respectively. Short-eared Owl eggs hatch asynchronously, and nestlings vary in age and size. We did not mark nestlings because they were distinctive until just prior to leaving their nests. Nestlings were banded when approximately 10-days-old with United States Fish and Wildlife Service aluminum bands. By the third week of May, all eggs had hatched. Nests were not visited during inclement weather.

Ricklefs (1983) stated that, in describing bird growth, the most straightforward approach is to fit the growth data to models with a few interpretable parameters. He further stated that growth among organisms can be compared intraspecifically and interspecifically, with each species having characteristic growth patterns. To describe Short-eared Owl growth, we used a logistic growth model for each nestling. Comparisons of growth rates between nests were made using these selected models. We did not assume that owl nestlings grew at the same rate; therefore, data were not pooled from individual nests.

Preliminary model fitting of various forms of the Richards' (1959) curve was used to choose the logistic model. The Richards' equation (Richards 1959) is $W(t) = [A^{m-1} + Be^{-kt}]^{1/(1-m)}$ where W is weight, t is time, 1/A is the asymptotic value of W, m is a shape parameter, B is a parameter related to the time of origin, and k is a constant proportional to overall growth rate. The logistic model is obtained by setting $m = 2$, (i.e., $W(t) = 1/(A + Be^{-kt})$. After the logistic form of the Richards model was determined to be sufficient, we used it for all data.

Parameter estimates were computed using the linearization method (Draper and Smith 1981). Model fit was assessed by plotting residuals against time (in days) and by inspecting the plots for evidence of bias (systematic over-or-under prediction) and non-constant variance.

The model which minimized the median absolute deviation of all weights about the fitted regression equation was chosen as a representative growth model for a given nest. Since the sample median minimizes the sample sum of the absolute deviations, we refer to this representative model as the median model. We did not feel enough data were collected to estimate asymptotic weights.

Results.—We used data from 18 nestlings from four nests (total of 110 weighings). Parametric estimates for all nestlings were similar among all nests except Cisco Beach, which only incorporated data from two nestlings (Table 1).

None of the models suffered from a notable degree of bias. The magnitude of all residuals tended to increase with time for all models. This evidence of non-constant variance does not detract from use of these models as descriptors of observed growth. This analysis has shown consistency among growth curves from three of four nests (Fig. 1). The remaining model from the Cisco Beach nest may be in error since hatching was estimated rather than observed.

For each of the median models, we estimated absolute body mass increments over four five-day-periods. These increments were chosen because they approximated nestling growth curves. Body mass increments were similar among all nests except Cisco Beach. The mean predicted body mass at hatching for nests 1, 3, and 4 was 14.7 g. These values were similar

TABLE 1

LOGISTIC GROWTH MODEL PARAMETER ESTIMATES FOR NESTLINGS AT FOUR NESTS

		Parameter			
Nestlings	Weighings	A[a]	B[b]	K[c]	Mean absolute deviation
Miacomet nest					
1	7	0.00304	0.0709	0.293	20.48
2	6	0.00351	0.0820	0.314	19.26
3	7	0.00433	0.1000	0.361	30.70
4*	8	0.00308	0.0913	0.307	16.20
5	8	0.00503	0.0899	0.387	45.31
6	7	0.00456	0.0907	0.309	48.81
Cisco Beach nest					
1*	7	0.00205	0.0429	0.187	24.95
2	8	0.00246	0.0735	0.263	27.14
Ram Pasture nest					
1	6	0.00380	0.0828	0.354	14.63
2*	5	0.00308	0.0828	0.304	12.81
3	4	0.00392	0.0799	0.375	19.52
Golf course nest					
1	6	0.00313	0.0771	0.325	44.38
2	5	0.00338	0.0771	0.323	45.78
3	5	0.00304	0.0680	0.316	48.82
4	4	0.00350	0.0749	0.337	43.93
5*	6	0.00320	0.0949	0.330	40.80
6	5	0.00329	0.1179	0.323	50.86
7	6	0.00594	0.0473	0.302	130.36

[a] Asymptotic value of weight (1/A).
[b] Parameter related to time of origin.
[c] K is a constant proportional to overall growth rate.
* Median growth model for each nest.

to the actual mean hatching body mass data (16.0 g, N = 8). There were no hatching data from nest number 2 and the value (26.6 g), estimated from the model represents day two (26.6 g), which is actually the predicted body mass for day two. According to the models, nestling Short-eared Owls gained an average of 8 g of body mass per day for the first five days of life, 19 g per day during the next five days, 21 g per day during the next five days, and 12 g per day during the last five days for which we have data (Table 2, Fig. 2). The Cisco Beach nest growth rates differed from the other nests. The predicted body mass gain for the Cisco Beach nest was less than for other nests for days 6–10 and more for days 16–20. It is interesting that the two nestlings from Cisco Beach nest grew faster in the fourth period (days 16–20) than nestlings from the other three nests (Table 2). We wonder if the small brood size, hatching date error or "compensatory growth" (I. L. Brisbin, pers. comm.) influenced these results.

Nestlings number 2 and 7 from Golf Course nest showed a decrease in body mass. This may be explained by: (1) the female owl's disappearing from the nest during the nestlings'

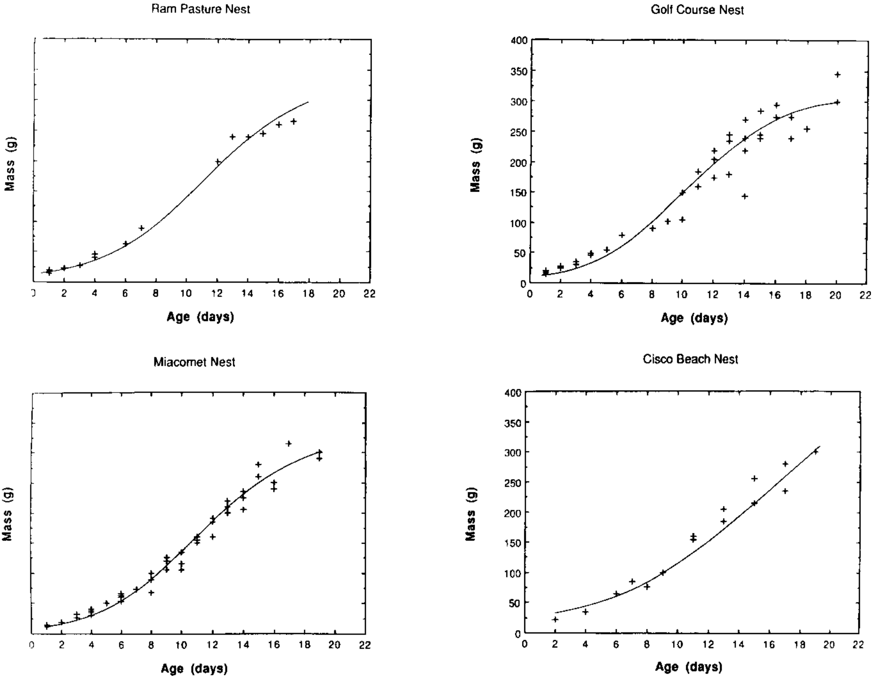

FIG. 1. Median growth models for all nests.

second week of growth. This may have put additional pressure on the male to provision food for seven nestlings; (2) we made errors in data recording; (3) other unknown factors.

Nestling growth was most rapid during periods 6–10 and 11–15. Nestlings gained almost twice the body mass during period 6–10 and almost three times the body mass during period 11–15, when compared with period 1–5 (Fig. 2). During the fourth period, body mass gains slowed as the owls gained an average of 12 g per day. Sexes of the nestlings could not be determined, so differential growth by sex is not reported.

In this study, flightless nestlings dispersed form their nests when approximately 16 days old ($\bar{x}$ = 15.7, SD = 1.11, range 14–17, N = 18). These pre-fledging dispersers moved up to 55 m from their nests for approximately a two-week period prior to their first flights. Pre-fledge dispersal coincided with growth period 11–15, at which time the owls gained most of their nestling body mass. The owls fledged when approximately 30 days old, although reluctant to fly initially. They also may have been influenced to fly by our activities.

Discussion.—Nice (1962) classified owls as semi-altricial. Short-eared Owls live in open habitats and nest on the ground. The nestlings are nidicolous. These habitats are characterized by food resources and climatic conditions which may have much annual variation (Cody 1985). Reasons for pre-fledging dispersal strategies in the Short-eared Owl have not been discussed in the literature. We believe that selective pressure favors rapid growth and development in nestling Short-eared Owls as an anti-predator adaptation because: (1) it minimizes the time predators have 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

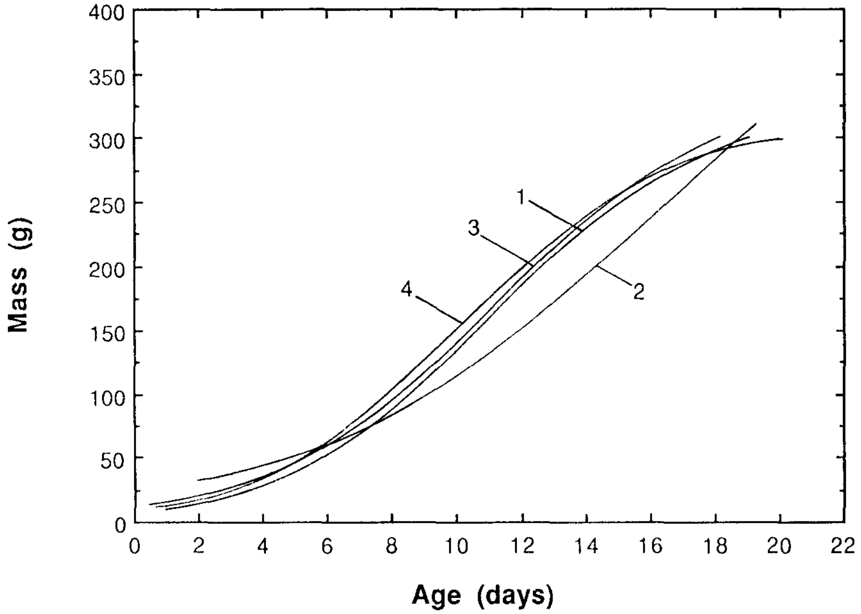

FIG. 2. Observed body masses and estimated median growth models for Short-eared Owl nests.

nesting period. Perhaps, pre-fledging dispersal also acts to reduce sibling brood cannibalism, but we are unsure if this is driven by natural selection or a by-product of pre-fledging dispersal. All cases of brood cannibalism in Short-eared Owls are reported to have occurred in the nest (Ingram 1962; D. Holt, unpubl. data).

Similar behaviors have been reported for the ground nesting Snowy Owl (*Nyctea scandiaca*) (Watson 1957, Taylor 1973) and Marsh Owl (*Asio capensis*) (Smith and Killick-Kendrick 1964). Ricklefs (1968) reported the Snowy Owl grows relatively more quickly than does the Barn Owl (*Tyto alba*) and Great Horned Owl (*Bubo virginianus*). He suggested that ground nesting Snowy Owls were subject to greater predation pressure than owls that nest above ground.

Wijnandts (1984) used the logistic model to compare growth for eleven species of owls. His growth constant (K) for the Short-eared Owl was 0.194, which is considerably lower than ours. Our Short-eared Owl growth constants were higher than those for any owls as computed by Wijnandts (1984) and buttress our argument that rapid growth for ground-nesting Short-eared Owls evolved as an anti-predator adaptation. Interestingly, Wijnandts' growth curves for ground nesting Snowy Owls (0.149) were much less than for Short-eared Owls. Ricklefs (1968) did state, however, that larger birds grow more slowly than smaller birds. Young Northern Eagle-Owls (*Bubo bubo*), whose nests are on the ground, disperse eight and 38 days before other Eagle-Owls that nest in trees or caves (Wijnandts 1984).

Clark (1975) provided the only other data describing Short-eared Owl nestling growth that we are aware of for North America. He reported data from three captive nestling Short-eared Owls. Two were hatched in an incubator, and a third was raised in captivity after

TABLE 2

DAILY INTERVALS AND ESTIMATED BODY MASS AT HATCHING AND BODY MASS INCREMENTS COMPUTED FROM THE MEDIAN MODELS

Intervals (days)	Estimated masses (g)		
	Start	End	Average daily change
Miacomet nest			
1–5	14.24	44.00	7.44
6–10	57.05	136.85	19.95
11–15	161.58	250.65	22.26
16–20	266.74	305.26	9.63
Cisco Beach nest			
1–5	26.60	53.05	6.61
6–10	62.58	115.82	13.31
11–15	133.17	216.01	20.71
16–20	238.76	326.85	22.02
Ram Pasture nest			
1–5	15.98	48.24	8.06
6–10	62.08	143.97	20.47
11–15	168.54	254.60	21.51
16–20	269.83	306.10	9.06
Golf Course Nest			
1–5	14.00	46.73	8.18
6–10	61.43	149.56	22.03
11–15	175.30	258.71	20.85
16–20	271.96	300.81	7.21

approximately 10 days of age. The two owls from the incubator weighed 16 and 18 g, respectively, at hatching and reached 210 and 230 g by approximately day 26. The owls grew slowly for the first eight to 10 days, and then rapidly from 10 to 20 days. The third owl grew rapidly from 7 to 18 days and then slowed. Its asymptotic weight was at approximately 385 g at age 27 days, its first flight day. The owl then fluctuated in weight between 360 g and 380 g from day 29 to 39 when data recording ceased. Clark's data are in agreement with our results.

Two of seven nestlings from the Golf Course nest lost body mass—the second oldest and the youngest. The mass loss of the youngest might be expected if food resources diminished or adults could not keep up with nestling needs. But why did the second oldest lose body mass? Lack (1954) stated that asynchronous hatching is an adaptation to food stress, with adults feeding the most active nestlings, usually the larger ones.

Gronlund and Mikkola (1969) reported mean hatching body mass for Short-eared Owls to be 15.4 g (range 14–17, N = 5), in Finland. They also reported that nestling Short-eared Owls leave their nests when 15 days old (range 14–18, N = 20). Watson (1972) reported that nestling Short-eared Owls in Scotland left their nest when 12 days old. Clark (1975) reported nestlings left when 13.6 days old (N = 6) in Manitoba, Canada. These pre-fledging dispersal dates are similar among studies reported as well as the present one. Our estimates of fledging are also within the range reported by Urner (1923), 31–36 days, and by Clark (1975), 27 days, in the United States and by Witherby et al. (1940), 24–27 days, in Europe.

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Frequency and timing of copulations in the Prairie Falcon.—Several authors (Birkhead et al. 1987; Møller 1987a, b; Birkhead and Lessells 1988) have commented on the high copulation frequencies in birds of prey compared to other avian taxa. However, there is a scarcity of observations on the copulatory behavior of birds of prey. Møller (1987a) described the copulation behavior of the Northern Goshawk (*Accipiter gentilis*), Birkhead and Lessells (1988) investigated copulatory behavior of the Osprey (*Pandion haliaetus*), and Sodhi (1991) that of the Merlin (*Falco columbarius*). Here, I describe the copulation frequency and timing of the Prairie Falcon (*F. mexicanus*), a large monogamous falcon of western North America (Palmer 1988).

Study area and methods.—From 1984–1987, I observed 52 breeding pairs of Prairie Falcons in the Snake River Birds of Prey Area (BOPA) and Reynolds Creek watershed in southwestern Idaho for 613 days (9085 h). A pair was considered breeding if eggs were laid (Steenhof 1987). The study area is part of the western intermountain sagebrush steppe, characterized by cold winters and hot, dry summers (West 1983). The vegetation is dominated by big sagebrush (*Artemisia tridentata*), winterfat (*Ceratoides lanata*), and shadscale (*Atriplex confertifolia*) associations (U.S. Dept. Interior 1979, West 1983). Observations started up to seven weeks prior to incubation and continued until young were 30–35 days old or the nesting attempt failed. Blinds placed at an average distance of 147 m (range = 70–250 m) from the aeries were used to make observations, aided by 10–45 × telescopes and 10 × 50 binoculars. Each nesting territory was observed, on average, once every six days by two observers, each on a half-day shift. I used an entire day as the sampling unit to avoid sampling problems related to daily behavioral cycles of the falcons (Altmann 1974). Observations started half an hour before sunrise and were terminated half an hour after sunset. Behavioral data were collected continuously, using focal animal sampling (Altmann 1974). Copulations were recorded as single events. I was not able to distinguish between successful (i.e., cloacal contact between mating birds) or unsuccessful copulations. Sex was determined by the larger size of the female and position of the falcons during copulations. Females solicited copulations and begged for food, unlike males. Falcons were not individually marked, but stylized drawings of each nesting falcon's facial pattern aided identification of individual birds. The establishment of stable territorial boundaries early in the nesting season (Ogden and Hornocker 1977, Sitter 1983, Holthuijzen, unpubl. data) and the general openness of the terrain further facilitated the distinction between nesting pairs and intruding falcons. The data presented here were collected as part of a larger behavioral study on Prairie Falcons. More details on the sampling procedure can be found in Holthuijzen (1990) and Holthuijzen et al. (1990).

Hatching dates were calculated by back-dating ages of young, using a photographic aging key (Moritsch 1983). Start of incubation was based on a 34-day incubation period (Burnham 1983). Observation days were categorized in six-day intervals based on the approximate stage of the nesting cycle relative to the female's estimated clutch completion date and labelled by midpoints (pre-incubation, N = 91 days of observation [DO]: days −51, −45, −39, −33, −27, −21, −15, −9, and −3; incubation, N = 267 DO: days 3, 9, 15, 21, 27,