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MASS GROWTH RATES, PLUMAGE DEVELOPMENT, AND RELATED BEHAVIORS OF SNOWY OWL (*BUBO SCANDIACUS*) NESTLINGS

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ABSTRACT.—In 1993 and 1995, we detailed body mass growth rates, plumage development, and related behaviors of Snowy Owl (*Bubo scandiacus*) nestlings from Barrow, Alaska. We recorded data from 71 of 80 nestlings from 14 of 20 nests in 1993 and 154 of 161 nestlings from 33 of 54 nests in 1995. Only nestlings for which we had data from hatching to at least 25 d of age were included in the growth model. Nestlings hatched between 1–3 d after "pipping" (creating a hole in) the eggshell. The semi-altricial young were covered in white protoptile (first) down plumage at hatching and weighed about 44–45 g. For about the first 7 d, their eyes were closed and movement was limited; the nestlings were dependent on the female for thermoregulation, food, and protection. Growth was rapid and by 8–9 d, the dark gray mesoptile (second) down had begun replacing protoptile down. By about 9–11 d, eyes were open, and by about 14 d, the owls were dark gray in color, and primary flight feather quills emerged. Mass gains were greatest the week prior to pre-fledging nest departure. The owls gained about 56 g every d, between 16–22 d. Around 21 d, the primary flight feathers erupted from their quills, and at approximately 25 d, tail (rectrices) feather quills erupted. After pre-fledging nest departure at approximately 21 d, the young owls roamed the tundra on foot and were fed and protected by both parents. We did not observe voluntary brood reduction; however, some young died in nests. Mass growth slowed substantially by about 34 d, while plumage development, particularly flight feather growth, increased rapidly. Young within and between nests, and years, grew at similar rates. Around 36–43 d, the young began their first attempts at flying, by hopping and pumping their wings. Also at this age, differences in plumage between presumed males and females were noticeable. Between 44 and 55 d, the young fledged, coinciding with the time when primary flight feather P8 reached 16.5 cm, and tail feather T1 reached 11.0 cm.

KEY WORDS: *Snowy Owl*; Bubo scandiacus; *growth rates*; *plumage development*; *related behavior*.

TASAS DE AUMENTO DE MASA, DESARROLLO DEL PLUMAJE Y COMPORTAMIENTOS RELACIONADOS DE POLLOS DE *BUBO SCANDIACUS*

RESUMEN.—En 1993 y 1995, detallamos las tasas de aumento de la masa corporal, el desarrollo del plumaje y los comportamientos relacionados de pollos de *Bubo scandiacus* provenientes de Barrow, Alaska. Registramos datos de 71 de 80 pollos provenientes de 14 de 20 nidos en 1993 y 154 de 161 pollos provenientes de 33 de 54 nidos en 1995. Solo se incluyeron en el modelo de crecimiento aquellos pollos para los que se tenían datos

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desde la eclosión hasta al menos 25 días de edad. Los pollos eclosionaron entre 1–3 días posteriores a la realización de un agujero en la cáscara del huevo. En el momento de la eclosión, los polluelos, semialtriciales, estaban cubiertos con plumón protoptilo blanco (primero) y pesaban 44–45 gramos. Los ojos de los pollos estuvieron cerrados durante sus primeros siete días de vida y su movimiento fue limitado. Durante este periodo los pollos también fueron dependientes de la madre para la termorregulación, alimentación y protección. El crecimiento fue rápido y hacia los días 8–9, el plumón mesoptilo gris oscuro (segundo) comenzó a reemplazar el plumón natal. En torno a los días 9–11, los pollos abrieron los ojos, y hacia el día 14 los búhos eran de color gris oscuro y emergieron los cañones de las plumas primarias de vuelo. El mayor aumento de la masa de los pollos tuvo lugar la semana anterior a la salida del nido previa al emplumamiento. Los búhos aumentaron alrededor de 56 gramos cada tres días, entre los días 16–22. En torno al día 21, las plumas remeras primarias emergieron de sus cañones mientras que los cañones de las plumas rectrices emergieron aproximadamente el día 25. Después de la partida del nido previa al emplumamiento, aproximadamente en el día 21, los pollos deambularon por la tundra a pie y fueron alimentados y protegidos por ambos padres. No observamos una reducción voluntaria de la nidada; sin embargo, algunos pollos murieron en los nidos. Cerca del día 34, el crecimiento de la masa disminuyó substancialmente, mientras que el desarrollo del plumaje, particularmente el crecimiento de las plumas de vuelo, se incrementó rápidamente. Los pollos crecieron a ritmos similares tanto dentro como entre nidos y años. Alrededor de los días 36–43, los pollos comenzaron sus primeros intentos de vuelo, a saltar y a batir sus alas. También durante este periodo, se hicieron notables las diferencias de plumaje entre presuntos machos y hembras. Entre los días 44–55, los pollos volaron del nido, coincidiendo con el tiempo en que la octava primaria P8 alcanzó los 16.5 cm y la primera plumas rectriz T1 alcanzó 11.0 cm.

[Traducción del equipo editorial]

The Snowy Owl (*Bubo scandiacus*) is a large, ground-nesting species that breeds in circumpolar regions of the northern hemisphere (Mikkola 1983, Cramp 1985, Holt et al. 1999, Mebs and Scherzinger 2000, König and Weick 2008, Potapov and Sale 2012). It is one of the largest owls in the world and has the most northerly distribution. In North America, wintering males weigh approximately 1600–1800 g, whereas females weigh approximately 2100–2280 g (Kerlinger and Lein 1988, Holt et al. 2015). During the nonbreeding season, many Snowy Owls migrate south to northern temperate latitudes, and are often considered nomadic (Mikkola 1983, Cramp 1985, Parmelee 1992) or irruptive migrants (Holt and Zetterberg 2008). Some Snowy Owls, however, winter at high latitudes in marine environments (Fay and Cade 1959, Irving et al. 1970, McRoy et al. 1971, Fuller et al. 2003, Therrien et al. 2011, Holt et al. 2015) and on their breeding grounds (D. Holt unpubl. data).

Several studies reported breeding ecology of Snowy Owls in North America and Europe (Murie 1929; Pitelka et al. 1955a, 1955b; Sutton and Parmelee 1956; Watson 1957; Hagen 1960; Tulloch 1968; Robinson and Becker 1986; Parmelee 1972; Taylor 1973; Wiklund and Stigh 1983, 1986; Petersen and Holt 1999; Menyushina 1994a, 1994b, 1994c; Potapov and Sale 2012). With exception of this study, and Menyushina (1994a, 1994b, 1994c), from Wrangel Island, Russia, most studies lasted a few seasons or less. Within these studies, authors reported some aspects of Snowy Owl growth (Murie 1929; Pitelka 1955a, 1955b; Sutton and Parmelee 1956; Hagen 1960; Tulloch 1968, 1969; Parmelee 1972; Taylor 1973; Robinson and Becker 1986, Potapov and Sale 2012). However, these data were difficult to interpret due to small samples, infrequent data points, and the mixing of data from captive-raised and wild young. Of these, four studies provided some detailed data of mass growth and plumage development (Watson 1957, from Canada; Hagen 1960, from Norway; Tulloch 1968, from Shetland Islands, Britain; Potapov and Sale 2012, from Russia), although sample sizes were small.

Because measuring avian growth can be complicated and growth of various body parts within a species highly correlated (Ricklefs 1983, Starck and Ricklefs 1998a), these authors suggested the most straightforward method was to fit growth data to equations with few interpretable variables (Starck and Ricklefs 1998b). Comparisons could then be made among individuals, cohorts, and groups. Models applied within and between years could then be used to compare growth in relation to sex, age, nesting chronology, and general health (Ricklefs 1968, Penteriani et al. 2005, Seidensticker et al. 2006). These parameters are an important source of intraspecific and interspecific life history information. In owls, the logistic function and its forms have been the growth model used most often (Wijnandts 1984, Holt et al. 1992, Starck and Ricklefs 1998b, Seidensticker et al. 2006). Consequently, this has allowed researchers an opportunity to compare studies (see Starck and Ricklefs 1998b).

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Owl nestlings are semi-altricial. They are nidicolous, and remain nest-bound for prolonged periods. Owl nestlings proceed through a slow physiological and morphological developmental period, and rely on parental care for thermoregulation, feeding, and protection for an extended time. Consequently, as a group, owls have bi-parental care until dependent young reach a certain age. (See species accounts by Bruce 1999, Holt et al. 1999, Mebs and Scherzinger 2000, König and Weick 2008). Herein we provide a standardized detailed approach to quantifying mass growth rates, plumage development, and related behaviors from hatching to fledging in Snowy Owl young, based on large sample sizes of Snowy Owls in Barrow, AK.

METHODS

Study Area. Our study (213 km^2) is located on the Arctic Coastal Plain, Barrow, AK, U.S.A. (71°18′N, 156°40′W). Barrow is bordered by the Chukchi Sea to the west and Beaufort Sea to the east. Topographic relief is low (sea level to 10 m), and ice wedge polygonal ground, shallow lakes, and underlying permafrost influence the landscape (Brown et al. 1980).

In Barrow, winters are long, dry, and cold, whereas summers are short, cool, moist, and windy. Snowmelt begins in June, and daylight lasts 24 hr per d from 10 May to 2 August (Bunnell et al. 1975, Brown et al. 1980).

Field Methods. From 1992 to 2015, DWH studied various aspects of Snowy Owl breeding ecology at Barrow. The owls do not breed every year. However, in 1993 and 1995, brown lemmings (*Lemmus trimucronatus*) were abundant and Snowy Owls bred in large numbers. Consequently, we recorded various aspects of Snowy Owl nestling growth. To locate nests, we hiked and used binoculars to scan the tundra. We initially searched for territorial male owls roosting alone on tundra mounds. Because of their highly reflective white plumage, they were easy to observe. If we located a male, we scanned the area for a female lying horizontally on a tall nest mound. The brown barring and spotting of the female's plumage rendered her more difficult to locate.

In 1993, we found 20 nests and visited them daily as did Watson (1957). We include data from 14 of these 20 nests, representing 71 of 80 nestlings. In 1995, we found 54 nests and visited them every third day. We include data from 33 of these 54 nests, representing 154 of 161 nestlings. Thus, we have detailed data for 225 nestlings from 47 nests. Nests were not visited during heavy fog or rain. In each year, one or two portable observation blinds were set up and moved to different nests when appropriate, so we could make behavioral observations.

During nest visits, we recorded clutch size and examined eggs for hatching. Where possible, we marked some freshly laid eggs with permanent marker, and then estimated incubation periods. Because Snowy Owls begin incubation with the first egg, and eggs were generally laid at 2-d intervals, we assumed that eggs hatched in the order laid, and thus assigned laying sequence beginning with the first egg to hatch. Our systematic nest visits provided confidence in these assumptions. Furthermore, for our purposes, knowing nestling hatching order was more important than knowing egg-laying order. We identified eggs as fractured (cracked shell) and "pipped" (hole in egg) where nestlings began emergence. After nestlings hatched, we recorded: hatchling weight, hatching intervals, mass growth, plumage development, eye-opening, iris color, egg tooth presence or absence, and related behaviors. Because Snowy Owl nestlings depart nests on foot at approximately 3 wk of age, we recorded relative distance young traveled from their nests until their first flights by pacing or visual estimation. We located young that had departed their nest by searching the nesting territory, observing food deliveries by adults, and listening for young making food-begging calls. We subjectively defined fledging as the ability to fly in a somewhat sustained fashion and to land with coordination. We monitored young until they died, could not be found, or fledged. Once young fledged, they roosted conspicuously together or in close proximity to each other on tundra mounds. Given our standardized nest visits, experience in locating young, and the owls' relatively predictable behaviors, we believe that young not found were sick or injured and destined to die, or already dead. In either case, they did not fledge. We monitored families until all young fledged or until 1 September when we left the study area. All but a few young were flying by this time, and the remaining few were usually only a few days from fledging. Thus, we were confident in assuming that they too fledged.

Nestlings were weighed with 100-, 300-, 500-, 1000-, 2000- and 2500-g Pesola (Schindellegi, Feusisberg, Switzerland) and Avinet (Dryden, NY U.S.A.) scales, with increments of 1, 2, 5, 10, and 50 g. One nestling from each nest was photographed and plumage and growth recorded during each nest visit. In 1995, we measured growth of the emerging eighth primary feather (P8) and central left and right tail feathers (T1 left and T1 right) to the nearest cm. Initially, all feathers were encased in sheaths. We measured growth of these flight

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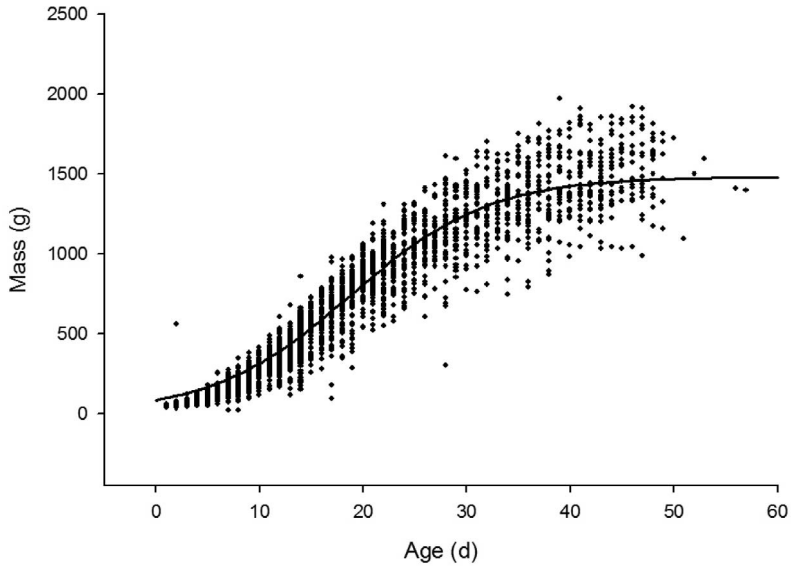


Figure 1. Fitted growth curves of mass verse age for Snowy Owl nestlings, 1993 and 1995.

feathers until they erupted from the sheath, after which time we measured growth of the erupted feather until owls fledged.

Because the eggs of Snowy Owls, and most owl species, hatch asynchronously, we were able to identify individual nestlings during nest visits. We noted marked differences in size, plumage patterning, and coloration prior to fledging, suggesting sexual size and color dimorphism. However, we had not developed a reliable sexing technique to separate males from females at that time (see Seidensticker et al. 2011). All nestlings were banded with number 8 or rarely number 9, United States Geological Survey (U.S.G.S) aluminum bands, when they were between 15–20 d old, just prior to pre-fledging nest departure. Thus, we were able to identify all individuals and monitor their growth and survival after nest departure.

Growth Model. To describe the owls' growth, we chose the logistic model (Ricklefs 1968, Wilson et al. 1987, Nagarajan et al. 2002, Starck and Ricklefs 1998b). We fitted the logistic equation $y = \frac{A}{1+\exp[-K(t-t_i)]}$ where y = mass (g) of nestling, A = parameter related to asymptote of growth, t_i = parameter related to the age at half the growth, K = parameter related to growth rate, t = age of nestling (d). A nonlinear mixed effects model was used due to the nested structure of the data (nestling within nest within year). We considered the asymptote parameter (K) as random. The mixed-effect model allowed us to report an average growth model of all nestlings. For the purposes of fitting the growth model, only nestlings for which we had data until at least 25 d old were included. All calculations were performed in R and the "nlme" function was used to fit the logistic growth curve (R Development Core Team 2007). The "nlme" function in R fits a nonlinear model to data allowing for a nested data structure. The function requires initial estimates of the parameters and the parameters are estimated by maximizing the log-likelihood.

RESULTS

Snowy Owls nested on the ground. Nests were located on mound tops approximately 1 m high. Females dug a circular bowl approximately 45 cm wide and 10 cm deep in the soil thaw zone. Eggs were laid on bare ground and no nest material was added. Nest mounds provided commanding views, and were the windiest sites on the tundra (Holt et al. 2009a).

Nestling Growth. In both years, the owls exhibited a sigmoidal-shape growth curve, similar to avian growth in general. The model fit with the observed data from combined 1993 and 1995 data was significant ($P < 0.0001$, $\hat{\sigma}_\varepsilon = 86.8$; Fig. 1). The estimate for the asymptote of the model, A, was 1483.1 g (SE = 7.9 g; Table 1). On average, young reached the asymptote at 1483.1 g with a 95% CI of 1476.6–1498.7 g (Table 1). The growth parameter, K, was 0.150 d^{-1} (SE = 0.0043 d^{-1}, 95% CI = 0.142–0.158 d^{-1};

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Table 1. Results of the mixed effects nonlinear logistic growth model for Snowy Owl nestlings in Barrow, AK U.S.A.

PARAMETER	ESTIMATE	STANDARD ERROR	*P*-VALUE	95% CONFIDENCE INTERVAL
A	1483.15	7.93	<0.0001	1476.6, 1498.7
K	0.150	0.0043	<0.0001	0.142, 0.158
Kt_i	18.8	0.113	<0.0001	18.58, 19.02

Table 1). Finally, the midpoint parameter, Kt_i, was 18.8 d (SE = 0.113 days, 95% CI = (18.58–19.02 d), which was interpreted as the average time for young to reach half of their growth (Table 1).

Development and Behavior. *Incubation and hatching period.* Eggs were white and nearly spherical in shape. Nestlings hatched out of the side of the egg, but toward the top end. Where approximated, eggs hatched after an incubation period of about 31–33 d. Eggs hatched asynchronously and generally in order laid, as in most species of owls. Nestlings vocalized from within the egg prior to hatching. Fracturing of the egg shell, the creation of the pipping hole, and the emergence from the shell took 1–3 d.

Nest-bound period. Nestlings were wet when hatched, but by end of the first day had dried and were covered in white, fluffy protoptile (first) down on all feather tracts. Actual hatching mass was 44.7 g, SE = 0.36, $n = 136$), although the model overpredicted the nestling hatching weight at 97.8 g (Table 2). Nestlings' eyes were closed and movement limited. The white egg tooth was present on the black bill, and the cere was grayish (Fig. 2a). The metatarsal pad and foot soles were bare of feathers and pink in color (Table 3). A soft twitter was the only vocalization.

Between hatching and day four, nestlings gained about 12.8 g/d (Table 2) and were still covered in white protoptile down (Table 3, Fig. 2a). Between 4–7 d, nestlings gained 28.3 g/d (Table 2). At this time, their fused eyelids began to open as a slit and gray mesoptile (second) down was visible subcutaneously to protoptile down on capital, humeral, spinal, and ventral feather tracts (Table 3, Fig. 2b). Movement was limited.

Between 7–10 d, nestlings gained about 55.6 g/d (Table 2). By 8–9 d, gray mesoptile down emerged through the skin and began pushing protoptile down out on all feather tracts (Table 3, Fig. 2c). Their eyes were yellow-gray, and opened fully by 9–11 d (Fig. 3a). A loud, long, screeching food-begging call was now the primary vocalization. We heard these vocalizations during nest visits and during observations made from the blind. By 14 d, nestlings were dark

Table 2. Snowy Owl mass at 3-d intervals. Mass on Day 1 equals hatching weight.

AGE IN DAYS (*n*)	MEAN MASS IN g (SE)	MASS CHANGE PER 3-DAY INTERVAL (g/3 d)	AVERAGE MASS GAIN PER DAY (g/d)	PREDICTED MASS FROM LOGISTIC MODEL (g)
1 (136)	44.7 (0.36)	—	—	97.8
4 (113)	83.0 (1.64)	38.3	12.8	147.44
7 (116)	167.8 (4.02)	84.8	28.3	218.3
10 (108)	334.7 (6.33)	166.9	55.6	315.2
13 (102)	410.1 (10.25)	75.4	25.1	440.1
16 (99)	588.2 (10.42)	178.1	59.4	589.6
19 (81)	747.5 (15.94)	159.3	53.1	753.1
22 (73)	918.3 (19.39)	170.8	56.9	915.5
25 (52)	1045.7 (19.02)	127.4	42.5	1062.0
28 (54)	1141.6 (31.57)	95.9	32.0	1183.1
31 (38)	1250.5 (30.70)	108.9	36.3	1276.1
34 (43)	1290.0 (28.91)	39.5	13.2	1343.7
37 (25)	1441.2 (43.50)	151.2	50.4	1390.8
40 (27)	1393.0 (36.60)	−48.2	−16.1	1422.7
43 (32)	1437.5 (32.58)	44.5	14.8	1443.8
46 (19)	1562.1 (51.55)	124.6	41.5	1457.7

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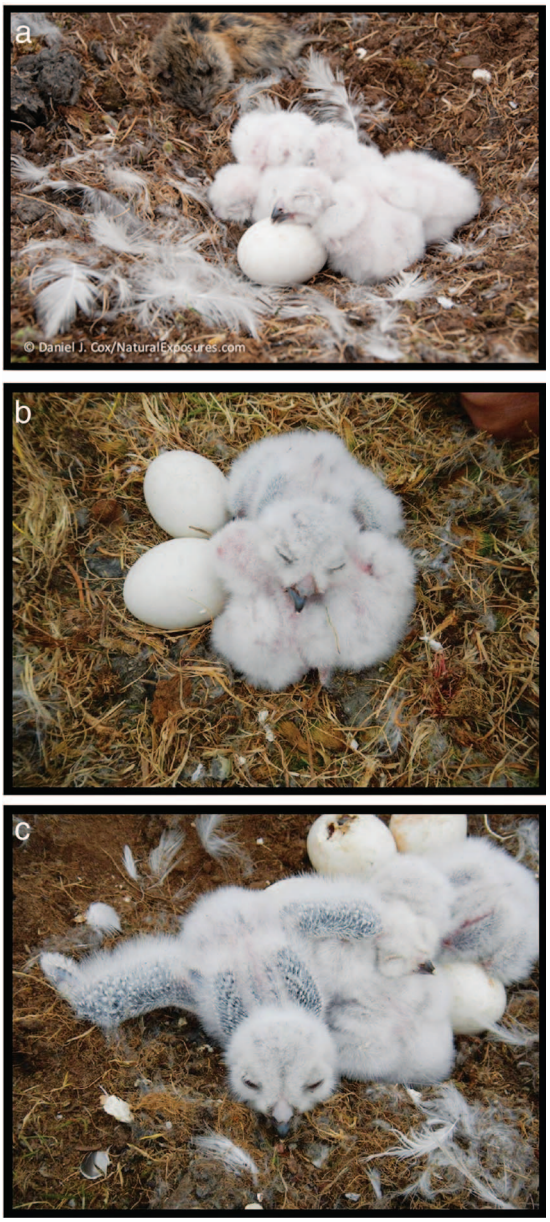


Figure 2. (a) White protopile down from hatching to about day four. (b) Gray mesoptile down appears subcutaneously about 4–7 d old. (c) Gray mesoptile down emerges through skin about 8–9 d and replaces protopile down.

gray in color, with white tips of the protoptile down clinging visibly to the tips of the mesoptile down (Fig. 3b). The nestlings were moderately mobile within the nest at this time. Tail feather quills were conspicuously absent. Leg and toe feathers were white. Also near 14 d, the primary (remiges) flight feather quills emerged. Between 15–21 d, the egg tooth disappeared, and primary flight feathers erupted from their sheaths. The nestlings were mobile, either on the nest mound or within a few meters. All young were predominately covered in gray mesoptile down (Fig. 3c). A surge in body mass occurred around 16–22 d, just prior to and near the time of nest departure. During this period, nestlings gained approximately 56 g/d (Table 2).

Nest-departure period. Nestlings moved in and around the immediate nest at about 15 d. However, they did not permanently depart their nest mounds on foot until about 3 wk of age (Fig. 4a). The owls were very mobile and moved in various directions for the next 3 wk. They generally stayed within 1 km of their nests, but were capable of travelling farther, depending on lemming populations and neighboring owl territories. They usually roosted alone, yet near each other, or occasionally in groups. Only two young wandered into another owl's territory, but did not mix with the other brood. Parents were usually within view of young, with female parents roosting closer to their young than males. After nest departure, mass gain began to slow, and around 22–31 d, young gained approximately 37 g/d.

Between 22–28 d, mesoptile down was long and deep gray in color. The white juvenile plumage began pushing out mesoptile down around the forehead and eyes, creating a white X on the face (4b). The tail quills (rectrices) were conspicuous around 21–22 d and erupted by 25 d (Fig. 4b). The eyes had begun turning a deep yellow color. Between 29–35 d, juvenile plumage around the eyes gave way to a white facial mask. The black and white body covert feathers were distinct. All juvenile primary and secondary flight and covert feathers had emerged, and were growing rapidly (Table 3, Fig. 4b, 4c). Young continued to gain body mass, albeit at a slower and more variable rate between days 31–46, averaging about 20.7 g/d (Table 2). Between 36–43 d, all flight feathers continued to grow rapidly. At this age, we noticed two distinct plumages we attributed to sexual dimorphism. Plumage of presumed males was whiter overall, with less barring and more spotting on the secondaries; presumed female plumage was overall darker, with more barring and less spotting on the secondaries (Fig. 5a). However, we developed a sexing technique at a later time (Seidensticker et al. 2011).

Fledging period. At about 40 d, the young began to jump and attempt flying, resulting in hops in which

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Table 3. Guide to Snowy Owl development from hatching to fledging, Barrow, AK U.S.A.

AGE (d)	DEVELOPMENT	BEHAVIOR
1–4	White protoptile down, eyes closed, egg tooth, talons whitish, feet and metatarsal pad pink (Fig. 2a).	Soft twitters (believed to be food-begging vocalization).
4–7	Gray mesoptile down appears subcutaneously under protopile, eyes slit and opening (Fig. 2b)	Helpless but moving in nest
8–14	Gray mesoptile down emerges through skin and replaces protoptile down, eyes open by 9–11 d, primary quill feathers emerge about 14 d, tail feather quills absent, leg and toe feathers white (Fig. 2c, 3a, 3b)	Gular flutter; holds head up; moderately mobile in nest; long, loud, food-begging scream
15–21	Rapid growth, primary feathers erupt from sheath, egg tooth disappears, tail feathers quills visible (Fig. 3c)	Very mobile in nest, pre-fledging departure from nest about 3 wk old
22–28	Eyes yellower, mesoptile down darker gray, plumage on forehead forming white X around eyes, tail feather quills erupt (Fig. 4a, 4b)	Mobile, runs, departs nest on foot
29–35	White feathers around eyes forming a mask, primary wing feathers and coverts show dark bars and spots, all juvenile flight feathers grow rapidly and synchronously (Fig. 4b, 4c)	Defense posture with wings outstretched
36–43	Wing and tail feathers well developed; noticeable differences in plumage between siblings, suggesting male and female differences; gray down retained on head, back, and breast (Fig. 5a)	First attempts at hopping and flying
44–55	Fledging, most birds flying with variable skills; juvenile plumage replaces down, with last down to be replaced on head (Fig. 5b)	May roost together or on nearby high mounds, still dependent on adults for food

they were briefly airborne. Due to the young's increased mobility, we had more difficulty collecting data. Primary, secondary, and tail feathers grew fastest during the 36–43 d period. At the time of fledging, the mean length of the longest primary flight feather (P8) was 16.5 cm (SD = 1.9, range 13–21.5, n = 80), and the mean length of the inner pair of tail feathers (T1) was 11.0 cm (SD = 1.5, range = 6.7–13.9, n = 80). Between approximately 44–55 d, most young were flying, with variable skill (Fig. 5b). At about 46 d old, the young weighed on average 1562 g (SE = 51.55 g; Table 2); however, data were more difficult to obtain and our sample sizes were small at this age.

Once fledged, yet still growing, broods often roosted together or near each other on tall mounds within their nesting territory. We were uncertain when family groups separated or when individuals began to disperse. We believe this occurred sometime in late September or early October, at the onset of migration, and as indicated by groups of recently fledged Snowy Owls seen at various locations, including onboard ships at sea, at this time.

DISCUSSION

The Snowy Owl breeding season, from courtship until young are independent, ranges from mid-May to late September/early October, approximately 4.5–5 mo. Snowy Owls have a long incubation (ca. 33 d), nest-bound period (ca. 21 d), pre-fledge walking period (ca. 25 d), fledging period (ca. 10 d), and perhaps another few weeks until independence. Thus, Snowy Owls have one opportunity to breed per year.

Incubation and Hatching Period. Where data are known, only female owls incubate eggs, initiating with the first egg in most species (Bruce 1999, Holt et al. 1999, Mebs and Scherzinger 2000, König and Weick 2008). In this study, only female Snowy Owls incubated, brooded, and fed nest-bound nestlings. Incubation periods for Snowy Owls were reported at 32–33 d (Murie 1929, Watson 1957, Tulloch 1968, Taylor 1973, Robinson and Becker 1986) and eggs hatch asynchronously at 1–2-d intervals, usually in the order laid (Murie 1929, Watson 1957). Our results were similar to these reports, although a few eggs hatched near synchronously, and some eggs hatched 3–5 d apart. Body mass and plumage descriptions at hatching from a small sample of nestlings from other studies were consistent with our results (Murie 1929, Watson 1957, Hagen 1960, Parmelee et al. 1967, Potapov and Sale 2012).

Nestling Period. In our study, the protopile (first) down was white, and nestlings acquired a gray

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Figure 3. (a) Eyes yellow-gray and open fully by 9–11 d. (b) Nestlings gray with frosted tips to mesoptile down; primary quills emerge by day 14. (c) Nestlings gray, tail quills visible, primary feathers erupt, surge in mass gains, very mobile, 15–21 d.



Figure 4. (a) Very mobile, can run, departs nest about 3 wk old, tail feathers conspicuous. (b) Eyes deeper yellow; juvenile plumage emerges, showing white X on face 22–28 d; tail quills erupt about 25 d. (c) White mask forms on face, juvenile upper wing coverts and flights feathers distinct at 29–35 d.

mesoptile (second) natal down at about 1 wk of age, and within 2 wk of age they were mostly covered in the mesoptile down. These findings were similar to other studies (Sutton and Parmelee 1956, Watson 1957, Tulloch 1968, Potapov and Sale 2012).

It is not known, in an evolutionary sense, why Snowy Owl nestlings replace the white protopile down with a gray mesoptile down. In all owl species where data are known, the protopile down is white

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Figure 5. (a) Distinct plumage patterns suggest sex differences between male and female at 36–43 d. Notice less barring and more spotting on male secondaries and more barring and less spotting on female secondaries. (b) Young fledge around 44–55 d.

(see Bruce 1999, Holt et al. 1999, König and Weick 2008), and mesoptile down varies in color among species. Most species of owls are nocturnal or active at low-light levels, and only females incubate and brood. Thus, we hypothesize that there is no need for eggs or nestlings to evolve cryptic coloration because they are almost constantly covered by the female. Thus, white may be a neutral or default color favored by natural selection, and energetically cheaper to produce.

The evolution of gray mesoptile down by Snowy Owls may be explained by two hypotheses, neither mutually exclusive. First, natural selection should favor cryptic coloration and plumage patterning to reduce detection by predators or harassment by other animals. Second, dark plumage should provide thermal advantages (solar heat absorption and retention) from harsh weather while young are out of the nest developing juvenile plumage. Dark colors absorb radiant energy and may have thermal advantages over lighter colors that reflect radiant energy (Marchland 1991).

Nest-departure Period. Snowy Owl nestlings in our study area departed nest mounds on foot when about 3 wk old. These results were similar to those of Petersen and Holt (1999), and Romero et al. (2006) for the same study area at Barrow, and other studies (Watson 1957, Tulloch 1968, Robinson and Becker 1986, Potapov and Sale 2012).

The surge in body mass gains prior to nest departure probably allows nestlings to gain endogenous reserves (i.e., fat) needed to survive the Arctic environment while flightless and still dependent on parents. Why do nestlings depart their nests when so young? Sutton and Parmelee (1956) suggested young left to keep cool, but Watson (1957) concluded there was no advantage. Our measures of stress hormones indicated nestlings did not experience elevated corticosterone levels prior to departing nests (Romero et al. 2006). These results supported our hypothesis that neither brood size nor food, often considered to be stressors leading to sibling rivalry or competition, influences nest departure (Romero et al. 2006, Holt et al. 2009b).

Potapov and Sale (2012) suggested sibling rivalry influenced nest departure in Snowy Owls. We saw no signs of intense rivalry. If this were the case, however, younger, less-dominant siblings should leave the nest before older siblings to gain relief from aggression. This did not occur in our study, as older nestlings always departed the nests first. Potapov and Sale (2012) also suggested nestlings left the nest in order to be seen first when adults returned with food. However, depending on brood size, even if one or two young have departed, the remainder of the brood is nest-bound, and most food deliveries occur at nests. It is our experience that young do wander, but spend much of the time hiding, occasionally giving food-begging calls. We believe flightless young that have left the nest try to hide from mammalian and avian predators. Furthermore, adults appear to know where all the young are located. When adults deliver food, the young scurry to meet them, get excited, often vocalize, and flash their wings as they grab food and maintain balance. In general, we did not observe young expose themselves until adults arrived with food. Potapov and Sale (2012) went on to suggest that older young leave the nest sooner because they are too large to be brooded and gain warmth under the female. It is our experience that larger nestlings nearing the age of nest departure are capable of withstanding all but the most severe

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rain and wet snow conditions (D. Holt unpubl. data). In fact, nestlings nearing this age often sat at the nest edge gular-fluttering, a sign of overheating. Furthermore, in inclement weather, young huddle at the nest, reducing heat loss from conduction and convection.

We suggest that natural selection favors rapid nestling growth and early nest departure as an anti-predator tactic due to the ground-nesting behavior of Snowy Owls, and the fact that numerous terrestrial carnivores exist throughout the owls' breeding range. A similar conclusion was reached by Ricklefs (1968). In our study area, Arctic fox (*Alopex lagopus*) and Pomarine Jaegers (*Stercorarius pomarinus*) do prey upon a few Snowy Owl young. Pre-fledging nest departure of Snowy Owls was similar to that of another obligate ground-nesting species, Short-eared Owls (*Asio flammeus*), which leave their nests at about 16 d (Holt et al. 1992). Although both species reached their greatest body mass gains just prior to leaving their nests on foot, Snowy Owls probably depart their nests about one week later than Short-eared Owls because of growth and developmental constraints of a larger bird. We agree with Ricklefs (1968) and Holt et al. (1992) who suggested early nest departure minimized time predators have to locate nests. Similarly, tree-nesting Long-eared Owls (*Asio otus*) that depart the nest at about 22 d may also be avoiding predation (Seidensticker et al. 2006, Holt et al. 2009b). Secondarily, asynchronous nest departure hedges against reproductive failure if nests are preyed upon at later stages of the nestling period.

Although Snowy Owl young generally stayed within 1 km of their nests, occasionally they ventured further. We were unsure of reasons driving this behavior. It may be interplay between general wandering, an adult strategy to move nestlings to safer areas to avoid predation, or to areas where food is more abundant. Neighboring Snowy Owl territories may also influence this behavior. Other studies reported young remain within a limited area of the nest (Hagen 1960); or within 250 m, 400 m, or 1 km of the nest (Watson 1957, Tulloch 1968). Potapov and Sale (2012) reported young to wander up to 3 km, and mix with other broods. We never observed brood-mixing or feeding by unrelated adults during the wandering period from our monogamous or polygynous nests. Our results were most similar to Watson's (1957) from Baffin Island, Canada.

Fledging Period. Results from other studies were consistent with ours. For example, first flight attempts have been reported at 30–37 d, and sustained coordinated flight at 44–60 d (Watson 1957, Parmelee et al. 1967, Tulloch 1968, Taylor 1973, Robinson and Becker 1986). And, once fledged, siblings conspicuously roosted on tops of mounds often near each other, similar to Watson's (1957) results.

Tulloch (1968) reported no sexual plumage differences at fledging; however, by 10 wk of age he saw differences ($n = 3$). We noted discernible plumage differences in young at 5 wk (see Results). Indeed, we predicted and confirmed with blood tests the sex of 140 individuals based on these plumage traits and were 100% correct (Seidensticker et al. 2011). We also wondered if males fledged before females due to their lighter body mass, but were not able to compare that during these years.

On Brood Reduction and Sibling Cannibalism. We never observed voluntary brood reduction or sibling cannibalism from 74 nests reported herein, or 235 nests for the entire study. We suspected that some females ate young that died in the nest, or fed dead young to hungry nestlings, and we know others did not. The disappearance of nest-bound nestlings, the discovery of their partially consumed bodies, and nestling remains in pellets led us to these conclusions. These events occurred during years of food abundance or food shortage. Our observations from blinds indicated females apportioned food somewhat equally to all nestlings (D. Holt unpubl. data). Nestlings showed minimal amounts of aggression toward each other, and when very young were too small and weak to inflict serious wounds. However, when food was scarce, older, larger, and mobile young outcompeted smaller siblings for food, until about 2–3 wk of age when competition seemed to decrease.

In species that hatch asynchronously, it is believed that an opportunity is thereby provided for larger nestlings to kill, eat, or be fed smaller nestlings, during situations of food stress. Thus, brood reduction supposedly increases chances for some successful nesting during food shortages (Lack 1947, Magrath 1990). Brood reduction and cannibalism were suspected for Snowy Owls (Ingram 1959), and reported for Barn Owls (*Tyto alba*) and Short-eared Owls (Ingram 1959, Holt 1992). In one observation, Wotton (1976) witnessed a female Snowy Owl feed a dead nestling to another nestling. However, this appeared to be scavenging, not brood reduction. We filmed a female specifically care for a sick nestling that eventually died. The female then fed this 2-wk-old nestling to the remaining four nestlings.

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However, we suggest that during times of food stress, the consumption of a few small nestlings may not substantially increase the survival of older siblings.

Comparisons with Other Studies. Mass growth comparisons can be made to other studies as long as the form of the nonlinear model is the same or the parameter estimates are standardized according to the method suggested by Ricklefs (1973). Because Starck and Ricklefs (1998b) standardized their parameter estimates to a logistic model, comparisons can then be made to their estimated values of the growth parameter. Sample sizes were small from other studies; however, our Snowy Owl growth values using the logistic equation (K = 0.154, 95% CI = 0.150, 0.158) were similar to those of Ricklefs (1968, 1983), and Starck and Ricklefs (1998b; K = 0.148) and Wijnandt's (1984; K = 0.149) recalculation's of Watson's (1957) data. These previous studies did not report error measurements, so it is not possible to determine whether our estimates differed significantly.

Potapov and Sale (2012) used a sigmoid equation to describe Snowy Owl growth parameters from a sample of wild owls from six nests and a few samples from the literature. Their most detailed growth data came from two captive-reared nestlings. They claimed their model was more biologically correct growth than models currently used in other ornithological studies. However, their growth curves are not comparable to most other studies of owls that used the logistic function.

Logistic growth models for tree-nesting *Bubo* species similar in size to Snowy Owls were: Eurasian Eagle-Owl (*Bubo bubo*) K = 0.060; Great Horned Owl (*B. virginianus*) K = 0.138; and Verreaux's Eagle-Owl (*B. lacteus*) K = 0.099 (Starck and Ricklefs 1998b). These three species grew at a similar growth rate as Snowy Owls, but Snowy Owls departed their nests earlier. Furthermore, the rapid growth of Snowy Owl flight feathers after nest departure may have evolved in response to terrestrial predation pressure. Indeed, tree-nesting owl species grow more slowly relative to size (Ricklefs 1968, Starck and Ricklefs 1998a), probably because they are released from some predation pressure incurred from ground nesting.

Conclusion. We provide a quantitative measure of mass growth and plumage development in Snowy Owl young. We also propose several hypotheses as to the evolution of these traits based on 24 yr of researching Snowy Owls in the Arctic. Our hypo-theses provide a foundation for future research questions–descriptive, quantitative, and experimental.

Compared to other *Bubo* species, Snowy Owls have a rather more rapid growth and development. This is probably influenced by its ground-nesting habits and by the short Arctic breeding season. Indeed, because Snowy Owls are obligate ground nesters, their rapid growth and development likely coevolved. Although Snowy Owls are large, powerful, and capable of vigorous nest defense, nestlings and young that have departed the nests are subject to occasional predation by mammalian and avian predators. Therefore, we suggest that natural selection favors rapid nestling mass growth, an early pre-fledging nest departure and hiding period, and rapid flight feather development as an antipredator adaptation. These traits are consistent with the life history of many other ground-nesting bird species.

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LITERATURE CITED

BROWN, J., K.R. EVERETT, P.J. WEBER, S.F. MACLEAN, JR., AND D.F. MURRAY. 1980. The coastal tundra at Barrow. Pages 1–29 *in* J. Brown, P.C. Miller, L.L. Teiszen and F. L. Bunnell [EDS.] An Arctic ecosystem: the coastal tundra at Barrow, Alaska. US/IBP synthesis series 12. Dowden, Hutchinson and Ross, Stroudsburg, PA U.S.A.

BRUCE, M.D. 1999. Tytonidae species accounts. Pages 67–75 *in* J. del Hoyo, A. Elliott and J. Sargatal [EDS.] Handbook of the birds of the world. Vol. 5. Lynx Edicions, Barcelona, Spain.

BUNNELL, F.L., S.F. MACLEAN, JR., AND J. BROWN. 1975. Barrow, Alaska, U.S.A. Pages 73–124 *in* T. Rosswall and O.W. Heal [EDS.], Structure and function of tundra ecosystems: IBP Tundra Biome V International Meeting on Biological Productivity of Tundra, Ecological Bulletin 20. Swedish Natural Science Research Council, Stockholm, Sweden.

CRAMP, S. 1985. Handbook of the birds of the western Palearctic: Europe, Middle East and North Africa. Vol. IV, Oxford Univ. Press, London, U.K.

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FAY, F.H. AND T.J. CADE. 1959. An ecological analysis of the avifauna of St. Lawrence Island, Alaska. *University of California Publication in Zoology* 63:73–150.

FULLER, M., D.W. HOLT, AND L. SCHUECK. 2003. Snowy Owl movements: variation on the migration theme. Pages 359–366 *in* P. Berthold, E. Gwinner and E. Sonnenschein [EDS.], Avian migration. Springer-Verlag Berlin, Heidelberg, Germany.

HAGEN, Y. 1960. The Snowy Owl on Hardangervidda in summer of 1959. *Meddelelser fra Statens Viltundersökelser* 2:1–25.

HOLT, D.W. 1992. Notes on Short-eared Owl (*Asio flammeus*) nest sites, reproduction, and territory sizes in coastal Massachusetts. *Canadian Field-Naturalist* 106:352–356.

———, R. BERKLEY, C. DEPPE, P.L. ENRIQUEZ-ROCHA, P.D. OLSEN, J.L. PETERSEN, J.L. RANGEL-SALAZAR, K.P. SEGARS, AND K.L. WOOD. 1999. Strigidae species accounts. Pages 153–242 *in* J. del Hoyo, A. Elliott and J. Sargatal [EDS.], Handbook of the birds of the world, Vol. 5. Lynx Edicions, Barcelona, Spain.

———, M.D. LARSON, N. SMITH, D.L. EVANS, AND D.F. PARMELEE. 2015. Snowy Owl (*Bubo scandiacus*). *In* A. Poole [ED.], The birds of North America online, No. 10. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu./bna/species/010 (last accessed 28 December 2015).

———, M.T. MAPLES, J.L. PETERSEN-PARRETT, M. KORTE, M. SEIDENSTICKER, AND K. GRAY. 2009a. Characteristics of nest mounds used by Snowy Owls in Barrow, Alaska, with conservation and management implications. *Ardea* 97:555–561.

———, S.M. MELVIN, AND B. STEELE. 1992. Nestling growth rates of Short-eared Owls. *Wilson Bulletin* 104:326–333.

———, A. PAULSON, AND L.M. ROMERO. 2009b. Corticosterone as a measure of stress in nest bound and nest departed Long-eared Owl *Asio otus* chicks. *Ardea* 97:593–596.

——— AND S.A. ZETTERBERG. 2008. The 2005 to 2006 Snowy Owl irruption migration to Montana. *Northwestern Naturalist* 89:145–151.

INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of birds of prey. *Auk* 76:218–226.

IRVING, L., C.P. MCROY, AND J.J. BURNS. 1970. Birds observed during a cruise in the ice-covered Bering Sea in March 1968. *Condor* 72:110–112.

KERLINGER, P. AND M.R. LEIN. 1988. Causes of mortality, fat condition, and weights of wintering Snowy Owls. *Journal of Field Ornithology* 59:7–12.

KÖNIG, C. AND F. WEICK. 2008. Owls of the world. Yale Univ. Press, New Haven, CT U.S.A.

LACK, D. 1947. The significance of clutch size. *Ibis* 89:302–352.

MAGRATH, R.D. 1990. Hatching asynchrony in altricial birds. *Biological Review* 65:587–622.

MARCHLAND, P.J. 1991. Life in the cold. Univ. Press of New England, Hanover, NH U.S.A.

MCROY, C.P., S.W. STROKER, G.E. HALL, AND E. MUKTOYUK. 1971. Winter observations of mammals and birds, St. Matthew Island. *Arctic* 24:63–65.

MEBS, T. AND W. SCHERZINGER. 2000. Die Eulen Europas: Biologie, Kennzeichen, Bestände. Franckh-Kosmos Verlags-GmbH and Co., Stuttgart, Germany.

MENYUSHINA, I.E. 1994a. Interspecies relation of the polar fox (*Alopex lagopus*) and the Snowy Owl (*Nyctea scandiaca* L.) during the breeding season in the Vrangel Island. Part I. *Lutreola* 3:15–21.

———. 1994b. Interspecies relation of the polar fox (*Alopex lagopus*) and the Snowy Owl (*Nyctea scandiaca* L.) during the breeding season in the Vrangel Island. Part II. *Lutreola* 4:8–14.

———. 1994c. Interspecies relation of the polar fox (*Alopex lagopus*) and the Snowy Owl (*Nyctea scandiaca* L.) during the breeding season in the Vrangel Island. Part III. *Lutreola* 5:15–19.

MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD U.S.A.

MURIE, O.J. 1929. Nesting of the Snowy Owl. *Condor* 31:3–12.

NAGARAJAN, R.K., K. THIYAGESAN, R. NATARAJAN, AND R. KANAKASABAI. 2002. Patterns of growth in Indian Barn Owls. *Condor* 104:885–890.

PARMELEE, D.F. 1972. Canada's incredible Arctic owls. *Beaver* (summer) 30–41.

———. 1992. Snowy Owl (*Nyctea scandiaca*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 10. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

———, H.A. STEPHENS, AND R.H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. *National Museum of Canada Bulletin* 222:1–229.

PENTERIANI, V., M.M. DELGADO, C. MAGGIO, A. ARADIS, AND F. SERGIO. 2005. Development of chicks and predispersal behavior of young in the eagle owl (*Bubo bubo*). *Ibis* 147:155–168.

PETERSEN, J. AND D.W. HOLT. 1999. Observations on the Snowy Owl (*Nyctea scandiaca*) at Barrow, Alaska: 1992–1998. North Slope Borough, Department of Wildlife Management, Barrow, AK U.S.A.

PITELKA, F.A., P.Q. TOMICH, AND G.W. TREICHEL. 1955a. Breeding behavior of jaegers and owls near Barrow, Alaska. *Condor* 57:3–18.

———, ———, AND ———. 1955b. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecological Monograph* 25:85–117.

POTAPOV, E. AND R. SALE. 2012. The Snowy Owl. T. AND A. D. Poyser, London, U.K.

R DEVELOPMENT CORE TEAM. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (last accessed 27 December 2015).

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

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———. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201.

———. 1983. Avian growth and development. Pages 1–83 *in* D.S. Farner, J.R. King and K.C. Parkes [EDS.], Avian biology, Vol. 7. Academic Press, New York, NY U.S.A.

ROBINSON, M. AND C.D. BECKER. 1986. Snowy Owls on Fetlar. *British Birds* 79:228–242.

ROMERO, L.M, D.W. HOLT, M. MAPLES, AND J.C. WINGFIELD. 2006. Corticosterone is not correlated with nest departure in Snowy Owl chicks (*Nyctea scandiaca*). *General and Comparative Endocrinology* 149:119–123.

SEIDENSTICKER, M.T., D.T. TYLER FLOCKHART, D.W. HOLT, AND K. GRAY. 2006. Growth and plumage development of nestling Long-eared Owls. *Condor* 108:981–985.

———, D.W. HOLT, J. DETIENNE, S. TALBOT, AND K. GRAY. 2011. Sexing young Snowy Owls. *Journal Raptor Research* 45:281–289.

STARCK, J.M. AND R.E. RICKLEFS. 1998a. Patterns of development: The altricial-precocial spectrum. Pages 3–30 *in* J.M. Starck and R.E. Ricklefs [EDS.], Avian growth and development: evolution within the altricial-precocial spectrum. Oxford Univ. Press, New York, NY U.S.A.

——— AND ———. 1998b. Avian growth rate data set. Pages 381–415 *in* J.M. Starck and R.E. Ricklefs [EDS.], Avian growth and development: evolution within the altricial-precocial spectrum. Oxford Univ. Press, New York, NY U.S.A.

SUTTON, G.M. AND D.F. PARMELEE. 1956. Breeding of the Snowy Owl in southeastern Baffin Island. *Condor* 58: 273–282.

TAYLOR, P.S. 1973. Breeding behavior of the Snowy Owl. *Living Bird* 12:137–154.

THERRIEN, J.-F., G. GAUTHIER, AND J. BÊTY. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. *Journal Avian Biology* 42:363–369.

TULLOCH, R.J. 1968. Snowy Owls breeding in Shetland in 1967. *British Birds* 61:119–132.

———. 1969. Snowy Owls breeding in Shetland. *British Birds* 62:33–36.

WATSON, A. 1957. The behaviour, breeding, and food-ecology of the Snowy Owl (*Nyctea scandiaca*). *Ibis* 99:419–462.

WIKLUND, C.G. AND J. STIGH. 1983. Nest defence and evolution of reversed sexual size dimorphism in Snowy Owls (*Nyctea scandiaca*). *Ornis Scandinavica* 14:58–62.

——— AND ———. 1986. Breeding density of Snowy Owls (*Nyctea scandiaca*) in relation to food, nest sites and weather. *Ornis Scandinavica* 17:268–274.

WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* 72:1–92.

WILSON, R.T, M.P. WILSON, AND J.W. DURKIN. 1987. Growth of nestling Barn Owls (*Tyto alba*) in central Mali. *Ibis* 129:305–318.

WOTTON, M. 1976. Summer of the white owl. *Audubon* 78:32–41.

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