

VARIATION IN PRIMARY MOLT IN THE LEAST AUKLET

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Abstract. Along with breeding and migration, molt is one of the most energetically expensive components of a bird's annual cycle. Auklets (tribe Aethiini) are apparently unique among the Alcidae in that flight-feather molt and breeding overlap. We compared the degree of overlap of primary molt with breeding in the Least Auklet (*Aethia pusilla*) at four colonies in varying oceanographic environments: Kiska Island (Aleutian Islands, Alaska, 52°N), St. George Island (Pribilof Islands, Alaska, 56°N), St. Paul Island (Pribilof Islands, 57°N), and Cape Ulyakhpen (Chukotka Peninsula, Russia, 64°N). We hypothesized that the onset and speed of feather replacement should be related to latitude or sea-ice dynamics. Flight-feather molt commenced during incubation with up to four primaries replaced by the end of chick rearing. At Kiska, we found no difference in molt rate between adult breeders and nonbreeders, but subadults started molt after adults and were more variable in when they started primary molt. At higher latitudes adult auklets replaced their first four primaries faster and initiated molt later although the length of the breeding season was similar. The increased energetic requirements of Least Auklets breeding and molting at higher latitudes are supported by the cold Anadyr Current, which advects lipid-rich oceanic copepods (*Neocalanus* spp.). In the Least Auklet and other members of the Aethiini, sequential primary molt, rather than the simultaneous molt typical of other alcids, may be possible because of auklets' lower body mass, lower wing loading, mass loss at hatching, and foraging on highly abundant prey.

Key words: molt, Least Auklet, *Aethia pusilla*, Bering Sea.

Variación de la Muda las Primarias en *Aethia pusilla*

Resumen. Junto con la reproducción y la migración, la muda es uno de los componentes más costosos en términos energéticos del ciclo anual de un ave. Las alcas (tribu Aethiini) son aparentemente únicos entre los Alcidae en que la muda de las plumas del vuelo y la reproducción se superponen. Comparamos el grado de superposición de la muda de las primarias con la reproducción en *Aethia pusilla* en cuatro colonias en ambientes oceanográficos variados: Isla Kiska (Islas Aleutianas, Alaska, 52° N), Isla St. George (Islas Pribilof, Alaska, 56° N), Isla St. Paul (Islas Pribilof, 57° N) y Cabo Ulyakhpen (Península Chukotka, Rusia, 64° N). Hipotetizamos que el inicio y la velocidad del reemplazo de las plumas deberían estar relacionados con la latitud o la dinámica del hielo marino. La muda de las plumas del vuelo comenzó durante la incubación con hasta cuatro primarias reemplazadas hacia el final de la cría del pichón. En Kiska, no encontramos diferencias en la tasa de muda entre los adultos criando y no criando, pero los sub-adultos comenzaron la muda luego de los adultos y fueron más variables en el comienzo de la muda de las primarias. A mayores latitudes, los adultos de alcas reemplazaron sus primeras cuatro primarias más rápido e iniciaron la muda más tarde aunque la duración de la estación reproductiva fue similar. El incremento de los requerimientos energéticos de los individuos de *A. pusilla* reproduciéndose y mudando a mayores latitudes están respaldados por la corriente fría de Anádyr, la cual transporta copépodos oceánicos (*Neocalanus* spp.) ricos en lípidos. En *A. pusilla* y otros miembros de los Aethiini, la muda secuencial de las primarias puede ser posible, más que la muda simultánea típica de otros álcidos, debido a la menor masa corporal de las alcas, menor carga alar, pérdida de masa en la eclosión y forrajeo basado en presas muy abundantes.

INTRODUCTION

The regular replacement of feathers through molt is costly both in energy and time (Murphy 1996, Rohwer et al. 2009). Despite the importance of molt, studies of inter-annual and inter-colony variation of molt of pelagic seabirds, and of possible influencing factors, are rare (Emslie et al. 1990, Underhill

and Crawford 1999). Because of the cost of feather synthesis and the aerodynamic and thermoregulatory costs of missing feathers, understanding patterns of molt can be crucial to investigations of avian physiology, ecology, and behavior (Hoye and Buttemer 2011).

Auklets (tribe Aethiini) are unusual among the Alcidae because several species molt their primary feathers sequentially

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beginning during the breeding season (Bédard and Sealy 1984, Emslie et al. 1990, Konyukhov 2001, 2009). Most other auks molt all their flight feathers simultaneously after they leave the breeding colony, rendering them flightless for several weeks (Stresemann and Stresemann 1966, Harris and Yule 1977, Sealy 1977, Bédard 1985, Ewins 1988, Harris and Wanless 1990, Bridge 2006, Pyle 2008). Patterns of molt of some species of auk, such as the Spectacled Guillemot (*Cephus carbo*), Craveri's Murrelet (*Synthliboramphus craveri*), and Japanese Murrelet (*S. wumizusume*) are largely unknown.

The Least Auklet (*Aethia pusilla*) is endemic to the Bering and Okhotsk seas and adjacent North Pacific Ocean, where it breeds at a few dense colonies (Gaston and Jones 1998). In North America, major colonies are in the western Aleutian Islands, on the Pribilof Islands, and in the northern Bering Sea (Bond et al. 2013). In Russia, Least Auklets breed on Ratmanov (Big Diomedé) Island (Bering Strait), on the Chukotka Peninsula, and on islands in the Sea of Okhotsk and Kuril Archipelago (Dement'ev et al. 1951, Kozlova 1957, Konyukhov et al. 1998, Kondratyev et al. 2000, Artukhin et al. 2001, Zelenkaya 2009). Northern colonies in the Bering Sea and Sea of Okhotsk are surrounded by sea ice during part of the year, whereas all Aleutian and most Kuril Island colony sites are ice-free year round (Fetterer et al. 2010).

Molt is often timed with birds' annual cycles (Dawson 1998, Dawson et al. 2001), and in the Least Auklet it is probably related to the timing of breeding. Auklets breed later at higher latitudes; e.g., Least Auklets nest 3–4 weeks later at St. Lawrence Island (63° 24' N) than at colonies in the Aleutian Islands (approximately 52°N) (Sealy 1975, Gaston and Jones 1998, Bond et al. 2013). We therefore predicted that the timing of the Least Auklet's molt would follow a similar gradient. Such latitudinal variation in timing and rate of molt has been observed in mammals (Todorovič 1955, King and Moody 1982) and land birds (Williamson and Emison 1971, Mewaldt and King 1978, Dawson et al. 2000), but ours is the first investigation of this phenomenon in a marine bird.

We recorded data from all of the Least Auklet's major breeding areas (northern Bering Sea, Pribilof Islands, Aleutian Islands, Chukotka Peninsula), to investigate how the timing of primary replacement varied with breeding phenology, age class, breeding status (breeder vs. nonbreeder), and latitude of the colony. Because Least Auklets begin replacing flight feathers during incubation and continue through chick rearing, we predicted that adults from more northerly colonies affected by sea ice and snowmelt should molt later and faster than adults farther south. On the basis of Bédard and Sealy (1984) and Emslie et al. (1990), we also predicted that subadults should initiate molt later but replace primaries faster than adults. We also used museum specimens collected outside the breeding season to determine the progress of the Least Auklet's primary molt away from the breeding colonies when the birds are at sea. Finally, we discuss why the tribe

Aethiini is unique among the Alcidae in overlapping primary replacement and breeding.

METHODS

CAPTURE AND MOLT STATUS OF WILD LEAST AUKLETS

We caught Least Auklets at Sirius Point, Kiska Island, Aleutian Islands, Alaska (52° 08' N, 177° 37' E) in June and July 2008 and 2009, at Ulakaia Ridge, St. George Island, Pribilof Islands, Alaska (56° 35' N, 169° 35' W), from June to August 2005, at Tolstoi Point, East Landing, and Zapadni Point on St. Paul Island, Pribilof Islands (57° 11' N, 170° 16' W) from June to August 2000 and in June and July 2004, and at Cape Ulyakhpen on the Chukotka Peninsula, Russia (64° 23' N, 173° 54' W) from June to September 1988–1990 (Fig. 1). Konyukhov (2009) summarized data from St. Paul, St. George, and Cape Ulyakhpen. We caught the birds with noose carpets or with a ground net placed over crevices in which the birds nest (Konyukhov 2009). We weighed, measured, and banded each bird and recorded the number of replaced and missing primaries. Adults were identified as having a black forehead with white streaks; subadults (individuals 11–13 months old) have a brown forehead and worn flight feathers (Pyle 2008). On Kiska Island only, we determined the apparent breeding status of each adult by resighting marked birds and recording whether they carried a meal for the chick, which is evident from the distended throat pouch (Portenko 1934, Bédard 1969). We identified a bird as a breeder if it was observed with a meal for a chick at least twice during the chick-rearing period (late June to late July). This criterion underestimates the number of actual breeders, as some captured birds were not seen after release and could have been breeding elsewhere in the colony, and because some breeders whose attempt failed during incubation would not have been seen carrying a meal (Jones et al. 2002).

At St. Paul Island, St. George Island, and Cape Ulyakhpen, we measured newly grown primaries to the nearest 0.1 mm with calipers. At Kiska Island, we scored feathers as "old" (0), missing (1), new, 25% grown (2), new, 50% grown (3), new, 75% grown (4), or new, fully grown (5). We then converted feather lengths to proportion of feather mass grown (Underhill and Summers 1993) by assuming that the deposition of mass within each new feather was linear and by using masses of fully grown primaries obtained from auklets encountered dead at Kiska (all feathers) or sampled for stable-isotope analysis (P1 and P10, Table 1). The proportion of feather mass grown is preferable, as it describes the energetic costs more accurately than do measured feather lengths (Underhill and Zucchini 1988), and counting replaced and missing feathers assumes that each feather is energetically identical (Rohwer 2008). The relationship between length and mass of Least Auklet primaries is not uniform (Table 1); the mass per mm of outermost primaries is greater than that of inner primaries.

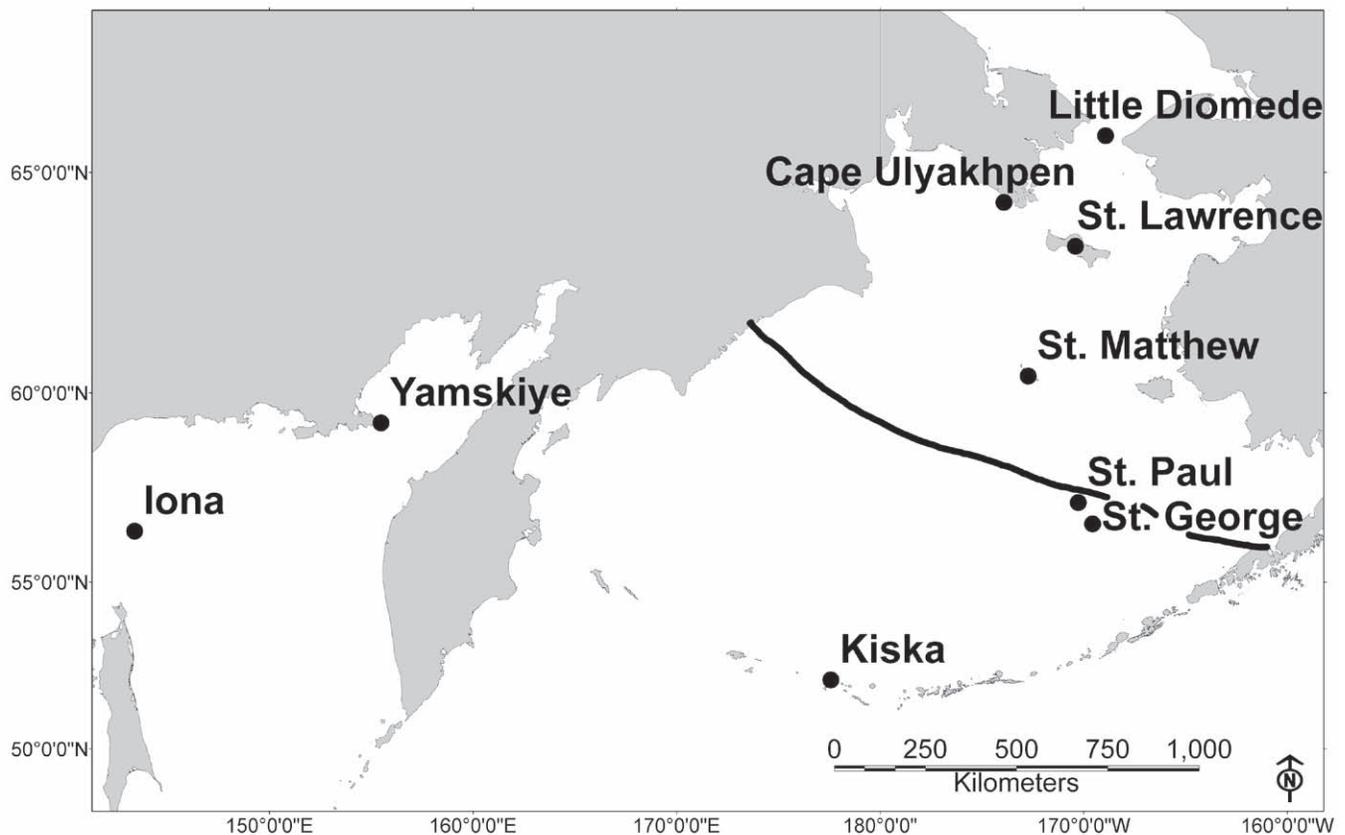


FIGURE 1. We investigated the Least Auklet's primary molt at four colonies in the Bering Sea: Cape Ulyakhpen, St. Paul, St. George, and Kiska islands. Other place names mentioned in the text are also shown. The solid line is the approximate maximum extent of sea ice extent, 2003–2007 (data from the National Snow and Ice Data Center).

We analyzed the proportion of feather mass grown in relation to the mass of the first four primaries, as only these are replaced during the breeding season (see Results).

MUSEUM SPECIMENS

To study the Least Auklet's molt outside the breeding season, we examined specimens collected from September to January and held in museum collections in Canada, the United States, Japan, and Russia (Appendix, available at <http://dx.doi.org/10.1525/cond.2013.110062>). As with live auklets, we aged each specimen as adult or subadult and scored each primary as "old" (0), missing (1), new, 25% grown (2), new, 50% grown (3), new, 75% grown, or new, fully grown (5). We then converted the values into proportion of feather mass grown of all 10 primaries (Remisiewicz et al. 2010). Because we assumed some mixing of winter populations, lacked any a priori knowledge about segregation of Least Auklets from different breeding areas during the nonbreeding season, and had a small sample, we analyzed all September–January specimens together.

STATISTICAL METHODS

Using the mass of each primary (Table 1), we converted the measured lengths of feathers to proportion of feather mass

grown for an Underhill–Zucchini type 5 analysis (Underhill and Zucchini 1988, Underhill et al. 1990; "U-Z 5" analysis). U-Z 5 is used when individuals sampled have either not yet started, or

TABLE 1. The mass and length of Least Auklet primaries used to calculate the proportion of feather mass grown for Underhill–Zucchini molt models ($n = 5$ individuals, except for P1 and P10, where $n = 13$ individuals). Lengths are from Konyukhov (2009). Total feather mass \pm SD is given for the five individuals of which all 10 primaries were weighed.

Primary	Mass \pm SD (mg)	Length \pm SD (mm)	Mean mg mm ⁻¹
1	11.1 \pm 1.3	43.1 \pm 1.7	0.26
2	12.9 \pm 2.3	46.0 \pm 1.9	0.28
3	14.3 \pm 2.7	48.7 \pm 1.5	0.29
4	16.5 \pm 2.6	51.1 \pm 2.0	0.32
5	18.3 \pm 2.8	54.5 \pm 1.4	0.34
6	19.1 \pm 3.2	55.9 \pm 1.7	0.34
7	19.8 \pm 3.6	57.1 \pm 1.6	0.35
8	20.8 \pm 3.7	57.8 \pm 2.1	0.36
9	22.8 \pm 3.4	58.3 \pm 1.7	0.39
10	24.5 \pm 2.8	56.5 \pm 1.8	0.43
Total	176.6 \pm 30.0		0.33

are currently molting primaries and no individual has finished primary molt at the end of the study (Underhill et al. 1990). U-Z models use a maximum-likelihood approach to estimate the duration (and therefore rate) of molt and date of molt initiation for a given population by proportion of feather mass grown. We constructed the models with the package “moult” (Erni et al. 2013) in R 2.12.1 (R Development Core Team 2011). To test for differences in measures of molt by group (breeders vs. nonbreeders, adults vs. subadults, among colonies) in a series of planned comparisons, we used paired *t*-tests, and corrected α values by both the false-discovery rate approach (Benjamini and Hochberg 1995) and Dunn–Šidák correction (Šidák 1967).

RESULTS

MOLT OF LEAST AUKLETS AT BREEDING COLONIES

On Kiska Island, we examined 214 live birds between 8 June and 26 July 2008 and 115 birds between 10 June and 19 July 2009. At St. George Island, we examined 232 adult birds between 30 June and 5 August 2005 and 143 adults between 25 June and 31 July 2007. At St. Paul Island, we examined 310 birds between 10 June and 9 August 2000 and 182 birds between 29 June and 30 July 2004. At Cape Ulyakhpen, we captured 129 adults between 4 June and 7 September 1988, 195 adults between 5 June and 25 August 1989, and 386 adults between 2 June and 31 August 1990. We found that Least Auklets begin growing up to four primary feathers sequentially during late incubation and early chick rearing.

Because of the small number of adult birds examined on Kiska in 2009 ($n = 65$), it was not possible to construct a meaningful U-Z model for this group, so we excluded it from subsequent analysis.

Overall, when compared with the data, fitted values from the U-Z 5 model had relatively high goodness of fit ($r^2 = 0.62$, $P < 0.001$); no outliers were detected. Conclusions from multiple comparisons by both the false-discovery rate and Dunn–Šidák correction were identical. At Kiska Island, the duration of primary molt of breeders and nonbreeders did not differ ($t_{153} = 0.80$, $P = 0.42$), nor did that of adults and subadults ($t_{209} = 0.21$, $P = 0.84$). Breeding and nonbreeding adults began primary molt at the same time ($t_{153} = 0.75$, $P = 0.45$), and the extent of individual variation in start date of both classes was the same ($t_{153} = 1.37$, $P = 0.17$), but subadults began molt 18 days later

than adults ($t_{209} = 2.66$, $P = 0.009$) and the date of the start of their molt was much more variable ($t_{209} = 12.70$, $P < 0.001$; Table 2).

With respect to the onset of primary molt, three groups emerged, following a general pattern of initiation earlier in the Aleutians, intermediate in the Pribilofs, and later at Cape Ulyakhpen. The auklets' molt began earliest in the Aleutians (Kiska 2008) + Pribilofs (St. Paul 2004, St. George 2005), then in the Pribilofs (St. George 2007, St. Paul 2000) + Chukotka (Cape Ulyakhpen 1989, 1990), latest at Cape Ulyakhpen in 1988 (Table 3). Variation in the start date was generally higher at southern colonies (Aleutians, Pribilofs) than at colonies on the Chukotka Peninsula (Table 3). At the Pribilofs the start date tended to be intermediate; there was no difference in SD of start date between St. George in 2007 and Cape Ulyakhpen in 1990 ($P = 0.86$) or among St. Paul in 2000 and Cape Ulyakhpen in 1988 and 1989 (all $P > 0.14$; Fig. 2, Table 3).

MUSEUM SPECIMENS

We examined 66 museum skins collected between September and January. Some birds had completed primary molt by the end of September, others a month later. No birds were molting primaries after 27 November (Fig. 3).

DISCUSSION

Least Auklets replace the innermost primary feathers at the breeding colony during chick rearing and complete primary molt by October or November. Our results contrast with patterns of molt of the closely related Cassin's Auklet (*Ptychoramphus aleuticus*), in which nonbreeding subadults tend to molt primary feathers faster than do breeding adults, presumably because the costs of breeding reduce the amount of energy and resources available for molt (Emslie et al. 1990). We found no difference: adults (breeders and nonbreeders or failed breeders) molted at the same rate as subadults. Neither did Bédard and Sealy (1984) find a difference between successful and failed breeders in progress of wing molt.

Subadult Least Auklets molt 18 days later than adults and were more variable in the timing of initiation of their molt, replacing their extremely worn flight feathers (Bond et al. 2013; originally grown a year before when the bird was a nestling), though the duration of their molt is similar to that of adults (Table 2). Subadult Least Auklets do not breed (Bond et al. 2013) and therefore do not

TABLE 2. At Kiska Island in 2008, breeding status and age class had no effect on the duration or initiation date of primary molt of adult Least Auklets. Subadults' initiation date was significantly more variable than that of adults. Groups sharing the same letter are not considered statistically different.

Group	<i>n</i>	Initiation date ± SE (days)	Initiation date SD ± SE (days)	Duration ± SE (days)
Adult breeders	84	16 Jun ± 5.9 ^a	18.3 ± 0.2 ^a	79.5 ± 24.8 ^a
Adult nonbreeders	71	11 Jun ± 3.7 ^a	18.7 ± 0.2 ^a	104.5 ± 16.8 ^a
All adults	155	13 Jun ± 3.0 ^a	19.5 ± 0.1 ^a	93.0 ± 12.4 ^a
Subadults	56	01 Jul ± 7.7 ^b	24.3 ± 0.5 ^b	100.7 ± 52.6 ^a

TABLE 3. Adult Least Auklets from the most northern colony (Cape Ulyakhpen) tended to molt their primaries faster and to start their primary molt later than did conspecifics in the Pribilofs (St. Paul, St. George), or the Aleutians (Kiska). Groups sharing the same letter are not considered statistically different; colonies are arranged from north to south.

Colony and year	<i>n</i>	Initiation date ± SE (days)	Initiation date SD ± SE (days)	Duration ± SE (days)
Cape Ulyakhpen				
1988	129	28 Jul ± 1.8 ^c	11.3 ± 0.1 ^b	54.4 ± 6.6 ^a
1989	195	6 Jul ± 2.5 ^b	11.3 ± 0.1 ^b	75.2 ± 8.3 ^{ab}
1990	386	12 Jul ± 2.2 ^b	10.2 ± 0.1 ^a	60.5 ± 7.2 ^{ab}
St. Paul				
2000	310	9 Jul ± 2.3 ^b	11.5 ± 0.1 ^b	66.1 ± 8.6 ^{ab}
2004	182	10 Jun ± 5.3 ^a	17.9 ± 0.2 ^c	114.0 ± 18.6 ^{bc}
St. George				
2005	232	14 Jun ± 6.3 ^{ab}	23.0 ± 0.2 ^e	133.2 ± 23.1 ^{bc}
2007	143	7 Jul ± 2.2 ^b	10.3 ± 0.1 ^a	76.6 ± 9.1 ^{ab}
Kiska				
2008	158	13 Jun ± 3.5 ^a	19.6 ± 0.1 ^d	93.6 ± 14.3 ^{ab}

need to carry the nutrient reserves required by breeding individuals (Gaston and Hipfner 2006), so they are less constrained in the timing of molt. The primary molt of subadult birds requires greater attention, and further study over multiple colonies and years to determine whether the trends we observed are typical or anomalous.

We found that breeding status had no relationship with the progress of molt, as Bédard and Sealy (1984) also noted for wing molt in the Crested (*Aethia cristatella*) and Parakeet (*A. psittacula*) as well as the Least Auklet. Two points must be considered, however: first, our method underestimates the number of actual breeders in our sample, as individuals that failed during incubation were not counted, and some breeders may be seen with a meal for the chick only once. Some birds captured with noose carpets were nonbreeders not tied to a specific part of the colony or were breeding birds that bred elsewhere in the colony (Jones et al. 2002). Second, the timing of primary molt differs by colony and year, and in other auklets both timing and rate vary from year to year (Emslie et al. 1990), so it is possible that breeders and nonbreeders molt at different rates in some years, perhaps in response to variation in food availability or other factors.

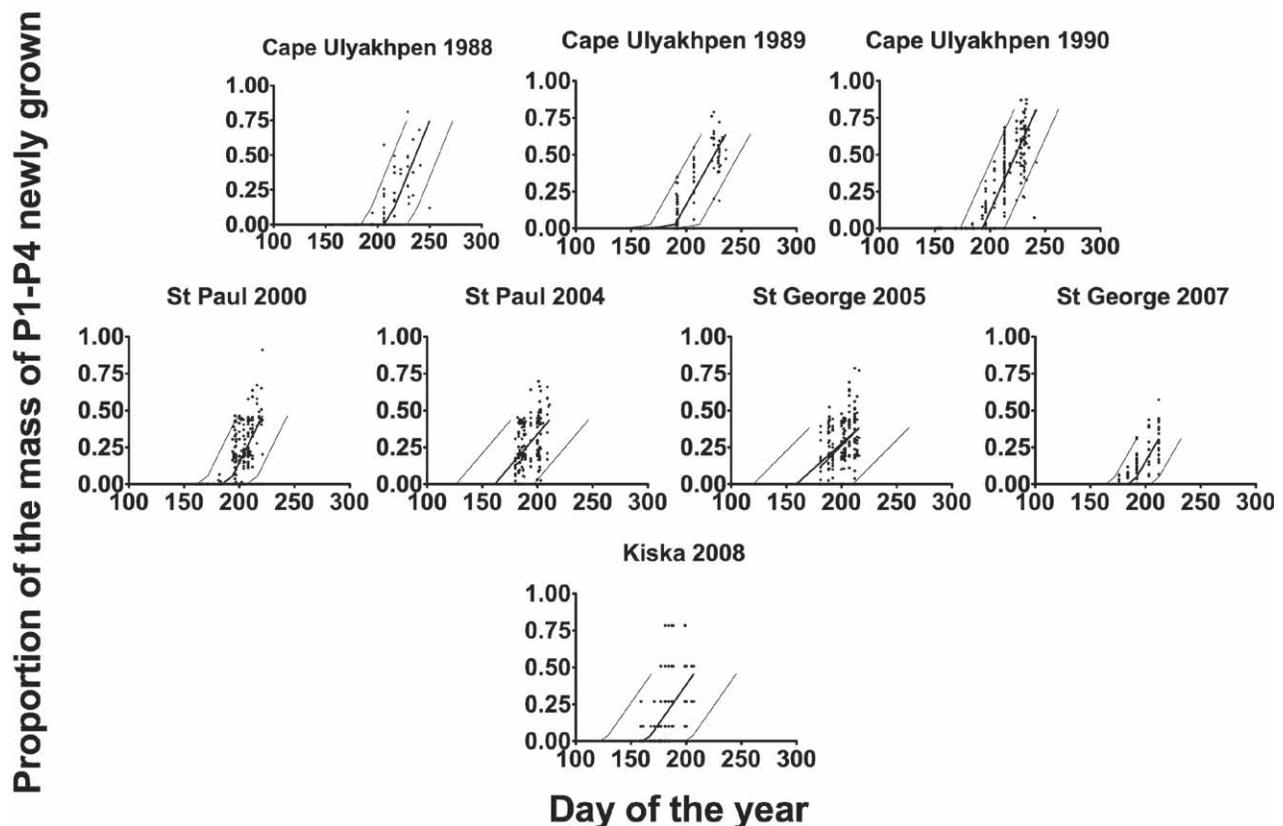


FIGURE 2. Duration and initiation date of primary molt in the Least Auklet varied by year and colony, with adults from the northernmost colony, Cape Ulyakhpen, molting later (higher *x*-intercept) and faster (greater slope). The solid lines are the estimated means and 95% confidence intervals; dots represent individual observations. Researchers arrived after the start of primary molt on St. Paul in 2004 and on St. George in 2005. Day 200 = 19 July.

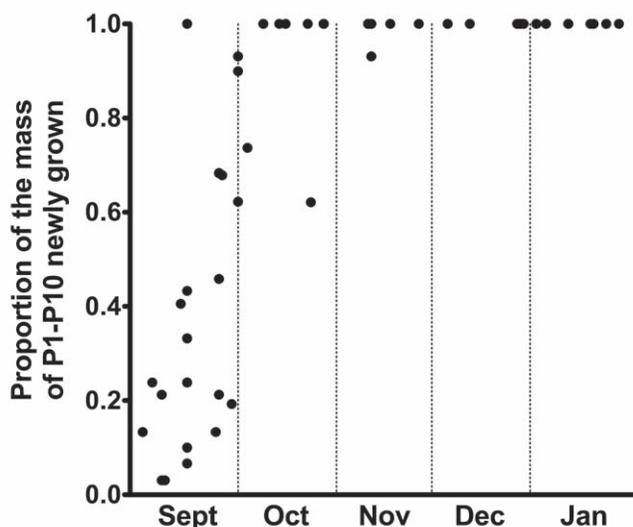


FIGURE 3. The majority of Least Auklets examined from museum collections had completed primary molt by the end of October, and all had completed primary molt by the end of November. Data for all locations, age classes, and years pooled.

Birds breeding at high latitudes often breed in a briefer period (e.g., Summers et al. 2004, Coppack 2007), and molt is often faster at more northerly locations, presumably to minimize overlap of the two life-history stages (Wingfield 2008). Delays in molt can result in an increase in molt rate and decrease in feather quality (Dawson 2004). In the Least Auklet, neither the breeding season nor the duration of molt is compressed at higher latitudes (cf. Cooper et al. 2011): at St. Lawrence Island (63° 24' N) the periods of incubation (30 days) and fledging (29 days; Piatt et al. 1990) are similar in duration to those in the Aleutian Islands (29 days; Renner 2005). There is little information on auklet molt outside the breeding season (i.e., in migration or winter), and few museum specimens have been collected between October and May. Auklets from more northerly locations face longer migrations, as colonies in the northern Bering Sea and the Sea of Okhotsk, unlike those in the Aleutian Islands, are embedded in sea ice, (Fetterer et al. 2010). Birds breeding at colonies surrounded by sea ice may therefore have to molt faster (de la Hera et al. 2009).

Least Auklets breeding in Chukotka likely exploit the cold Anadyr Current, which advects oceanic zooplankton such as *Neocalanus* copepods (Springer et al. 1987, Piatt and Springer 2003). The surface temperature of the Anadyr Current is colder than that around the Pribilof and Aleutian islands (Piatt and Springer 2003). These oceanographic conditions, combined with the rate of molt at Cape Ulyakhpen being faster than at the other colonies we studied, lead us to conclude that Least Auklets breeding farther north must consume more calories per unit time than their southern conspecifics—a situation made possible by the Anadyr Current's advection of oceanic copepods.

We estimate that growth of the Least Auklet's P1 takes around 20–30 days (Konyukhov 2009, Rohwer et al. 2009).

Our modeled values for primary initiation indicate that molt starts during incubation and that the first primary is often replaced by the mean hatch date. The rate of increase per day in proportion of feather mass grown is not likely linear through the sequence of primaries, so estimating a molt-completion date in the absence of a large sample of birds is difficult. On the basis of museum specimens, primary molt concludes before the end of November. Thus duration of the Least Auklet's molt is similar to that estimated for the similar-sized (118 g) Whiskered Auklet (*A. pygmaea*) at Buldir Island, Aleutian Islands, where Konyukhov (2001) predicted molt to end around October. Values of stable isotopes in feathers usually represent exogenous nutrients at the time of synthesis (Hobson and Clark 1992). In adult auklets, it is therefore possible to select feathers representing three different times in the annual cycle: the last (outermost) primary grown the previous winter after young have fledged, body feathers grown during the spring (Pyle 2008), and the first primary grown during incubation.

Unlike other auks, *Aethia* auklets show a high degree of overlap between primary molt and breeding. The Least Auklet is the smallest species of auk and has the lowest wing loading (body mass per unit wing area). It can therefore fly with missing primaries. With the exception of the auklets (*Aethiini*, 5 species), all other auks molt their primaries simultaneously, resulting in a period of flightlessness (Livezey 1988, Thompson et al. 1998, Bridge 2006). The Least Auklet's ecological counterpart in the Atlantic, the Dovekie (*Alle alle*), is also a small planktivore, but its primary molt is functionally simultaneous (Salomonsen 1944, Thompson et al. 1998, Stempniewicz 2001). It's likely that the difference in molt strategy between the Least Auklet and Dovekie is the result of phylogeny, as all extant members of the tribe Alcini (murrelets, *Uria* spp., Razorbill, *Alca torda*, and Dovekie) replace their primaries simultaneously, and have a period of flightlessness (Bédard 1985, Thompson et al. 1998).

Molt–breeding overlap is also associated with limited post-breeding migration or dispersal (Bridge 2006). The Least Auklet's winter range is largely unknown, but the birds are more abundant in the western Pacific during the winter and spring (Vyatkin 1981, Sydeman et al. 2010), and some winter in the Sea of Japan off the coast of Primorye, Russia (Shuntov 1965, Velizhanin 1977, Kondratyev et al. 2000). Sea-ice cover in the Bering Sea and Sea of Okhotsk, however, requires some auklets to disperse up to 1000 km from their breeding colony (Fetterer et al. 2010). Bridge (2006:9) classified the Least Auklet as “dispersive,” among “birds that leave the breeding area after fledging chicks but that spend the nonbreeding period in the general area or region of the breeding site.” It is clear, however, that Least Auklets breeding in the northern Bering Sea (Chukotka Peninsula, Ratmanov, Little Diomedea, St. Lawrence, St. Matthew islands) and the Sea of Okhotsk [Yamskiy Islands, and Iona (St. Jonah) Island, for example] must disperse at least hundreds of km during winter (Fetterer et al. 2010). The Least Auklet may therefore be an exception to the general trade-off between dispersal and molt–breeding overlap.

We found that the Least Auklet's primary molt varies with latitude, likely because of local oceanographic conditions that facilitate upwelling of copepod prey. Physiological and behavioural factors, including mass loss and a change in foraging area, allow Least Auklets to molt during chick rearing, presumably the time of greatest food availability.

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Appendix

Catalogue numbers of Least Auklet specimens examined at the American Museum of Natural History (New York, New York, USA; AMNH), Academy of Natural Sciences (Philadelphia, Pennsylvania, USA; ANSP), Cowan Vertebrate Museum (Vancouver, British Columbia, Canada; CVM), Delaware Museum of Natural History (Wilmington, Delaware, USA; DMNH), Denver Museum of Nature and Science (Denver, Colorado, USA; DMNS), Field Museum of Natural History (Chicago, Illinois, USA; FMNH), Moscow State University Zoological Museum (Moscow, Russia; ZMMU), Harvard Museum of Comparative Zoology (Cambridge, Massachusetts, USA; MCZ), University of Michigan Museum of Zoology (Ann Arbor, Michigan, USA; UMMZ), National Museum of Natural History–Smithsonian Institution (Washington, D.C., USA; USNM), San Diego Natural History Museum (San Diego, California, USA; SDSNH), and the Yamashina Institute for Ornithology (Chiba, Japan; YIO).

AMNH: 30040, 30041, 30043, 95335, 653500, 748234, 748235, 748241, 749236, 749240, 753496, 753497, 753498, 753499, 753501, 753503, 753504; ANSP-55379, 148119, 148121; CVM-13290; DMNH-55060; DMNS-11636; FMNH-159117, 159118, 159119; MCZ-66704, 158779, 250852, 250853, 250854, 250860, 250861, 276930, 317567, 319889, 337388; UMMZ-150027; USNM-92980, 237505, 406336, 406337; SDSNH-16083, 16084, 16085, 16086, 39723; YIO-12768, 12769, 12771, 12777, 12778, 12779; ZMMU-42421, 42724, 64650, 70035, 70777, 79193, 81118, 85668, 85669, 98295, 98296, 98297, 119171.