EFFECTS OF HUMAN DISTURBANCE ON BREEDING LEAST AND CRESTED AUKLETS AT ST. LAWRENCE ISLAND, ALASKA

JOHN F. PIATT, BAY D. ROBERTS, WAYNE W. LIDSTER,
JOHN L. WELLS, AND SCOTT A. HATCH
Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 USA

ABSTRACT.—We studied breeding success, chick growth, and diets of Least (*Aethia pusilla*) and Crested (*A. cristatella*) auklets on St. Lawrence Island, Alaska, in summer 1987. Least Auklets had higher breeding success on control plots (50–66%) than on disturbed plots (36%). Crested Auklets had a breeding success of 42% on disturbed plots. Predation by microtine rodents and weather accounted for most natural chick mortality. Least Auklet chicks grew at a maximum rate of 4.9 g/day, and Crested Auklet chicks at 12.8 g/day. Least Auklet chicks were fed mostly copepods (*Neocalanus plumchrus*), whereas Crested Auklet chicks were fed *Thysanoessa* euphausiids. *Received 13 December 1988, accepted 30 November 1989.*

LEAST Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) are the most abundant planktivorous seabirds in the North Pacific, and breeding populations coexist at many colonies in the Bering Sea (Sowls et al. 1978). Both species lay their eggs in natural crevices formed in the rubble of talus slopes. There have been few detailed studies of auklet breeding biology, probably because auklet colonies are remote, and breeding sites are difficult to observe. We studied Least and Crested auklets on St. Lawrence Island in summer 1987 to learn more about their basic breeding biology and to evaluate methods used to measure breeding success.

After several years of study on St. Lawrence Island, Bédard (1969a, b) described the breeding habitat and diets of auklets, and Sealy (1968) reported on chick growth and development (Sealy 1973, 1981), factors that influence breeding chronology (Sealy 1975, 1984) and survival of eggs and chicks (Sealy 1982). Elsewhere, Knudtson and Byrd (1982) estimated Least and Crested auklet breeding success at Buldir Island in the western Aleutians, and Roby and Brink (1986) studied Least Auklet breeding biology during two summers at St. George Island in the Pribilofs.

All previous investigators have noted the negative effect of human disturbance on auklet breeding success, but this factor has never been quantified. We attempted to measure the effect of human disturbance on auklet breeding success and to identify natural sources of egg and chick mortality. Selected Least Auklet study plots were subjected to three levels of disturbance. Because fewer Crested Auklets were found, they were studied at only one (high) level of disturbance. We also measured chick growth and collected food samples to determine the composition of auklet diets.

STUDY AREA AND METHODS

The study was conducted from 28 May to 2 September 1987 at Kongkok Bay (63°24'N, 171°49'W) near the southwestern cape of St. Lawrence Island (Fig. 1). The avifauna, climate, and seabird breeding habitats of St. Lawrence Island have been described elsewhere (Fay and Cade 1959, Bédard 1969a, Sealy 1975).

We established sixteen 200-m^2 auklet study plots on the southeast-facing (inland) talus slope of Owalit Mountain (Fig. 1). At least 20,000 auklets (2:1 Least/Crested) breed on those slopes (Searing 1977, Piatt et al. 1990). All 16 plots were inspected 3-4 times over 13 days during the early egg-laying period to locate eggs, check the status of previously located eggs, and mark breeding sites. Some eggs were located after minor excavation, but most were located by a line-of-sight search with strong flashlights. All inspections were conducted during mid-day (1400–1800) when attendance by adults on the surface of talus slopes was minimal (Piatt et al. 1990). Least Auklet breeding sites on one set of eight "Intensive" plots were checked every day weather permitted through the hatching period (27 July–13 August), every 2–4 days up to early fledging (25 August), and every day possible thereafter until 2 September. We recorded weights and wing-chord lengths of Least Auklet chicks on Intensive plots only. To reduce disturbance, Least Auklet breeding sites in the other set of eight "Control" plots on Owalit Mountain were inspected only four times after the initial search for eggs (but see below). Least Auklet chicks were not handled on Control plots. The

final check of breeding sites on all plots (including those below) was especially thorough, and excavation was sometimes used to determine the status of chicks. On 23–25 July, in another set of eight control plots on the north-facing talus slope of Kongkok Basin (Fig. 1), we searched Least Auklet breeding sites for eggs. These plots were then checked twice before chicks fledged to determine the status of chicks. Observer disturbance in Kongkok was minimal compared with Owalit, where observers were on the slopes daily to check plots and weigh chicks. Least Auklet densities were higher at Kongkok, and total numbers were far greater (ca. 1 million birds; Searing 1977, Piatt et al. 1990) than at Owalit. Because we located fewer Crested Auklet breeding sites, we studied them on all 16 Owalit plots with the same level of intensity as the "Intensive" Least Auklet study plots. Crested Auklet chicks were weighed and measured in all 16 study plots. Although we tried to avoid disturbing Least Auklets in their breeding crevices, our work on Crested Auklets increased disturbance to Least Auklets on the eight "Control" Owalit plots.

It is difficult to monitor the breeding status of Least and Crested auklets because neither builds a nest, and eggs or chicks are never in plain view. Detailed written instructions with reference to orange spray-painted marks and numbers on rocks were used to locate breeding sites again. When eggs and chicks disappeared between site-checks, their fate was difficult to assess. Many reappeared on subsequent checks, but those that never were located again may have been taken by predators, moved permanently, or died of other causes.

Estimates of hatching success were biased because eggs found at a late stage of incubation were more likely to hatch than those found earlier (Mayfield 1975, Johnson 1979). To correct for that effect, we calculated hatching success (Mayfield 1975) as follows: (1) we divided the total number of egg-days observed by the total number of eggs lost, which yielded the egg-survival rate per day; (2) we multiplied that rate by itself n times, where n is the average number of incubation days, which yielded the egg-survival rate per season; and (3) we multiplied that rate by the proportion of eggs surviving to hatching age (i.e. eggs that actually hatched).

For describing and contrasting chick growth rates, we followed Sealy (1973) and Gaston (1985) to determine the "instantaneous (maximum) growth rate" at the inflection point of the growth curve. We determined maximum growth rates from our own and published data by fitting the steepest possible tangent to composite growth curves (Gaston 1985). We calculated median chick weights for comparative purposes as the midweight between hatching and asymptotic weights (Gaston 1985). We also calculated $t_{10\text{-}90}$, the time (days) it took for chicks to grow from 10 to 90% of asymptotic weight (Ricklefs 1967).

Adult body weights were obtained from birds shot

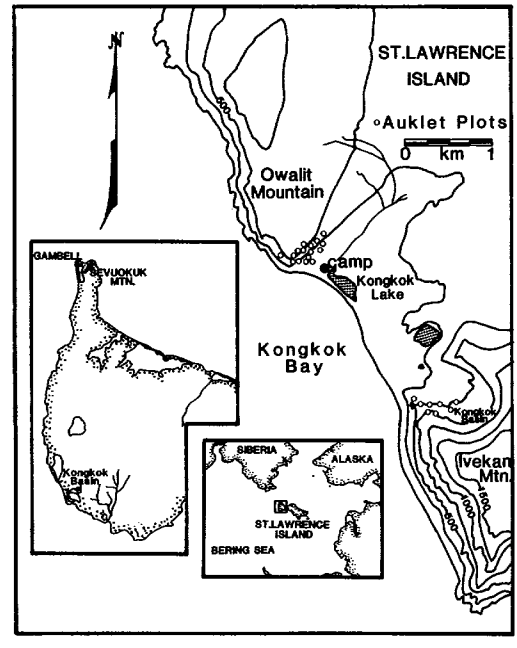

Fig. 1. Locations of auklet study plots on Owalit Mountain and in Kongkok Basin.

by native hunters in Gambell in May and from birds shot near Kongkok Bay for diet studies in June and July. To obtain samples of chick meals, we mist-netted 56 Least Auklets and 5 Crested Auklets on Owalit Mountain between 7 August and 1 September, and we retrieved the contents of food regurgitated from gular pouches. Food samples from 18 Least and 49 Crested auklets were obtained from gular pouches of adults shot near Kongkok Bay on 30 August. Collected meals were preserved in 5% formalin and later subsampled and sorted to identify prey items. Weights of the various taxa identified were extrapolated from numbers occurring in subsamples (Springer and Roseneau 1985).

Results

Breeding chronology.—We first observed Least and Crested Auklets near shore on 15 May, and at colonies near Gambell on 18 May. We inspected breeding habitat at Owalit and Kongkok throughout June, and first eggs were found on 27 June at Owalit (4 Least and 1 Crested). Because we were rarely sure we had found an egg on the first day of incubation, only a few records were used to estimate auklet incubation periods (Table 1). Combined with hatching data (Table 1, Fig. 2), we suggest that median laying occurred around 1–2 July. Only 4 of 369 eggs

TABLE 1. Breeding chronology of Least and Crested auklets on St. Lawrence Island in 1987.

	Least Auklet			Crested Auklet		
	n	$\bar{x} \pm$ SE	Range	*n*	$\bar{x} \pm$ SE	Range
Incubation period (days)	31	30.1 ± 0.51	25–39	20	33.8 ± 0.63	29–40
Chick-rearing period (days)	34	29.3 ± 0.37	25–33	6	33.2 ± 0.05	27–36
Median laying date	—	1 July[a]		—	2 July[a]	
Median hatching	76	30 July		75	4 August	
Median fledging	38	28 August		—	6 September[a]	

[a] Extrapolated from median hatching dates using mean incubation and chick-rearing periods.

(1.1%) were suspected to have been re-lays (Table 2).

Hatching was highly synchronous (Fig. 2). Approximately 80% of Least and Crested auklet eggs hatched over 7- and 10-day periods, respectively. Fledging of Least Auklets was also highly synchronous (ca. 80% over 7 days). The longer incubation and fledging periods of Crested Auklets produced median fledging around 6 September. Fledging began a few days before our departure on 2 September.

Breeding success.—Least Auklet hatching success was higher at Kongkok than at the Intensive study plots on Owalit Mountain ($\chi^2 = 5.06$, df = 1, $P < 0.05$; other comparisons were not significant, Table 2). The biggest difference between sites was the high rate of nonhatching or abandonment of eggs on the Intensive study plots. A higher proportion of eggs disappeared for unknown reasons on the less disturbed plots. Most Crested Auklet egg losses were from nonhatching or abandonment. A smaller proportion was lost to vole predation (as evidenced by teeth marks and punctures of the shell, Sealy 1982). Estimates of hatching success using the Mayfield correction were ca. 5–10% lower than estimates made from raw data.

The losses of Least Auklet chicks from unexplained disappearances, mortality, and predation were higher on heavily disturbed (Intensive) plots than on the moderately disturbed (Control) plots on Owalit and the lightly disturbed plots at Kongkok. This produced progressively higher fledging success from Inten-

TABLE 2. Breeding success of Least and Crested auklets on St. Lawrence Island in 1987. Values in parentheses are percentages of hatched eggs.

	Least Auklet						Crested Auklet	
	Intensive		Control		Kongkok		Intensive	
	n	%	*n*	%	*n*	%	*n*	%
Visits	28		7		3		28	
Total eggs found	109	100.0	101	100.0	56	100.0	103	100.0
Egg losses due to:								
Non-hatch/abandoned	24	22.0	7	6.9	3	5.4	14	13.6
Unknown	4	3.7	13	7.9	4	7.1	4	3.9
Breaking	2	1.8	4	4.0	1	1.8	5	4.9
Vole predation	3	2.8	1	1.0	0	0.0	2	1.9
Eggs re-laid[a]	2	—	1	—	—	—	1	—
Hatching success (A)	~76	69.7	76	75.3	48	85.7	78	75.7
(Mayfield estimate [B])		66.4		69.8		80.5		65.6
Chick losses due to:								
Disappearance	16	(21.1)	16	(21.1)	6	(12.5)	18	(23.1)
Death	12	(15.8)	5	(6.8)	3	(6.3)	6	(7.7)
Vole predation	7	(9.2)	1	(1.3)	0	(0.0)	2	(1.9)
Fledging success (C)	41	(53.9)	54	(71.1)	39	(81.3)	50	(64.1)
Breeding Success (A × C)		37.6		53.5		69.7		48.5
(Mayfield estimate, B × C)		35.8		49.6		65.5		42.0

[a] Not included in subsequent calculations.

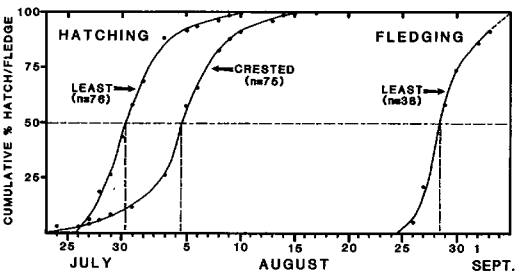

Fig. 2. Breeding phenology of Least and Crested auklets.

sive to Control plots ($\chi^2 = 5.32$, df = 1, $P < 0.05$), and from Control to Kongkok plots ($\chi^2 = 3.91$, df = 1, $P < 0.05$; Table 2). However, chick losses did not vary consistently with levels of disturbance. For example, similar proportions of chicks disappeared on Control and Intensive plots (but see below), and similar proportions of chicks were found dead on Control and Kongkok plots. Crested Auklet chick mortality rates were similar to those of Least Auklets on Owalit, with an overall fledging success that was intermediate between Least Auklet success on Intensive and Control plots.

Vole predation was highest on Intensive study plots (Table 2). Voles did not usually kill chicks outright, but removed flesh from the lower back or flank regions. Death or disappearance usually followed vole attacks by a few days. Thus, many of the chicks that "disappeared" on the Control plots were probably killed by voles, but vanished between inspections. Presumably they were removed by an adult or scavenger, buried, or washed away. Vole predation was most intense on chicks 5–20 days old (Fig. 3). Chicks were protected by attending adults in the first few days of life (Fig. 4), and were able to fend for themselves at a later age (>20 days).

Most chick mortality occurred within a week of hatching (Fig. 3). Overall, 38% (Least Auklet) and 30% (Crested Auklet) of all chicks that died or disappeared were handled by us for measurements. Many dead chicks were found saturated with water, and it is likely that rain and hypothermia contributed to mortality. More than twice as much rain fell between 2 and 17 August (5.1 cm) than in the previous months of June and July (2.1 cm), and much of this fell over two periods (2–3 and 9–12 August) immediately following chick hatching.

No chicks older than 22 days were found dead

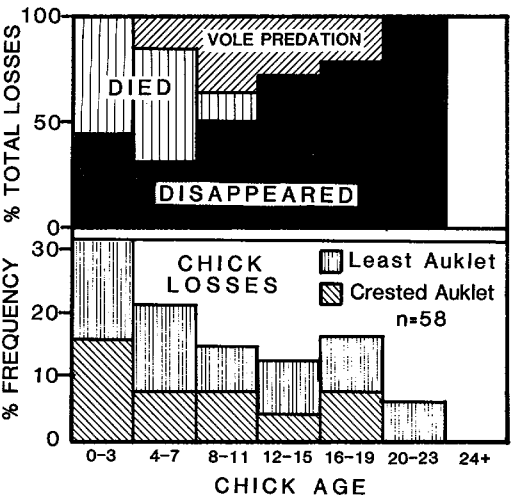

Fig. 3. Sources and frequency of auklet chick mortality with age (days) of chicks.

(Fig. 3). The proportion of chick losses ascribed to "disappearance" increased with age up to 22 days. Some of those chicks may have wandered from their breeding sites and starved, been eaten, or survived undetected. Most chicks were located again on repeated inspections. The few that could not be located after surviving to >23 days old were assumed to have fledged in our calculations of breeding success.

Overall breeding success of Least Auklets varied significantly among study plots ($\chi^2 = 16.1$, df = 2, $P < 0.001$), and reflected the different hatching and fledging rates among plots (above, and Table 2). Breeding success was significantly

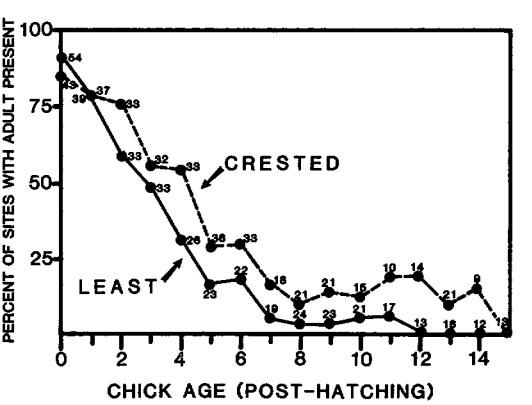

Fig. 4. Frequency of attendance of adult auklets with chicks of varying age (days). Sample sizes indicated next to each data point.

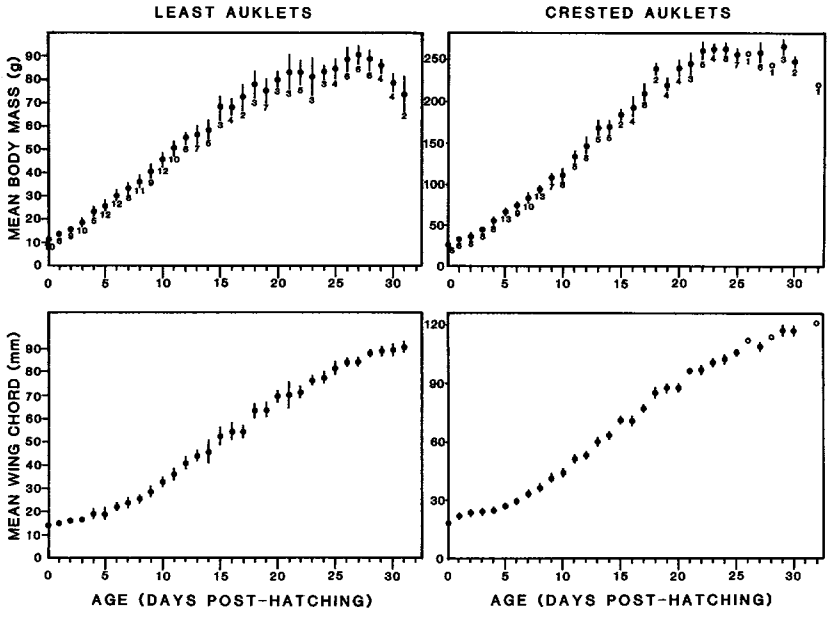

Fig. 5. Increase in body mass and wing lengths ($\bar{x} \pm$ SE, and sample sizes) of auklet chicks with age.

higher on Kongkok plots than on Control plots ($\chi^2 = 3.9$, df = 1, $P < 0.05$), which in turn exceeded success on Intensive plots ($\chi^2 = 5.32$, df = 1, $P < 0.05$). Crested Auklets had a higher breeding success than Least Auklets on Intensive plots, but the difference was not significant ($\chi^2 = 2.58$, df = 1, $P > 0.05$). The Mayfield correction reduced estimates of auklet breeding success 2–6% below estimates from raw data.

Chick growth.—The mean mass of Least Auklet chicks increased steadily for ca. 21 days post-hatch, reached an asymptote at 27 days, and declined thereafter (Fig. 5). The mean mass of chicks older than 22 days, or at fledging, was close to that of adults in late June (Table 3). Maximum chick growth rates, midweights, and development times appeared to be "normal" for St. Lawrence Island (Table 4), but statistical evaluation based on variance of individual growth rates was not possible because only composite data were available from previous studies. After an initial lag as primaries developed, wing lengths increased steadily to 90% of adult wing lengths at 31 days post-hatch.

Crested Auklet chick mass increased steadily up to 23 days and reached an asymptote at 29 days post-hatch. Maximum growth rates and midweights were slightly higher than in previous years (Table 4). No fledging weights were obtained, but the average mass of chicks older than 22 days post-hatch was similar (98%) to adults in mid-July (Table 3). Crested Auklet chick wing lengths increased after an initial 5-day lag to a maximum of 85% of adult lengths.

Diets.—Least Auklet chick meals sampled between 7 August and 1 September were dominated by calanoid copepods, particularly *Neocalanus plumchrus* (Table 5). A variety of other prey were taken in much smaller quantities. These included *Parathemisto* amphipods, *Thysanoessa* euphausiids, and *Pandalus* shrimp zoeae. Most Crested Auklets were collected on one day (30 August), when meals consisted largely of *Thysanoessa* euphausiids. Copepods and amphipods contributed only slightly to the diets of Crested Auklets.

DISCUSSION

Chronology.—Breeding of auklets on St. Lawrence Island followed the same chronology as in most previous years (1964–1967, 1976, 1981; Bédard 1969b, Sealy 1968, Searing 1977, Roseneau et al. 1985), which is 7–10 days later than at St. Matthew Island (60°27′N; Springer et al. 1985a, b), 2–3 weeks later than at St. George Island in the Pribilofs (56°55′N; Roby and Brink 1986), and 3–4 weeks later than at Buldir Island in the western Aleutians (52°21′N; Knudtson and Byrd 1982). The differences are probably

TABLE 3. Mass and wing-chord length of adult auklets and chicks from St. Lawrence Island, 1987.

	Least Auklet			Crested Auklet		
	n	$\bar{x} \pm$ SE	Range	*n*	$\bar{x} \pm$ SE	Range
Adult mass (g)						
May 18–20				18	283 ± 5.6	250–315
June 6	18	86.6 ± 1.5	77–101	6	272 ± 6.0	256–298
June 30	8	82.0 ± 1.8	76–90	34	260 ± 2.4	227–285
July 18				22	265 ± 3.2	228–294
Chick mass (g)						
Asymptote	6	90.8 ± 3.1	81–100	3	269 ± 6.1	258–279
Fledgling	12	82.2 ± 2.8	72–99			
22+ days	46	85.0 ± 1.3	64–105	38	261 ± 2.8	221–290
Wing length (mm)						
Adult	18	97.6 ± 0.5	95–102	20	143 ± 0.9	137–153
Fledgling	12	87.9 ± 1.1	83–95	1	122 (max)	

related to the timing of prey availability in each region (Sealy 1968, Birkhead and Harris 1985), although cold temperatures and snow may also delay breeding at northern colonies in some years (Sealy 1975).

Least and Crested auklets are synchronized in laying eggs, but hatching is out of phase by ca. 5 days, and fledging by ca. 9 days. Like Sealy (1968, 1981), we found that Least Auklets incubated eggs for ca. 31 days and Crested Auklets for 34 days. Incubation times may vary considerably depending on the degree of disturbance to incubating birds (Sealy 1968, 1984), but incubation periods reported for Least Auklets (35–36 days) and Crested Auklets (40–41 days) at Buldir Island (Knudtson and Byrd 1982) were probably inflated because breeding sites were not checked frequently enough to pinpoint laying and hatching dates (Sealy 1984; V. Byrd pers. comm.). Chick-rearing periods were similar to those reported at St. Lawrence Island and elsewhere (Sealy 1968, 1984; Roby and Brink 1986).

Breeding success.—All previous investigators have suggested that their estimates of hatching success for auklet eggs were biased upwards because of early egg losses to predation or other causes (Sealy 1968, Searing 1977, Knudtson and Byrd 1982, Roby and Brink 1986). We concur and believe that hatching success was probably overestimated by 5–10%, and breeding success by 2–6%.

Our measure of egg-hatching success was biased downwards by human disturbance that led to high rates of nonhatching and abandon-

TABLE 4. Auklet growth at St. Lawrence Island (SLI) and other colonies in the Bering Sea (St. Matthew Island [SMI] and the Pribilofs [PRI]).

Area	Year	MGR (g/day)[a]	Mid-weight[b]	$t_{10\text{-}90}$ (days)[c]	Sources
			Least Auklet		
SLI	1987	4.9	51.4	20	This study
SLI	1981	4.7	—	—	Roseneau et al. 1985
SLI	1976	4.4	50.5	19	Searing 1977
SLI	1966–1967	5.3	49.7	18	Sealy 1968
PRI	1981–1982	5.7	53.9	17	Roby and Brink 1986
SMI	1982	4.9	—	—	Springer et al. 1985a
SMI	1983	3.9	—	—	Springer et al. 1985b
			Crested Auklet		
SLI	1987	12.8	147.8	17	This study
SLI	1976	11.1	146.0	20	Searing 1977
SLI	1966–1967	12.5	144.9	22	Sealy 1968

[a] MGR is maximum growth rate.
[b] Mid-weight is the average weight of chicks mid-way through growth to asymptotic weight.
[c] $t_{10\text{-}90}$ is the time (days) for growth between 10 and 90% of asymptotic weight.

TABLE 5. Composition of Least (n = 74) and Crested (n = 54) auklet chick meals collected at St. Lawrence Island between 7 August and 1 September, 1987.

Prey species	Least Auklet			Crested Auklet		
	n	% No.	% Wt.	n	% No.	% Wt.
Neocalanus cristatus	725	1.4	2.4	280	3.2	0.6
Neocalanus plumchrus	44,417	82.9	87.0	909	10.4	1.2
Calanus marshallae	5,646	10.5	5.5	285	3.3	0.2
Calanoid copepod	690	1.3	1.0	20	0.2	0.1
Metridia pacifica	40	0.1	0.1	0	0	0
Eucalanus bungii	286	1.5	0.3	0	0	0
Euchaeta elongata	2	0.1	0.1	0	0	0
Apherusa glacialis	1	0.1	0.1	0	0	0
Anisogammarus pugettensis	48	0.1	0.1	0	0	0
Parathemisto libellula	135	0.3	1.0	9	0.1	0.1
Parathemisto pacifica	571	1.1	0.7	24	0.3	0.1
Parathemisto spp.	28	0.1	0.1	27	0.3	0.1
Thysanoessa spp. adult	36	0.1	0.8	7,048	80.3	97.8
Thysanoessa spp. furcilia	413	0.8	0.1	165	1.9	0.1
Pandalus spp. zoea	525	1.0	1.0	13	0.1	0.1
Paguridae spp. zoea	23	0.1	0.1	0	0	0
Limacina helicina	3	0.1	0.1	0	0	0
Squid	1	0.1	0.1	0	0	0
Fish	1	0.1	0.1	0	0	0

ment. Knudtson and Byrd (1982) and Searing (1977) also reported high rates (29% and 24%, respectively) of nonhatching and abandonment for Least Auklets. Similarly, Crested Auklet egg losses from nonhatching and abandonment observed by Searing (50%), Knudtson and Byrd (22%), and us suggest that human disturbance interferes with incubation activities and reduces hatching success. High egg losses from nonhatching and abandonment have also been reported for other crevice- or burrow-nesting alcids. These include the Parakeet Auklet (*Cyclorrhynchus psittacula*; 20%, Sealy and Bédard 1973), Cassin's Auklet (*Ptychoramphus aleuticus*; 23–30%, Vermeer and Lemon 1986), Xantus' Murrelet (*Synthliboramphus hypoleucus*; 14%, Murray et al. 1983), and Ancient Murrelet (*S. antiquus*; Gaston et al. 1988). Auklet fledging success was also reduced by human disturbance as evidenced by the high rates of chick death and disappearance on disturbed plots. Similarly, most chick losses of both species on St. George and Buldir islands resulted from death or disappearance (16–19%, Roby and Brink 1986, Knudtson and Byrd 1982).

Least Auklet *breeding success* (number of chicks fledged per egg laid) on the least disturbed Kongkok plots (66%) was higher than at Buldir Island (51%) and a little lower than at St. George Island (67–73%). Given differences in methodology and levels of disturbance, however, it is impossible to say whether these values reflect differences in the biology of Least Auklets among areas or years. The same is true for Crested Auklets, where breeding success was lower on disturbed plots at St. Lawrence Island (42%) than at Buldir Island (51%).

Other factors may also bias estimates of breeding success. For example, optimal breeding sites for auklets (especially Crested), are in deep, inaccessible crevices, where the effects of human disturbance, predation, and weather are less pronounced than near the surface (Bédard 1969a, Sealy 1968). Also, auklets occur in much higher abundance and density in Kongkok Basin than on Owalit Mountain, and breeding success may be correlated positively with bird density (Birkhead 1985). If we assume that Least Auklet breeding success at Kongkok was most representative for the population in our study area in 1987, and divide the 10 unaccounted for egg and chick losses proportionately between all observed outcomes (i.e. 7 chicks fledged), then "typical" breeding success might approach 82%. Similarly, Crested Auklet breeding success might have been much higher than measured.

Effects of predation and weather.—Red-backed Voles (*Clethrionomys rutilus*) were abundant and widespread on breeding slopes, and frequently preyed on auklet eggs and chicks. Sealy (1968,

1982) and Searing (1977) observed similar rates of predation (1–11%) by voles. Predation on seabirds by microtine rodents is unusual (Sealy 1982), but it has also been reported (Sealy and Bédard 1973, Murray et al. 1983, Gaston et al. 1988). We could not account for the losses of auklet eggs and chicks from predation by Arctic foxes (*Alopex lagopus*), but auklets are not predominant prey of foxes that den near seabird colonies on St. Lawrence Island (Fay and Stephenson 1989).

We confirmed (Roby and Brink 1986) that adult attendance of Least and Crested auklet chicks decreased rapidly during the first 10 days after hatching. As chicks do not become homeothermic until they are ca. 4–5 days old (Sealy 1968), unattended chicks are particularly vulnerable to cold, wet weather in the first week of life. This accounts for the increased chick mortality that followed two prolonged periods of rain in August.

Chick diets and growth.—Auklets had no difficulty feeding and rearing chicks in 1987. Median masses, maximum growth rates, development times, and diets were similar to those found in other years and locations. The composition of diets was similar to that reported by Bédard (1969b) for Crested Auklets, but was markedly different for Least Auklets. Whereas we, and others (Searing 1977, Springer and Roseneau 1985), found that Least Auklets consumed predominantly *Neocalanus plumchrus*, and generally much lower proportions of *Calanus marshallae* and *N. cristatus*, Bédard reported that *C. finmarchicus* (now *C. marshallae* in the Pacific) was the dominant calenoid copepod in auklet diets and reported no *N. plumchrus*. However, it seems likely that Bédard identified *N. plumchrus* as *C. finmarchicus* (Bédard 1969b: 1036). The remainder of prey identified by Bédard were similar to those reported by later investigators.

Acknowledgments

We thank the Sivuqaq and Savoonga Native Corporations for permission to work on St. Lawrence Island. Lane Iyakitan (Sukilpaq) provided invaluable assistance at our camp and in locating auklets and study plots. We appreciate the help provided on St. Lawrence Island by Darlene Apangalook, Gerome Apatiki, Chris Haney, Joel Hubbard, Lewis Iyakitan, Gerrard Kanooka, and Bruce Rasmussen. Alan Springer, Martha Springer, and Amy Stone identified the contents of auklet chick meals. Alan H. Brush, Vern Byrd, Tony Gaston, Chris Haney, Ed Murphy, David Nettleship, and Alan Springer improved this manuscript with their helpful comments and discussions. This work was supported jointly by the Minerals Management Service (Intra-agency Agreement No. 14-12-0001-30391), the Alaska Fish and Wildlife Research Center, the Alaska Maritime National Wildlife Refuge, and Mr. Theodore Cross of New York.

Literature Cited

Bédard, J. 1969a. The nesting of the Crested, Least, and Parakeet auklets on St. Lawrence Island, Alaska. Condor 71: 386–398.

———. 1969b. Feeding of the Least, Crested, and Parakeet auklets around St. Lawrence Island, Alaska. Can. J. Zool. 47: 1025–1050.

Birkhead, T. R. 1985. Coloniality and social behavior in the Atlantic Alcidae. Pp. 355–383 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Orlando, Florida, Academic Press.

———, & M. P. Harris. 1985. Ecological adaptations for breeding in the Atlantic Alcidae. Pp. 205–231 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Orlando, Florida, Academic Press.

Fay, F. H., & T. J. Cade. 1959. An ecological analysis of the avifauna of St. Lawrence Island, Alaska. Univ. of Calif. Publ. Zool. 63: 73–150.

———, & R. O. Stephenson. 1989. Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. Can. J. Zool. 67: 1986–1994.

Gaston, A. J. 1985. Development of the young in the Atlantic Alcidae. Pp. 319–354 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Orlando, Florida, Academic Press.

———, I. L. Jones, & D. G. Noble. 1988. Monitoring Ancient Murrelet breeding populations. Colon. Waterbirds 11: 58–66.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651–661.

Knudtson, E. R., & G. V. Byrd. 1982. Breeding biology of Crested, Least, and Whiskered auklets in Buldir Island, Alaska. Condor 84: 197–202.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456–466.

Murray, K. G., K. Winnett-Murray, Z. A. Eppley, G. L. Hunt, & D. B. Schwartz. 1983. Breeding biology of the Xantus' Murrelet. Condor 85: 12–21.

Piatt, J. F., B. D. Roberts, & S. A. Hatch. 1990. Attendance patterns and populations of Least and Crested auklets on St. Lawrence Island. Condor 92: 97–106.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978–983.

Roby, D. D., & K. L. Brink. 1986. Breeding biology of Least Auklets on the Pribilof Islands, Alaska. Condor 88: 336–346.

ROSENEAU, D. G., A. M. SPRINGER, E. C. MURPHY, & M. I. SPRINGER. 1985. Population and trophic studies of seabirds in the northern Bering and eastern Chukchi Seas, 1981. U.S. Dep. Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Final Rep. 30: 1–58.

SEALY, S. G. 1968. A comparative study of breeding ecology and timing in plankton-feeding alcids (*Cyclorrynchus* and *Aethia* spp.) on St. Lawrence Island, Alaska. M.S. thesis, Vancouver, Univ. British Columbia.

———. 1973. Breeding biology of the Horned Puffin on St. Lawrence Island, Bering Sea, with zoogeographical notes on the North Pacific puffins. Pacific Sci. 27: 99–119.

———. 1975. Influence of snow on egg-laying in auklets. Auk 92: 528–538.

———. 1981. Variation in fledging weight of Least Auklets *Aethia pusilla*. Ibis 123: 230–233.

———. 1982. Voles as a source of egg and nestling loss among nesting auklets. Murrelet 63: 9–14.

———. 1984. Interruptions extend incubation by Ancient Murrelets, Crested Auklets, and Least Auklets. Murrelet 65: 53–56.

———, & J. BÉDARD. 1973. Breeding biology of the Parakeet Auklet (*Cyclorrhynchus psittacula*) on St. Lawrence Island, Alaska. Astarte 6: 58–68.

SEARING, G. F. 1977. Some aspects of the ecology of cliff-nesting seabirds at Kongkok Bay, St. Lawrence Island, Alaska during 1976. U.S. Dep. Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Annu. Rep. 5: 263–412.

SOWLS, A. L., S. A. HATCH, & C. J. LENSINK. 1978. Catalog of Alsakan seabird colonies. U.S. Dep. Interior, Fish Wildl. Serv. FWS/OBS-78/78.

SPRINGER, A. M., E. C. MURPHY, D. G. ROSENEAU, & M. I. SPRINGER. 1985a. Population status, reproductive ecology, and trophic relationships of seabirds in northwestern Alaska. U.S. Dep. of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Final Rep. 30: 127–242.

———, D. G. ROSENEAU, E. C. MURPHY, & M. I. SPRINGER. 1985b. Populations and trophic studies of seabirds in the Northern Bering and eastern Chukchi Seas, 1983. U.S. Dep. Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Final Rep. 30: 59–126.

———, & ———. 1985. Copepod-based food webs: auklets and oceanography in the Bering Sea. Mar. Ecol. Prog. Ser. 21: 229–237.

VERMEER, K., & M. LEMON. 1986. Nesting habits and habitats of Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands, British Columbia. Murrelet 67: 34–44.