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ASSESSING THE EFFECTS OF INTRODUCED NORWAY RATS (*RATTUS NORVEGICUS*) ON SURVIVAL AND PRODUCTIVITY OF LEAST AUKLETS (*AETHIA PUSILLA*)

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Abstract.—We assessed potential effects of introduced Norway rats (*Rattus norvegicus*) on Least Auklets (*Aethia pusilla*) breeding at Sirius Point on Kiska Island, the largest auklet colony in the Aleutian Islands, Alaska. We compared productivity, chick growth, and adult survival of Least Auklets during 2001–2003 at Kiska and two nearby, rat-free Least Auklet colonies on Buldir and Kasatochi islands. During 2001 and 2002 (when rats were abundant), productivity at Kiska was the lowest ever recorded for this species (0.09–0.16 chicks fledged per eggs laid), primarily because of high mortality of newly hatched chicks. Growth rates and mean fledging mass were both lower on Kiska than on rat-free islands, though there were some interannual differences in these patterns. Adult survival rates were highly variable among years but strongly concordant among colonies, and survival from 2001 to 2002 on Kiska (0.881 ± 0.033) did not differ significantly from long-term averages on either Buldir (0.853 ± 0.014, 1990–2003) or Kasatochi (0.893 ± 0.027, 1996–2003) islands. Although we found little evidence at nesting crevices of predation on adults, eggs, or chicks, low productivity and slow chick growth were both consistent with disturbance caused by rats, particularly through disruption of adults attempting to brood or provision young chicks. Breeding failure may have been exacerbated by low prey availability for chick provisioning, but the lack of concordance in either productivity or chick growth rates between Kiska Island and nearby rat-free Buldir Island cast doubt on this possibility.
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Key words: *Aethia pusilla*, chick growth, island conservation, Least Auklet, non-indigenous species, productivity, survival.

Évaluer les Effets de *Rattus norvegicus* Introduits sur la Survie et la Productivité de *Aethia pusilla*

Résumé.—Nous avons évalué les effets potentiels de *Rattus norvegicus* intorduits sur *Aethia pusilla* nichant à Sirius Point sur l'île Kiska, la plus grande colonie de *Aethia* dans les îles Aleutian, Alaska. En 2001–2003, nous avons comparé la productivité, la croissance des jeunes et la survie des adultes issus de colonies de *Aethia pusilla* situées sur les îles Kiska, Buldir et Kasatochi. Ces colonies sont toutes situées proches les unes des autres mais les deux dernières ne présentent pas de *Rattus norvegicus*. En 2001–2002 (quand les *Rattus norvegicus* étaient abondants), la productivité à Kiska était la plus faible jamais enregistrée pour cette espèce (0,09–0,16 oisillons à l'envol par œuf pondu), principalement à cause d'une forte mortalité des oisillons nouvellement éclos. Le taux de croissance et le poids moyen à l'envol étaient plus faibles sur Kiska que sur les îles sans *Rattus norvegicus*, malgré des

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différences interanuelles dans ces patrons. Le taux de survie adulte était très variable entre les années mais fortement concordant entre les colonies. La survie de 2001 à 2002 sur Kiska (0,881 ± 0,033) ne différait pas significativement des moyennes à long terme sur les îles Buldir (0,853 ± 0,014; 1990–2003) et Kasatochi (0,893 ± 0,027; 1996–2003). Bien que nous ayons trouvé peu de preuves de prédation sur les adultes, les œufs et les oisillons dans les fissures de nidification, la faible productivité et la faible croissance des oisillons supportent l'hypothèse du dérangement causé par *Rattus norvegicus*, particulièrement par l'interruption des adultes qui tentent de s'accoupler ou d'approvisionner les jeunes oisillons. L'échec de la nidification pourrait avoir été amplifié par la faible disponibilité des proies nécessaires à l'approvisionnement des oisillons. Mais, le manque de support basé sur la productivité et le taux de croissance des oisillons entre les îles Kiska et Buldir (qui située à proximité et ne présente pas de *Rattus norvegicus*) jette le doute sur cette possibilité.

PREDATION BY NON-INDIGENOUS species, especially rats (*Rattus* spp.), is the second-most important cause (after habitat destruction) of endangerment, extirpation, and extinction of island birds (King 1985). Approximately 54% of island bird extinctions have been attributed to introduced rats (King 1985), which currently inhabit >80% of major islands (Shrader-Frechette 2001). Rats have been implicated in the population declines of many seabirds, including Ancient Murrelets (*Synthliboramphus antiquus*) at Langara Island (Bertram 1995); Xantus' Murrelets (*S. hypoleucus*), Ashy Storm-Petrels (*Oceanodroma homochroa*), and Cassin's Auklets (*Ptychoramphus aleuticus*) on Anacapa Island (McChesney and Tershy 1998); and Dark-rumped Petrels (*Pterodroma phaeopygia*) in the Galápagos Islands (Harris 1970). Direct evidence of rat predation, however, has been documented in only a few cases, such as predation on Laysan Albatrosses (*Phoebastria immutabilis*) by Polynesian rats (*Rattus exulans*) on Kure Atoll, Northwest Hawaiian Islands (Kepler 1967).

During military occupation in the 1940s, Norway rats (*R. norvegicus*) were accidentally introduced onto Kiska Island in the western Aleutian Islands, Alaska (Murie 1959). A colony of Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*), probably the largest auklet colony in Alaska (G. V. Byrd pers. obs.), is located at Sirius Point on the northern tip of the island. Least Auklets are small, planktivorous seabirds that breed colonially in rock crevices throughout the Aleutian Islands and on other remote islands in the Bering Sea (Bédard 1969, Knudtson and Byrd 1982, Jones 1993a). One of the most abundant seabirds in North America (Sowls et al. 1978), Least Auklets are the smallest of the alcids, weighing less than half the mass of adult Norway rats (see Roby and Brink 1986, Moors 1990, Piatt et al. 1990). Given that Norway rats are so large, they may have a greater effect on seabirds than other species of *Rattus* (Imber 1975). Least Auklets may be particularly susceptible to predation by Norway rats not only because of their small size and colonial breeding behavior but also because birds nesting in burrows or on or near the ground are particularly vulnerable (Atkinson 1985). Our goal here was to assess the effects of Norway rats on Least Auklets at Kiska Island by comparing productivity, chick growth, and adult survival at the Sirius Point colony with similar data available from two nearby, rat-free colonies on Buldir and Kasatochi islands.

METHODS

Study area.—This study was conducted from 2001 to 2003 within the Alaska Maritime National Wildlife Refuge (AMNWR) on Kiska Island, the second-largest island in the Rat Islands group in the western Aleutian Islands, Alaska (Fig. 1). A large auklet colony, encompassing 1.8 km^2, is situated on two lava domes at the base of Kiska Volcano on the northern tip of the island at Sirius Point (52°08′N, 177°37′E). This colony was occupied in 2001 by >1 million Least and Crested auklets (I. L. Jones unpubl. data). To monitor productivity of Least Auklets, we established three 800-m^2 study plots that were representative of the variability in habitats at the colony. The "New Lava" plot was sparsely vegetated with lichens; the "Old Lava Low" plot was heavily vegetated with *Carex* spp., *Calamagrostis* spp., and ferns (*Thelypteris* and *Athyrium* spp.) growing on basalt

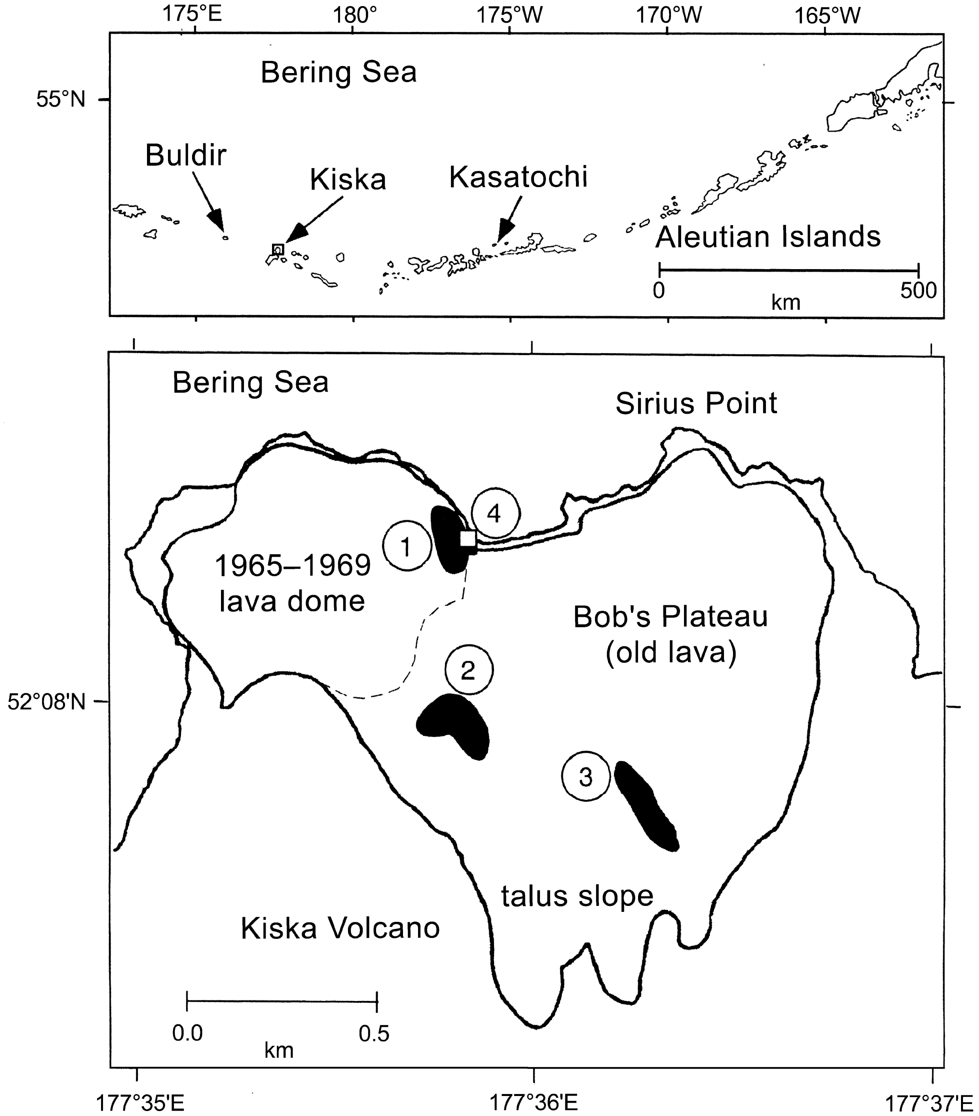

Fig. 1. Locations of Buldir, Kiska, and Kasatochi islands in the Aleutian Islands, Alaska. Lower map of the northern part of Kiska Island indicates the location of Sirius Point, the Least Auklet colony boundaries (solid line), and locations of the three productivity-monitoring plots: (1) New Lava, (2) Old Lava Low, (3) Old Lava High, and (4) the survival plot. Dotted line indicates the boundary between the 1965–1969 lava dome and Bob's Plateau.

blocks; and the "Old Lava High" plot was moderately vegetated with *Carex* spp. and ferns.

Data from Kiska were compared with those collected during long-term monitoring by AMNWR personnel (previously unpublished data) at Least Auklet colonies on two rat-free islands: Buldir Island (119 km west of Kiska) and Kasatochi Island (467 km east of Kiska) (Fig. 1). Productivity was monitored at samples of crevices widely scattered over the Main Talus colony on Buldir Island (52°23′N, 175°55′E) and Thundering Talus on Kasatochi Island (52°10′N, 175°31′W).

Productivity.—On all three islands, we searched for Least Auklet breeding crevices within the study plots, permanently marked them with acrylic paint, and checked them once every four days from late May (laying and early incubation period) through early August (fledging) each year to assess productivity. We monitored 190–202 crevices annually at Kiska from 2001 to 2003, 50–83 at Buldir from 1988 to 2003, and 85–100 at Kasatochi from 1996 to 2003. Each year, we rechecked all crevices that had been monitored previously and monitored any that were reoccupied; we added new crevices each year when needed to maintain consistent sample sizes. Because eggs may have been lost before our first crevice check, estimates of hatching success may have been biased high. However, this bias would be present in all our estimates (i.e., for all islands and all years); thus, validity of our interisland comparisons remains strong.

Least Auklets lay single-egg clutches in bare rock crevices; thus, we defined hatching success as the proportion of monitored crevices in which the egg hatched, fledging success as the proportion of hatched eggs that produced a fledged chick, and productivity as the proportion of monitored crevices that produced a fledged chick. To evaluate the amount of bias, we also calculated Mayfield (1975) estimates of hatching and fledging success at Kiska for 2001–2003; we assumed a mean incubation period of 30 days and a fledging period of 30 days. If a crevice failed, it was carefully checked for the cause of failure, including signs of rat predation on adults, eggs, and nestlings. In addition, we carefully checked all chicks that were found dead to determine the proximate cause of death. To compare hatching and fledging success between islands and years we used log-linear analysis, testing for interactions using PROC GENMOD with SAS, version 8.0 (SAS Institute, Cary, North Carolina).

Chick growth.—We measured a sample of chicks from 40 crevices at Kiska Island every four days from hatching until fledging, death, or disappearance during 2002 and 2003. Chick age was estimated at time of discovery: a wet chick was presumed to be one day old; dry but wobbly, two days old; and dry, alert, and coordinated, three days old. We measured mass to the nearest gram and wing chord to the nearest millimeter; we present all measurements as means ± SE.

For comparison with chick growth data from St. Lawrence Island (Sealy 1973, Piatt et al. 1990) and the Pribilof Islands (Roby and Brink 1986) we used methods similar to those outlined by Ricklefs (1967) and the statistical software MINITAB, version 14 (Minitab, State College, Pennsylvania). We fit a logistic growth curve to each chick's measurements from 2003 (data were insufficient from 2002) and calculated the mean (±SE) growth parameters from linear regressions for each chick. The mean and maximum instantaneous growth rates were then compared with those found at St. Lawrence Island (Sealy 1973, Piatt et al. 1990) and the Pribilof Islands (Roby and Brink 1986).

For comparison to chick growth data from Kasatochi Island, where each bird was measured only twice during the linear growth phase (6–18 days old; Piatt et al. 1990), we used similar methods and calculated the slope of the regression line for each bird. Using ANOVA, we compared growth rates for mass and wing chord length from 2002 and 2003 to those measured at Kasatochi during the same years.

Adult survival.—We captured Least Auklets on noose carpets set out on the colony surface within a single 50-m^2 (surface area) study plot located near the New Lava study area. We used noose carpets because they are believed to catch breeding and nonbreeding birds randomly from the population (Jones 1992a, b, 1993b). Each captured adult Least Auklet was given a numbered stainless steel leg band and a unique combination of three Darvik plastic color bands. We did not color-band subadult birds (two-year-olds, identified by criteria described by Jones and Montgomerie [1992] and Jones [1993b]) or include them in the survival analysis. We resighted color-marked Least Auklets on study plots (except during the most severe weather) during their main activity periods (0900–1400 hours and 2200–0030 hours, Hawaii–Aleutian Standard Time) from mid-May to early August, which encompassed the birds' laying, incubation, and chick-rearing periods. Similar methods were used at both Buldir and Kasatochi islands to mark and resight adult Least Auklets.

We used MARK (White and Burnham 1999) to estimate adult apparent survival (ϕ) and recapture (p) rates using methods described in Lebreton et al. (1992) and Burnham and Anderson (1998). For analysis, we included data from Kiska ($n = 224$ birds; 1 year), Buldir ($n = 338$ birds; 13 years), and Kasatochi ($n = 488$ birds; 8 years) islands. We expected that some individuals ("prospectors") might show lower site-fidelity and, hence, lower survival rates after their first capture; whereas after this first year, permanent emigration would be low and constant (Pradel et al. 1997, Prévot-Julliard et al. 1998, Bertram et al. 2000). To account for this, we included a transient term in which we modeled survival rates in the year after the initial capture independently of survival in subsequent years, thereby minimizing bias resulting from permanent emigration (Pradel et al. 1997). We defined the most general model as that in which survival rate included the transient term and varied by year and among islands for newly banded and previously banded adults. Similarly, recapture probability also varied by year and among islands.

We tested the goodness-of-fit of this model to the data using a parametric bootstrap approach by comparing the rank of the observed deviance relative to ranked deviances from 100 parametric bootstraps, as described in Cooch and White (2006). We also used the bootstraps to estimate the variance inflation factor, $\hat{c}$, which is a measure of extrabinominal variation in the data that can arise when some model assumptions, such as independence or homogeneity in survival or recapture rates among individual animals, are not met (Burnham and Anderson 1998). To do so, we divided the deviance estimate from the original data by the mean of the simulated deviances to estimate $\hat{c}$ (White et al. 2001).

Based on the most general model, we then constructed a set of competing models with reduced numbers of parameters. We first determined the best structure for recapture rates and then modeled survival rates (Lebreton et al. 1992). We used standard linear model notation to indicate relationships among factors and explicitly described the parameterization of each transient class (a_1 = first year after capture, a_2 = all subsequent years; Lebreton et al. 1992). Models were selected using the Quasi-Akaike's Information Criterion (QAIC_c) adjusted for overdispersion and small sample size, in which those models with the lowest QAIC_c values were judged the best compromise between good-fitting models and those with fewer explanatory variables (Burnham and Anderson 1998, Anderson and Burnham 1999). We also calculated QAIC_c weights, which provide a relative measure of how well a model fits the data, compared with other models (Anderson and Burnham 1999).

RESULTS

Productivity.—Mayfield estimates of hatching and fledging success were not different from those calculated using proportions (Table 1); thus, we have used the proportional estimates for all comparisons between islands. Hatching success varied both across islands ($\chi^2 = 13.9$, df = 2, $P = 0.001$) and across years ($\chi^2 = 6.4$, df = 2, $P = 0.04$) in a consistent pattern (island*year interaction not significant, $\chi^2 = 6.5$, df = 4, $P = 0.17$). Fledging success also varied both across islands ($\chi^2 = 122.0$, df = 2, $P < 0.001$) and across years ($\chi^2 = 11.7$, df = 2, $P = 0.003$), but the island*year interaction was highly significant ($\chi^2 = 73.4$, df = 4, $P < 0.001$), primarily because of extremely low productivity at Kiska in 2001 and 2002.

Productivity at Kiska was extremely low during both 2001 (0.13 chicks fledged per crevice) and 2002 (0.09), but not during 2003 (0.50), compared with productivity at Kasatochi (0.52–0.73) and Buldir (0.34–0.60) in the same years (Table 1). Chick death was the most frequent cause of breeding failure at Kiska in 2001 and 2002 (39% and 45% of crevices monitored, respectively; Table 2). By comparison, dead chicks were found in only 12% of the crevices at Kiska in 2003 and in 5–10% of the crevices at Kasatochi and Buldir in 2001–2003. Chicks disappeared without a trace from an additional 17–20% of crevices at Kiska during all three years (Table 2); rates of disappearance of chicks at Kasatochi and Buldir were highly variable (4–47% of crevices).

There was little direct evidence at nesting crevices of depredation of eggs or chicks by rats at Kiska. Six of 18 eggs found broken were attributed to rat predation, but rates of egg loss were similar to those at Kasatochi and Buldir. Very few of the chicks found dead (0–20% year^{-1}) showed signs of trauma or predation. Most (52–100% year^{-1}) of the chicks found dead at Kiska had died within a week of hatching, before they were able to thermoregulate independently; we presumed that they had died of exposure, though no detailed postmortems were performed.

Chick growth.—At Kiska in 2002, of 41 crevices monitored for chick growth, only two Least Auklet chicks survived until fledging age. In 2003, of 40 crevices monitored, 18 chicks survived until fledging age. Chicks increased steadily in mass until ~20 days of age in 2003 (Fig. 2A); they fledged at 32 ± 1.2 (range: 26–35,

Table 1. Least Auklet hatching success (chicks hatched per egg laid), fledging success (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid) at Kiska, Kasatochi, and Buldir islands, Alaska, 2001–2003. Number of crevices monitored is given in parentheses for each year.

	Kiska			Kasatochi			Buldir		
	2001 (190)	2002 (195)	2003 (202)	2001 (85)	2002 (97)	2003 (110)	2001 (65)	2002 (50)	2003 (83)
Hatching success	0.78 ± 0.05	0.65 ± 0.03 0.68[a]	0.81 ± 0.03	0.76 ± 0.05	0.82 ± 0.04	0.86 ± 0.03	0.85 ± 0.04	0.86 ± 0.05	0.90 ± 0.03
95% CI	0.72–0.84	0.58–0.72	0.75–0.86	0.66–0.85	0.73–0.89	0.78–0.92	0.74–0.92	0.73–0.94	0.82–0.96
Fledging success	0.21 ± 0.03	0.14 ± 0.03 0.06[a]	0.61 ± 0.04	0.72 ± 0.06	0.62 ± 0.05	0.84 ± 0.04	0.65 ± 0.06	0.70 ± 0.07	0.37 ± 0.06
95% CI	0.14–0.28	0.09–0.21	0.53–0.68	0.60–0.83	0.51–0.73	0.75–0.91	0.51–0.78	0.54–0.83	0.26–0.49
Productivity	0.16 ± 0.03	0.09 ± 0.02 0.06[a]	0.50 ± 0.04	0.55 ± 0.05	0.52 ± 0.06	0.73 ± 0.04	0.55 ± 0.06	0.60 ± 0.07	0.34 ± 0.04
95% CI	0.11–0.22	0.06–0.14	0.42–0.57	0.44–0.66	0.41–0.62	0.64–0.81	0.42–0.68	0.45–0.74	0.24–0.45

[a] Mayfield estimate.

Table 2. Proportion of Least Auklet breeding attempts that failed for various reasons at Kiska, Kasatochi, and Buldir islands, Alaska, 2001–2003. See Table 1 for numbers of crevices monitored.

	Kiska			Kasatochi			Buldir		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
Adult found dead	0.01	0	0.01	0	0	0	0	0	0
Egg abandoned or displaced	0.09	0.14	0.09	0.13	0.14	0.04	0.08	0.06	0.05
Egg broken or depredated	0.01	0.05	0.03	0.06	0.01	0.05	0	0	0.02
Egg disappeared	0.11	0.15	0.04	0.05	0.02	0.04	0.08	0.08	0.02
Chick disappeared	0.17	0.17	0.20	0.16	0.21	0.04	0.23	0.20	0.47
Chick found dead	0.45	0.39	0.12	0.05	0.10	0.10	0.06	0.06	0.10

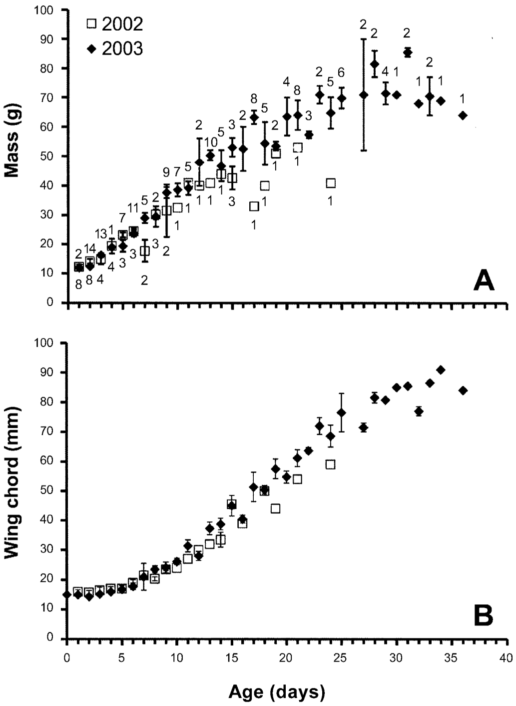

FIG. 2. Age-specific body mass (A) and wing chord (B) of Least Auklet nestlings at Kiska Island, Alaska, 2002–2003. Data are shown as means ± SE, with 2003 sample sizes above mean values and 2002 sample sizes below them.

n = 7) days of age with a body mass of 73.2 ± 4.3 g (range: 62–86, *n* = 6), significantly less (*F* = 10.16, df = 1 and 261, *P* = 0.002) than body mass (80.9 ± 0.36 g; range: 63–105, *n* = 257) of adults measured on the plots from 2001 to 2003. Wing chord also increased steadily throughout the linear growth phase (Fig. 2B) and was 80.3 ± 3.4 mm (range: 65–87, *n* = 6) at fledging, significantly shorter (*F* = 258.27, df = 1 and 244, *P* < 0.001) than adult wing chord (97.9 ± 0.15 mm; range: 90–104, *n* = 240).

Linear rates of mass gain of Least Auklet chicks from 6 to 18 days of age were significantly lower on Kiska than on Kasatochi island (*F* = 54.09, df = 1 and 48, *P* < 0.001), but differences between 2002 and 2003 (*F* = 8.17, df = 1 and 48, *P* = 0.006) were not consistent between islands (island*year: *F* = 6.23, df = 1 and 48, *P* = 0.016). Growth rates of wing chord length also showed a significant interaction between island and year for linear rates of mass gains of Least Auklet chicks from 6 to 18 days of age. Additionally, significant differences were found between islands (*F* = 10.18, df = 1 and 46, *P* = 0.003), with growth rates lower on Kiska than on Kasatochi during 2002 but not 2003 (Table 3). Growth rates and asymptotic and fledging masses of Least Auklet chicks at Kiska were markedly lower than any corresponding measurements ever recorded at other colonies in Alaska (Table 4).

Adult survival.—The data provided a good fit to our most general model of apparent adult survival with three island classes, time dependence, and a transient term. The variance inflation factor as calculated by the parametric bootstrap goodness-of-fit test was 1.996 for the most general model. Thus, we used the $\mathrm{QAIC_c}$ for survival estimation and model fitting. The model with the lowest $\mathrm{QAIC_c}$ and greatest empirical support (70%) in the candidate model set was the additive model ϕ(island+year) *p*(island*year), in which survival rates were correlated among islands across years but recapture rates differed by both island and year (Table 5 and Fig. 3). In the second-best model, survival and recapture rates varied independently by both island and year (ϕ[island*year] *p*[island*year]: $\Delta\mathrm{QAIC_c} = 4.02$; 9% support). There was virtually no support for the transient model,

TABLE 3. Growth rates (mean ± SE) of Least Auklet chicks during their linear growth phase (6–18 days) at Kiska Island in 2002 and 2003 compared with annual and long-term (1996–2003) estimates at Kasatochi Island.

	Kiska		Kasatochi		
	2002 (*n* = 5)	2003 (*n* = 23)	2002 (*n* = 10)	2003 (*n* = 14)	1996–2003 (*n* = 83)
Mass (g day^{-1})	1.1 ± 0.5	3.0 ± 0.2	4.4 ± 0.2	4.1 ± 0.4	4.1 ± 0.1
Range	(–0.2 to 2.2)	(1.4 to 4.8)	(3.6 to 5.4)	(–1.5 to 5.8)	(–1.5 to 6.2)
Wing chord (mm day^{-1})	2.0 ± 0.3	2.7 ± 0.2	3.8 ± 0.2	2.7 ± 0.3	3.2 ± 0.1
Range	(1.0 to 2.9)	(0.5 to 4.4)	(3.0 to 5.1)	(0.5 to 4.3)	(0.5 to 5.1)

TABLE 4. Growth parameters of Least Auklet chicks from Kiska Island during 2003 in comparison with those from other studies in Alaska.

Island	Asymptotic mass (g)	Adult mass (g)	Fledging mass (g) [a]	K [b]	$K(a)/4$ [c]	Source
St. Lawrence	86.5	92	81 (88%)	0.244	5.28	Sealy (1968, 1973)
St. Lawrence	90.8 ± 3.1	82.0 ± 1.8	82 ± 2.8 (100%) [d]	0.216 [e]	4.90	Piatt et al. (1990)
Pribilof Islands	95.8	84.5 ± 0.8 [e]	91.5 ± 3.5 (108%) [e]	0.239	5.72 [e]	Roby and Brink (1986)
Kiska Island	73.0 ± 2.2	80.9 ± 0.4	73.2 ± 4.3 (90%)	0.184 ± 0.02	3.36 ± 0.3	Present study

[a] Fledging mass (percentage of adult mass).

[b] Mean instantaneous growth rate calculated from individual chicks fit to logistic model.

[c] Maximum instantaneous growth rate, where a = asymptotic mass (Hussell 1972, Sealy 1973).

[d] 30 June measurement. Piatt et al. (1990) also measured adult mass at 86.6 g on 6 June.

[e] Estimated using data from source manuscript (Roby and Brink 1986).

TABLE 5. Top candidate models in comparison with global model to assess island, year, and transient effects on survival and recapture probabilities of adult Least Auklets on Kiska, Kasatochi, and Buldir islands, 1990–2001. A transient term was included in the global model to assess effects on apparent survival in the year after initial capture (a_1) versus subsequent years (a_2). Model likelihood adjusted for overdispersion by $\hat{c} = 1.996$.

Model	Number of parameters	Deviance	QAIC_c	ΔQAIC_c	Model QAIC_c
ϕ(island+year) p(island*year)	36	590.06	2538.91	0	0.70
ϕ(island*year) p(island*year)	41	583.84	2542.93	4.02	0.09
ϕ(island) p(island*year)	25	616.76	2543.20	4.29	0.08
ϕ(year) p(island*year)	34	598.98	2543.74	4.83	0.06
ϕ(island*year) p(year)	34	599.81	2544.58	5.67	0.04
ϕ(.) p(island*year)	23	623.56	2545.94	7.03	0.02
$\phi[(a_1, a_2\text{*year})\text{*island}]$ p(island*year) [a]	44	586.00	2551.24	12.34	0

[a] Global model.

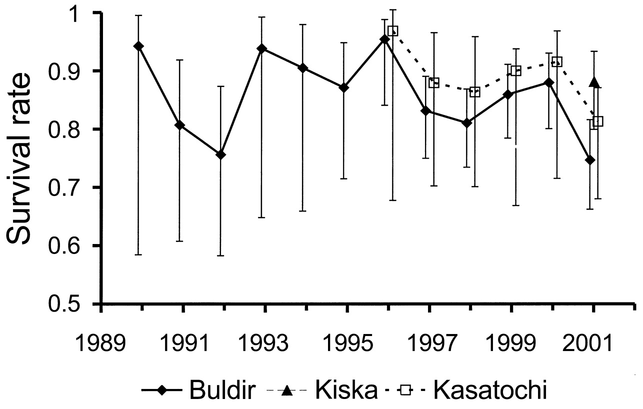

FIG. 3. Estimates (± SE) of annual survival rates of adult Least Auklets from Buldir, Kasatochi, and Kiska islands, Alaska (1990–2001), estimated by the most parsimonious model (ϕ[island+year] p[island*year]), with $\hat{c} = 1.996$.

in which survival differed between the year following capture and subsequent years (Table 5).

Although the most parsimonious model suggested a significant difference in adult survival rates among islands, confidence limits for the point estimates at Kiska in 2001 (0.88 ± 0.03), the only year estimated there, overlapped those from both Buldir (0.75 ± 0.04) and Kasatochi (0.81 ± 0.03) islands that year (Fig. 3). Point estimates for survival varied from 0.75 to 0.97 on Buldir Island over 12 years and from 0.81 to 0.97 on Kasatochi Island over six years (Fig. 3). Recapture probability on Kiska Island in 2001 was high (0.94 ± 0.02; 95% CI: 0.87–0.98), but was highly variable among years on other islands, averaging 0.82 ± 0.02 on Buldir (95% CI: 0.77–0.87) and 0.85 ± 0.03 on Kasatochi (95% CI: 0.77–0.92).

Discussion

Introduced rats have been implicated in the declines of many breeding seabird species (Atkinson 1985), yet there has usually been limited direct evidence isolating rat predation as the unequivocal and sole cause of population declines. Nevertheless, if rats were negatively affecting the Least Auklet population at Kiska, we would expect to find lower Least Auklet adult survival or productivity, or both, compared with those on rat-free islands. However, because both rats and Least Auklets breed underground in mostly inaccessible rock crevices on Kiska, obtaining direct evidence of rat predation and evaluating its effects on Least Auklet populations was a challenging proposition. Furthermore, although seabirds can normally outlast periods of unfavorable feeding conditions, in rare circumstances they may be limited by the amount of food available and experience breeding failure and consequent population declines (e.g., Atlantic Puffins [*Fratercula arctica*] on St. Kilda Island; Boddington 1960). Thus, decreased Least Auklet adult survival (e.g., Jones et al. 2002), low productivity, and slow chick growth might be expected in years of extraordinarily poor oceanographic conditions with scarce prey availability, which could provide an alternative explanation for breeding failure at Kiska.

In 2001 and 2002, Least Auklets experienced near-complete breeding failure at Kiska, with productivity by far the lowest ever recorded for this species. Least Auklet chicks there also grew more slowly and, overall, fledged at lower mass in comparison with all other Least Auklet colonies measured. These unprecedented events, occurring in years when other Aleutian Least Auklet colonies had normal productivity, suggested that a factor unique to Kiska, the only Alaskan Least Auklet colony with rats present, was the cause of breeding failure. Enigmatically, our single survival estimate for 2001–2002 at Kiska was close to the mean survival rate at rat-free Buldir and Kasatochi islands over the previous decade, which suggests that neither rats nor a shortage of prey was having a drastic effect on adult Least Auklet survival during that period. To address the difficult question of what caused breeding failure at Kiska, we evaluated how our data fit with two hypotheses (rats and food supply) concerning why Least Auklets at Kiska experienced such different conditions compared with those breeding at other colonies.

Rat hypothesis.—Least Auklets breeding at Kiska experienced two seasonal phases of rat activity. In the first phase, adult Norway rats that survived the winter killed and hoarded adult Least Auklets when the birds returned to the island in late May and early June, at which time female rats also began breeding (Major 2004, Major and Jones 2005). In the second phase, the offspring of these females became independent and dispersed through the Least Auklet colony beginning in mid- to late June, greatly increasing the number of rats present. Rat abundance early in the season varied greatly from year to year, perhaps in relation to the severity of the preceding winter, but by the time Least Auklet chicks began to hatch, these independent juvenile rats were conspicuous in the Least Auklet colony (Major and Jones 2005).

Our data provided no direct evidence for an effect on Least Auklets during the first phase of rat activity. Hedgren's (1980) age–experience hypothesis, which has been supported for many species of birds, including alcids (e.g., Thick-billed Murres [*Uria lomvia*]; De Forest and Gaston 1996), suggests that the earliest birds to arrive at breeding colonies are those that are older and more experienced. In years when many rats survive the winter, early-season killing and hoarding would be expected to remove high-quality individual Least Auklets that are older and more likely to fledge a chick. Loss of these individuals in sufficient numbers would be expected to result in relatively inexperienced birds raising chicks at Kiska, with decreased hatching and fledging success. In addition, previous studies have found that eggs laid earlier in the breeding season produce chicks that grow faster and fledge heavier, compared with eggs laid later in the breeding season (Birkhead and Nettleship 1981, Ydenberg et al. 1995). Thus, slow chick growth and light fledging mass would be expected with an increased proportion of inexperienced, late breeders. However, neither our survival data nor our hatching success data supported the suggestion that the first phase of rat activity negatively affected the Least Auklet population at Kiska. Our survival estimate was limited to one representative plot (located in an area with rats present) during a single year, but showed no evidence of reduced survival compared with Least Auklet colonies with rats absent. Our hatching success data, from three plots representative of the colony, similarly showed no evidence of reduced hatching success compared with rat-free Least Auklet colonies. Rats could have had a negative effect on productivity by taking high-quality birds early in the season before laying (we found one rat-depredated female Least Auklet with an egg in its oviduct), but we were not able to quantify this.

The second phase of rat activity on Kiska, which combined the effects of adults and their newly independent offspring in mid- to late June, seemed more likely to have had negative effects on Least Auklets. In both 2001 and 2002, we recorded extremely low productivity, whereas in 2003, Least Auklet productivity at Kiska returned to rates considered normal for the species (~0.50; Jones 1993a). Concomitantly, abundance of Norway rats early in the Least Auklet breeding season was high in both 2001 and 2002, and low in 2003 (Major 2004, Major and Jones 2005). The correspondence across years of Least Auklet breeding failure with rat abundance early in the breeding season was some of the best evidence that rats negatively affected the Least Auklet population. At Kiska in 2001 and 2002, the most frequent causes of breeding failure were chick death (small chicks found in crevices dead, often with no apparent injuries) and disappearance. We believe that the best explanation for the resulting low fledging success was rat activity. Rats were expected to leave few traces of their activities at Least Auklet crevices, because carcasses of depredated adults and chicks were removed and consumed elsewhere. Like other long-lived birds, Least Auklets would be expected to abandon their current breeding effort in situations where their survival or reproductive effort in future years was threatened (Williams 1966). Even disturbance of a crevice by rats, causing the adult Least Auklet to leave the breeding site temporarily, would be expected to lead to chick deaths by exposure, because independent thermoregulation of Least Auklet chicks begins at five to six days of age (Sealy 1968). At Kiska, chick growth rate was the lowest recorded when compared with rates in all other colonies, which is consistent with lack of parental attentiveness (i.e., rat predation and disturbance causing reduced chick growth rates by deterring parents' chick provisioning). Even for 2003, when rats were less abundant, depressed chick growth rates are believed to be attributable to rat disturbance. Ironically, the breeding failures of 2001 and 2002, in which most birds that attempted breeding did not raise chicks, may have resulted in increased adult survival rates, because breeders left the Sirius Point colony without having experienced the energetic stress and risk associated with provisioning of offspring (Stearns 1992). This could explain our high estimate of adult survival rate from Kiska, even with the observed rat predation on adult Least Auklets.

Food hypothesis.—Least Auklet survival and productivity are believed to be influenced by large-scale variations in climate and oceanography that affect ocean productivity and the consequent abundance of zooplankton prey (e.g., Pacific decadal oscillation; Jones et al. 2002). Thus, the Least Auklet population at Kiska would be expected to experience reduced adult survival rates (e.g., as at nearby Buldir Island; Jones et al. 2002) during unfavorable oceanographic conditions. Least Auklet breeding failure has not been documented before in any colony, but with extremely poor ocean conditions it might be expected to occur, as has been documented for Tufted Puffins (*F. cirrhata*; Gjerdrum et al. 2003). We considered the possibility that breeding failure and reduced chick growth at Kiska in 2001 and 2002 were caused by shortages of food owing to ocean conditions, as an alternative explanation to rat predation. If food shortage was responsible for breeding failure at Kiska, we would expect the following predictions to have been met: (1) oceanographic indexes for 2001 and 2002 should have shown values corresponding to unusually poor ocean productivity for the western Aleutian Islands; (2) interannual trends in productivity of Least Auklets should have been closely correlated at Kiska and Buldir, and both islands should have shown reduced productivity in 2001 and 2002; and (3) chick starvation and slow growth should have occurred at Kiska in 2001 and 2002.

With respect to prediction (1), climate indexes—such as the Pacific decadal oscillation (Mantua et al. 1997), the North Pacific index (Trenberth and Hurrell 1994), and the Aleutian low-pressure index (Beamish et al. 1997)—for 2001 and 2002 were not anomalously poor for ocean productivity, so there was no independent indication that oceanographic conditions would have led to a food shortage on Kiska in these years.

With respect to prediction (2), Least Auklets at Buldir showed no evidence of reduced productivity in 2001 or 2002 (Table 1), even though Least Auklets from Buldir and Kiska (119 km apart) likely forage in the same area (I. L. Jones and H. L. Major pers. obs.). Kasatochi Island also had normal Least Auklet productivity in 2001 and 2002 (Table 1). Least Auklets from Buldir experienced productivity near the long-term average in 2001 and 2002, whereas Least Auklets at Kiska were failing, but productivity at Buldir was unusually low in 2003, the year in which Kiska birds had near-average productivity for the species. Thus, productivity at Buldir and Kiska was strongly uncorrelated, which suggests that some factor other than local food supply explains the breeding failure measured at Kiska in 2001 and 2002. Kiska has one of the largest Least Auklet colonies in Alaska; therefore, in years of poor oceanic productivity, this colony may experience a greater density-dependent food shortage than smaller colonies. Ashmole (1963) suggested that large seabird colonies locally deplete the food supply, which results in a food-shortage halo. If these factors helped determine Least Auklets' productivity at Kiska, we would have expected to see a similar pattern of interannual variability in productivity across Kiska and other colonies, but with more extreme dips in productivity at Kiska in poor years. The complete lack of covariation in reproductive performance across colonies provides no support for such a process. However, the strong correlation in adult survival between Buldir and Kasatochi suggests that Least Auklet survival at widely spaced colonies is influenced strongly by the same large-scale environmental or oceanographic factors. Breeding failure at Kiska could have been attributed to food shortage if we were able to identify some oceanographic or other mechanism for very localized reduction in Least Auklets' highly mobile zooplankton prey, but no such mechanism is known. Finally, the observed high survival rate (close to the average for Buldir, 0.87 ± 0.04; Jones et al. 2002) of Least Auklets at Kiska between 2001 and 2002 was not indicative of a shortage of prey during the 2001 breeding season.

With respect to prediction (3), we observed slow chick growth at Kiska during the years of reproductive failure, which is consistent with a shortage of food. However, low fledging success was more strongly determined by the death of chicks less than one week old. These chicks apparently died of exposure attributable to lack of parental attentiveness rather than directly to starvation. In cases of starvation at other colonies, Least Auklet chicks normally disappeared from crevices after languishing for weeks (I. L. Jones pers. obs.). Taken together, the observed chick death by exposure, low chick growth, and lighter fledging masses at Kiska in comparison with all other islands measured are generally consistent with the food hypothesis, but could equally be explained by predation or disturbance to adults during chick rearing.

Considering all the data arising from the present study, there was little direct evidence that breeding failure at Kiska resulted from rats alone. Nevertheless, hundreds of rat-depredated eggs, adults, and chicks were found throughout the Sirius Point colony outside our study crevices, particularly in 2001 and 2002 (Major and Jones 2005), and comparisons between Kiska and rat-free colonies suggested that some factor unique to Kiska was responsible for the breeding failures of 2001 and 2002. Our data support more strongly the hypothesis that rats are having a negative effect on the Least Auklets breeding at Kiska than the hypothesis that prey shortage caused breeding failure. Nevertheless, a precise quantification of the relative importance of rats and prey abundance in determining population processes at Kiska remains unavailable. Future studies should continue to monitor adult survival and reproductive success at Kiska in comparison with that at other Aleutian Island colonies, and especially to determine the role of food supply in the reproductive performance at different Least Auklet colonies.

We believe that the Least Auklet colony at Kiska is of great importance, given that the colony site is subject to continual renewal and growth through volcanic activity, whereas most nearby colonies (e.g., Buldir) are decreasing in area because of encroaching vegetative cover. The presence of introduced rats at Kiska is of great concern, and we recommend their ultimate eradication. However, our current understanding of the processes underlying the reproductive failure of Least Auklets at Kiska remains limited, and we stress that continued targeted research aimed at this question is extremely important.

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