P   -   species, espe-
cially rats (*Ra us* spp.), is the second-most
important cause (a er habitat destruction) of
endangerment, extirpation, and extinction of
island birds (King 1985). Approximately 54%
of island bird extinctions have been a ributed
to introduced rats (King 1985), which cur-
rently inhabit >80% of major islands (Shrader-
Freche e 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 evi-
dence of rat predation, however, has been docu-
mented in only a few cases, such as predation on
Laysan Albatrosses (*Phoebastria immutabilis*) by
Polynesian rats (*Ra us 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, plank-
tivorous 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, Pia et al. 1990).
Given that Norway rats are so large, they may
have a greater e ect on seabirds than other
species of *Ra us* (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 e ects 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.

M

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 km², 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 pro-
ductivity of Least Auklets, we established three
800-m² 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
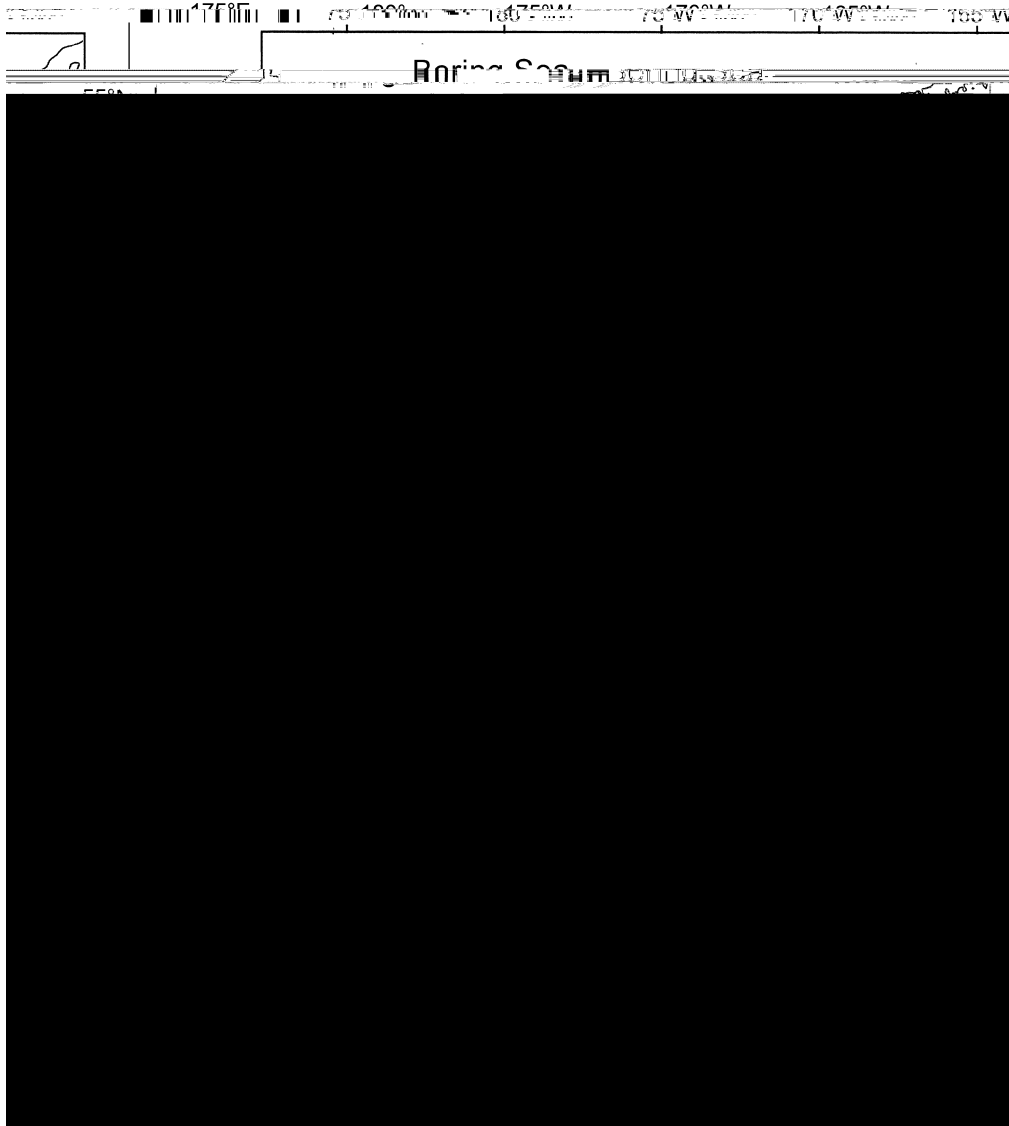(*Thelypteris* and

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, Pia et al. 1990) and the Pribilof Islands (Roby and Brink 1986)

we used methods similar to those outlined by Ricklefs (1967) and the statistical so ware MINITAB, version 14 (Minitab, State College, Pennsylvania). We fit a logistic growth curve to each chick's measurements from 2003 (data were insu cient 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, Pia 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; Pia 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 ( ) 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 a er their first capture; whereas a er 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 a er 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

T   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.

T   2. Proportion of Least Auklet breeding a empts 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

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 signifi-

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 <

T 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	Pia 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. Pia 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).

T 5. Top candidate models in comparison with global model to assess island, year, and transient e

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 Ne leship 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 a ected 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 e ect 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 e ects of adults and their newly independent o spring in mid- to late June, seemed more likely to have had negative e ects 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 a ected 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, o en 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

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 quantifi

colonies, and especially to determine the role of food supply in the reproductive performance at di erent Least Auklet colonies.

We believe that the Least Auklet colony at

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