

SURVIVAL AND REPRODUCTIVE SUCCESS OF CRESTED AUKLETS *AETHIA CRISTATELLA* IN THE PRESENCE OF INTRODUCED NORWAY RATS *RATTUS NORVEGICUS*

ALEXANDER L. BOND^{1,2}, IAN L. JONES¹, JEFFREY C. WILLIAMS³ & G. VERNON BYRD³

¹*Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9, Canada*

²*Present address: Department of Biology, University of Saskatchewan, and Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5, Canada (alex.bond@usask.ca)*

³*Alaska Maritime National Wildlife Refuge, US Fish and Wildlife Service, 95 Sterling Highway, Suite 1, Homer, Alaska 99603, USA*

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SUMMARY

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Introduced predators, including Norway rats *Rattus norvegicus*, can have devastating effects on island avifauna. Nevertheless, at Kiska Island in the Aleutian Islands, one of the largest auklet colonies in Alaska, Least Auklets *Aethia pusilla* and Crested Auklets *A. cristatella* appear to be persisting in the presence of introduced Norway rats. We gathered information on annual reproductive success and adult survival of Crested Auklets at Kiska during 2001–2010 and compared these demographic rates with those of Crested Auklets at rat-free Buldir and Kasatochi Islands in the Aleutian Islands. Although those on Kiska frequently had the lowest reproductive success among the islands in a given year, we did not detect a statistically significant mean difference with our relative small samples from Kiska. Restricting the analysis to years when rats were abundant at Kiska (2001–2002), Crested Auklets on Kiska had lower reproductive success than those on rat-free islands. Adult survival at Kiska declined through our study period and was estimated at <80% near the end of our study. The data we gathered provides the basis for a more detailed study in the future to more clearly determine the impacts of introduced Norway rats on Crested Auklet populations at Kiska.

Key words: Kiska Island, Aleutian Islands, Crested Auklet, demography, introduced predator, Norway rat

INTRODUCTION

Introduced predators can have severe effects on island avifauna populations, including seabirds (Jones *et al.* 2008, Towns *et al.* 2011). Introduced rats (*Rattus* spp.) cause reduced breeding success and adult survival in seabirds, especially in crevice- or burrow-nesting species (Atkinson 1985, Jones *et al.* 2008, Lavers *et al.* 2010). However, deciphering and quantifying the effect of rats on seabird demography is challenging because evidence for rat-caused

mortality is sometimes difficult to confirm, and both mortality and breeding success depend on other potentially confounding variables (Major *et al.* 2006, Jones *et al.* 2008).

Kiska Island (52°08'N, 177°37'E; Fig. 1), in the western Aleutian Islands, Alaska, is the site of one of the world's largest seabird colonies, comprised mostly of auklets *Aethia* spp. (Sowls *et al.* 1978, Rauzon 2007). In 1835, Arctic foxes *Vulpes lagopus* were introduced for fur farming (Ashbrook & Walker 1925) and presumably began to affect seabirds there as they did elsewhere in the Aleutians (Bailey 1993, Ebbert & Byrd 2002). Another introduced predator, the Norway rat *Rattus norvegicus*, was accidentally introduced between 1941 and 1946 (Murie 1959). Following fox eradication in 1987 (Deines & McClellan 1987a, b), the predation of breeding Least Auklets *Aethia pusilla* and Crested Auklets *A. cristatella* at the large colony at Sirius Point, the northern tip of the island, could be more easily attributed to rats (Deines & McClellan 1987a). Before eradication, foxes had routinely patrolled beaches and the intertidal zone at Kiska, whereas, following fox removal, rats became more visible in this habitat (JCW, GVB, pers. obs.). The relative abundance of rats fluctuated widely during a 10-year monitoring effort (2001–2010), with very high numbers present (based on observations of droppings and other sign) during 2001–2002, coincident with breeding failure of Least Auklets (Major *et al.* 2006). In other years, signs of rats were relatively scarce and Least Auklet productivity returned to higher levels (Bond *et al.* 2010).

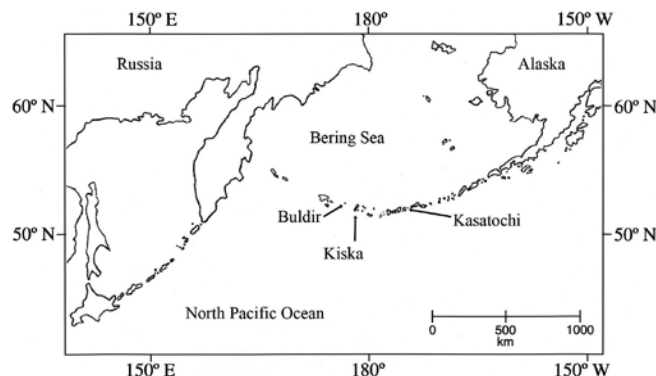


Fig. 1. The north Pacific Ocean showing our study sites at Buldir, Kiska, and Kasatochi islands.

An estimated 332 000 pairs of Crested Auklets breed at Sirius Point, making it one of the largest colonies in the Aleutian Islands (Byrd *et al.* 2005), constituting almost 40% of the Aleutian population and just over 5% of the estimated global population (Gaston & Jones 1998). The eruption of Kasatochi Volcano in August 2008, a former auklet colony with tens of thousands of breeding Crested Auklets, left that island with few breeding crevices (Williams *et al.* 2010). Major *et al.* (2006) suggested that birds forced from colonies by volcanism or vegetative succession may have emigrated to Kiska, where there is abundant available breeding habitat. The presence of periodically abundant rats on Kiska, and their predation on breeding auklets, means that Kiska could act as a “population sink”: a site that has high immigration from other populations, but low emigration and bouts of high mortality (Pulliam 1988). Understanding the demographic impact of rats on Crested Auklets at the Sirius Point colony is therefore of great importance.

Auklets are challenging to census because of their subterranean nests, variable colony attendance by adults and juvenile pre-breeders, and mixed nesting colonies (Jones 1992, Sheffield *et al.* 2006, Renner *et al.* 2011). Establishing reliable and repeatable population estimates is therefore difficult, and measuring demographic vital rates may provide the only insight into population changes before catastrophic decline or rapid increase. Our goals were therefore to review the available evidence on the reproductive success and survival of Crested Auklets breeding at Sirius Point, and to compare these data with those collected on predator-free colonies in the Aleutian Islands to assess the possible effects of Norway rats.

STUDY AREA AND METHODS

Reproductive success

Crested Auklet reproductive success was monitored on three of the Aleutian Islands: Buldir (1990–2010), Kiska (2001–2010), and Kasatochi (1996–2008); data from 1990–2008 were taken from Bond *et al.* (2011), and study areas were described by Major *et al.* (2006). The Sirius Point colony comprises two adjacent areas: a vegetation-free 1 km² coastal lava dome formed during 1964–1969, and a geologically older 800 m² volcanic formation called Bob’s Plateau. Habitat is more limited at most other breeding sites in the Aleutian Islands, where vegetative succession has reduced access to subterranean breeding crevices (Major *et al.* 2006). Each year, we monitored Crested Auklet nest sites (rock crevices) from late May until early August, encompassing the entire breeding season (for a detailed description of methods, see Bond *et al.* 2011). Crested Auklet breeding sites were much more difficult to locate and monitor than those of Least Auklets at Kiska and were more difficult to locate at Kiska than at other islands, likely because they were at greater depth within the porous lava at Kiska. For example, the proportion of Crested Auklet crevices in the sample of all auklet crevices monitored at Kiska averaged only 15% during 2001–2010 (Bond *et al.* 2010). We visited breeding sites every 4–7 days, and determined their status (empty, egg, chick, adult, unknown). We considered sites active when we found an egg or an adult in incubation posture on two consecutive visits. We scored sites as successful in fledging a chick if the chick disappeared after 26 days (Fraser *et al.* 1999). We defined reproductive success as the proportion of active nests from which chicks fledged. We looked for and noted all evidence of rat predation on eggs and chicks (e.g., eggs or dead chicks with bite marks; Major *et al.* 2006). Theoretically, Crested Auklet eggs and chicks are at greater risk

of rat predation than Least Auklets eggs and chicks because they have a longer breeding period. Crested Auklet eggs are incubated for 33–36 d (Fraser *et al.* 1999) compared with 30–32 d for Least Auklets (Roby & Brink 1986a, Piatt *et al.* 1990). Crested Auklet chicks remain nest-bound for 34 d (Fraser *et al.* 1999), while Least Auklets fledge after 28–29 days (Piatt *et al.* 1990, Renner 2005). In total, Crested Auklet nests face 67–70 d of potential rat predation, while those of Least Auklets experience 58–62 d of exposure (12% less time than nests of Crested Auklets).

We tested for differences in reproductive success among three islands: Kiska Island, rat-free Buldir Island (119 km west of Kiska Island; data from Tucker *et al.* 2010) and Kasatochi Island (469 km east of Kiska Island; data from Bond *et al.* 2011) using two generalized linear models with a binomial distribution and logit link function in SPSS 16 (SPSS Inc., Chicago, IL, 2007) — one for hatching success and one for reproductive success. We conducted pairwise comparisons of reproductive success among islands for each year, as we were interested in whether Crested Auklets’ reproductive success was lower on Kiska than on Buldir or Kasatochi islands. Comparisons were made following Šidák correction (Šidák 1967) and considered significant when $P < 0.05$. Because rats were highly abundant in 2001 and 2002 only, we also analyzed island differences in reproductive success in these two years. To evaluate statistical power post hoc, we used G*Power 3.1 (<http://www.psych.uni-duesseldorf.de/abteilungen/aap/gpower3>) and calculated observed power when $\alpha = 0.05$ using data from Kiska and Buldir in 2010 (year of the highest sample size on Kiska) and 2001 (year of lowest reproductive success on Kiska, and greatest difference between Kiska and rat-free colonies). We chose these years to illustrate the most extreme examples.

Adult survival

In 2001, a population of marked individuals of unknown age was established at Sirius Point, Kiska, on the 1960s lava dome (Major *et al.* 2006), but annual samples were relatively small until 2007, when we increased our emphasis on Crested Auklets (the emphasis earlier had been on Least Auklets; Table A2 available in the Appendix on the Web site). Birds were captured on a 50 m² plot using noose carpets, and adults were marked with a uniquely numbered metal band and combination of Darvik colour bands following Jones *et al.* (2004b). We did not colour-band subadults (one-year-old individuals, identified by worn, brown flight feathers and coverts and a dull orange bill), and they were not included in the analysis. We resighted colour-marked auklets during their main daily activity periods (09h00–15h00 and 22h00–00h30 Hawaii-Aleutian Standard Time) from late May to early August each year, encompassing the entire breeding cycle. To minimize resighting errors, individuals seen at least twice were considered “alive” in a given year. Using procedures described in Lebreton *et al.* (1992), annual probabilities of survival (ϕ) and resighting/recapture (p) were generated using Program MARK (White & Burnham 1999). Further details are given in Appendix 1, available on the Web site.

Model selection was based on quasi-Akaike Information Criteria adjusted for small sample size and overdispersion (QAICc). Models with lower QAICc values were considered the best compromise between a good fit to the data and overparameterization of the models (Burnham & Anderson 2002). We also calculated Akaike weights, which indicate how well a model fits the data when compared with other models (Burnham & Anderson 2002). We used

year classes rather than age classes as the marked individuals were of unknown age.

Observations of rat predation

We obtained anecdotal evidence of rat predation on Crested Auklets by examining the contents of rat caches where dead birds and eggs are stored early in the season for future consumption (Major & Jones 2005). Each year, entrances to rat caches around the auklet colony were excavated, the contents removed and identified. Clearly some auklets died from causes other than rats, but we considered birds found in caches with neck bites and evidence of bleeding to have been victims of rat predation and not just scavenged dead birds. We tested rat scavenging in the smaller Least Auklet, which should have been easier to carry by rats, by placing a series of seven wind-killed carcasses along a 400 m transect with rat sign evident. Over a period of 4 weeks in June and July 2009 during rats' presumed peak annual abundance, we saw no evidence of scavenging (ALB, unpublished data; freshly killed Crested Auklets were not available).

RESULTS

Reproductive success

The mean reproductive success of Crested Auklets at Kiska Island was lowest among the three islands at 0.59 (95% CI 0.54–0.65; $n = 275$) compared with 0.66 (95% CI 0.63–0.69; $n = 561$) at Buldir and 0.65 (95% CI 0.62–0.68; $n = 904$) at Kasatochi, but this difference was not statistically significant either among islands (Wald $\chi^2 = 3.80$, $P = 0.15$) or among years (Wald $\chi^2 = 8.57$, $P = 0.48$). Crested Auklets responded differently in different years on each island; the island \times year interaction was significant in the model of reproductive success (Wald $\chi^2 = 75.43$, $P < 0.001$). Crested Auklets on Kiska exhibited an opposite trend from those on Buldir from 2006–2010 (Spearman's $\rho = -1.0$, $P = 0.017$). Following Šidák correction, reproductive success was statistically similar among the islands in all years, except in 2003, when success was lower on Buldir than on either Kiska or Kasatochi. Comparing islands during

years of high rat abundance on Kiska, reproductive success was similar on Buldir and Kasatochi ($\chi^2 = 0.39$, $P = 0.53$) and lower on Kiska ($\chi^2 = 3.77$, $P = 0.049$).

Our monitoring efforts provided little direct evidence of rat predation on Crested Auklet chicks, but our sample sizes of Crested Auklet crevices monitored for reproductive performance were low in most years (range 24–46/year; Table 1). Only 3/275 (1.09%) monitored crevices from 2001–2010 lost eggs that we were able to ascribe to rat predation, and we did not document directly any rat predation of the chicks we followed in our study crevices. Crested Auklet reproductive success was correlated with Least Auklet reproductive success at Kiska Island ($n = 10$ years, $r^2 = 0.40$, $P = 0.07$; Least Auklet data from Bond *et al.* 2011), suggesting that similar factors may be affecting the reproductive success of both species.

A power analysis using data from Buldir and Kiska showed that the probability of detecting a significant difference in reproductive success between islands in 2010 was 0.24, but using data from 2001, when Crested Auklets on Kiska had the lowest reproductive success (coincident with high perceived rat abundance and Least Auklet breeding failure), our ability to detect a significant difference was 0.75. In both cases, increasing the sample size of crevices on Kiska to equal those monitored on Buldir increased the statistical power (2001: 0.92, 2010: 0.36).

Adult survival

The mark-recapture data provide a good fit with our global model, and overdispersion was calculated from parametric bootstraps as $\hat{c} = 1.146$. We therefore used QAICc for parameter estimates and model selection (Table A1, available in the Appendix on the Web site). The top-ranked model included a transient effect, in which local survival during the period immediately following banding was lower than on other occasions (Table 2). Crested Auklet survival has been declining steadily at Kiska from 2001 through 2009; survival was < 0.80 from 2006–2009, and dropped to a low of 0.731 ± 0.131 in 2007/2008 (Table 2). Data from Buldir and Kasatochi

TABLE 1
Crested Auklet reproductive success (number of chicks fledged per egg laid) from three plots at Sirius Point, Kiska Island, Alaska from 2001 to 2010^a

Year	Number of active nests	Number of eggs hatched	Hatching success (% of eggs laid that hatch)	Number of chicks fledged	Reproductive success (% of eggs laid from which chicks fledged)
2001	28	22	79	13	46
2002	24	20	83	10	42
2003	24	19	79	13	54
2004	31	25	81	21	68
2006	34	33	97	29	85
2007	36	29	81	21	58
2008	29	23	79	17	59
2009	23	21	91	13	52
2010	46	36	78	28	61
Total	275	228	83	165	60

^a No monitoring occurred in 2005.

TABLE 2
Crested Auklet survival at Sirius Point, Kiska Island, Alaska:
estimates (ϕ) and encounter probabilities (p) for 2001–2009

Parameter ^a	Estimate	Standard error	95% confidence interval
ϕ_{Initial}	0.746	0.045	0.648–0.824
$\phi_{2002-2003}$	1.000	0.001	0.999–1.000
$\phi_{2003-2004}$	1.000	0.001	0.999–1.000
$\phi_{2004-2005}$	0.969	0.102	0.034–1.000
$\phi_{2005-2006}$	0.908	0.115	0.366–0.993
$\phi_{2006-2007}$	0.794	0.109	0.511–0.934
$\phi_{2007-2008}$	0.731	0.131	0.425–0.909
$\phi_{2008-2009}$	0.744	0.089	0.538–0.878
p_A (2002, 2003, 2009) ^b	1.000	0.001	0.999–1.000
p_B (2004, 2006, 2007, 2008)	0.907	0.037	0.807–0.959
p_C (2005)	0.421	0.121	0.215–0.658

^a Determined by model A from Program MARK, adjusted for $\hat{c} = 1.146$.

^b Resight probability group.

showed a similar decline until 2003, but contra Kiska, rose from 2003–2008, and was negatively correlated with Kiska (Buldir: $r = -0.95$, $P = 0.01$; Kasatochi: $r = -0.64$, $P = 0.36$) (Jones 2010). As with reproductive success, the trends at the two rat-free colonies were the opposite of the trend at Kiska.

Observed rat predation

Before fox eradication in 1987, auklet predation was largely attributed to foxes (R.H. Day, B.R. Lawhead, pers. comm.). Following a brief visit in August 1996, during which rat predation was explicitly noted (Williams 1996), and a two-week expedition in 2000 that noted auklet predation in general (A.L. Sowls, M.J. Rauzon, pers. comm.), field crews were present at Kiska for the entire breeding season from 2001–2010 (except 2005). Based on observations of rat sign (direct sightings, droppings, trails, prey caches), rats were abundant at Sirius Point in 2001–2002, but present in relatively low numbers thereafter (Major *et al.* 2006, Bond *et al.* 2010). From 2001–2010, many Least Auklet eggs, chicks and adults were found in caches or otherwise depredated by adult rats (e.g., 59 rat-predated Least Auklet adults or eggs but only 12 rat-predated Crested Auklet adults or eggs in 2010; Bond *et al.* 2010). Over the study period, 33 Crested Auklet eggs and six adults were found depredated by rats (Table A3 available in the Appendix on the Web site, Fig. 2).

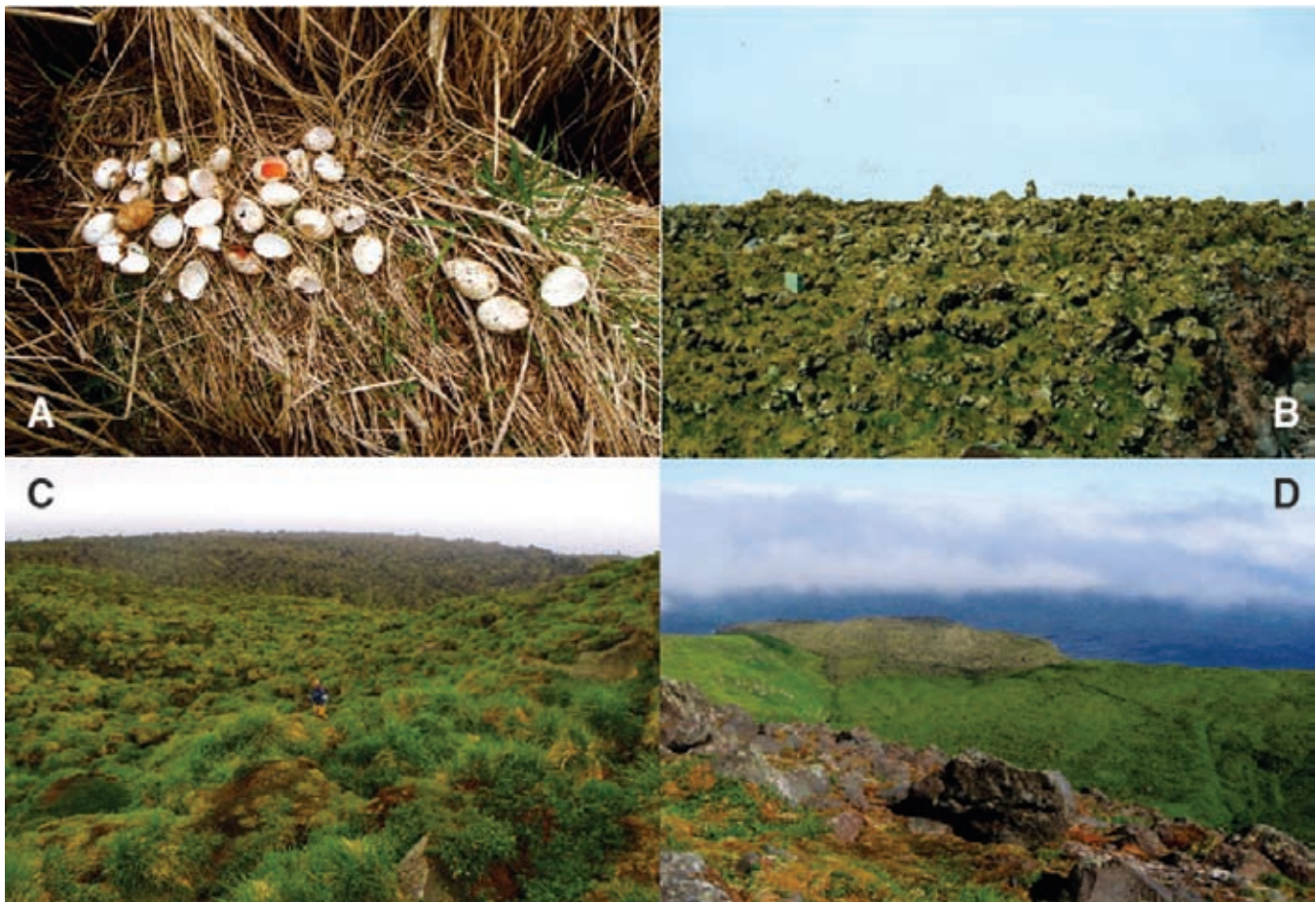


Fig. 2. A rat cache on Kiska Island with 29 Least Auklet eggs (left), and 3 Crested Auklet eggs (right) from June 2010 (A), the 1969 lava dome (B), Bob's Plateau (C), and entire auklet colony (D). Photos by ALB.

DISCUSSION

Reproductive success

We expected that Norway rats at Kiska Island would have a negative impact on breeding Crested Auklets, as they did on smaller Least Auklets (Major *et al.* 2006). The response variables likely to indicate an effect were reproductive success (reductions based on loss of eggs or chicks to rats) and adult survival (predation of adults).

Crested Auklets at Sirius Point, Kiska Island, Alaska, experienced hatching and overall reproductive success that was statistically similar to two other rat-free colonies in the Aleutian Islands over the long term, but during years of high rat abundance on Kiska, Crested Auklets experienced lower reproductive success. However, our analysis is conservative, given the small sample size on Kiska, and therefore had relatively low power to detect small (but potentially biologically important) differences in reproductive success among islands. Rats were abundant at Sirius Point only in 2001–2002, coincident with Least Auklet breeding failure and low Crested Auklet productivity in those years (Major *et al.* 2006). In other years, reduced Crested Auklet breeding success was not expected, as evidence of rats was rare and Least Auklet productivity was close to average for that species across all Aleutian monitoring sites. Thus, detecting a negative effect of rats was only likely during years when rats were abundant (only 2 of 10 years). Furthermore, we did note different patterns in auklet productivity among islands over time, as indicated by the significant island \times year interactions. Crested auklet reproductive success at Buldir and Kasatochi covaried with ocean basin-wide oceanographic indices in the North Pacific (Bond *et al.* 2011) but success at Kiska did not, suggesting that something local (i.e., restricted to this island alone) was influencing variation in reproductive success on Kiska.

We believe that the presence of rats on Kiska is the only difference among the three colonies that could explain the observed demographic differences. The effects of rats might not be limited to direct predation, but could also involve disturbance of auklet nest sites, resulting in abandonment by adults (Piatt *et al.* 1990, Major *et al.* 2006). Disturbance by prospecting conspecifics may have reduced the breeding success of Crested Auklets at post-eruption Kasatochi (JCW, unpubl. data). Despite abundant breeding habitat on Kiska, many crevices were used in one year and subsequently abandoned (ALB unpubl. data), suggesting that disturbance (by rats and/or conspecifics) may have contributed to crevice abandonment. The effects of disturbance are likely colony-specific (Fraser *et al.* 1999, Kitaysky 1999). It is therefore possible that the disturbance and increased risk by introduced rats could result in decreased reproductive success of adult Crested Auklets at Kiska Island, in the absence of direct predation of nest-bound chicks.

Adult survival

Small samples of marked birds hampered our ability to detect small differences in survival. Nevertheless, our estimates of local survival were robust, as indicated by the low level of overdispersion ($\hat{c} = 1.146$; Allard *et al.* 2010), and because our recapture/resight probability was high in each year except 2005, when logistic constraints resulted in a shorter field season. Note that survival estimates of 100% in 2001–2002 and 2002–2003 are the result of subsequently observing all marked individuals (Table A2 available

in the Appendix on the Web site). Because our methods permit estimation of local survival only, the measurements could reflect permanent emigration (e.g., resulting from disturbance caused by rats) as well as mortality. In either case, Crested Auklets' adult survival declined to <0.75 in the final two intervals (2007–2009), likely below that required for a stable population.

Vegetative succession and auklet colony persistence

The decline in survival at Kiska Island is particularly troubling because of the large area of available breeding habitat compared with other Aleutian colony sites. The auklet colony on Kiska Island covers approximately 1.8 km², 50% of which is on a lava dome less than 50 years old that is highly porous (i.e., with abundant crevices suitable for auklet nesting) and sparsely vegetated (Coats *et al.* 1961, Simkin *et al.* 1981, Jones *et al.* 2001). Vegetation succession and soil deposition can reduce access to breeding crevices within three to four auklet generations, or about 50 years (Roby & Brink 1986b). With the exception of Kiska Island, all other Aleutian Crested Auklet colonies are in the mid-to-advanced stages of succession. Furthermore, only auklet colonies at Gareloi, Kiska and Kasatochi islands have been active volcanically since 1900 (Alaska Volcano Observatory staff, pers. comm.), and, excluding Kiska, the remaining two islands comprise just over 10% of the Aleutian population of Crested Auklets (Byrd *et al.* 2005).

The influence of rats on auklet demography

Rat abundance has been extremely variable at the auklet colony at Sirius Point during 2001–2010 (Major *et al.* 2006, Bond *et al.* 2010), with the high rat abundance years 2001 and 2002 corresponding with nearly complete breeding failure of Least Auklets and the lowest reproductive success of Crested Auklets ever recorded. Highly variable abundance is typical of other Aleutian Islands with introduced rats (e.g., Adak, GVB unpubl. data). The frequency of years with high rat abundance and near-complete auklet breeding failure will determine the colony's future. A population viability analysis for Least Auklets indicates that, with more than two years of high rat abundance per decade and corresponding low adult survival, the colony will decline by $>70\%$ over 20 years (Major *et al.* in press). The results presented here are the first attempt at a similar analysis for Crested Auklets, but because of the small number of marked individuals and monitored nests, we caution that the conclusions are only preliminary. As with Least Auklets on Kiska (Major *et al.* in press), lack of significant differences among islands in demographic rates may not mean that the Crested Auklet population is unaffected; rather, there may be greater demographic variability, which could make it vulnerable to stochastic events (Hubbell 2001, Hilborn *et al.* 2003).

There has been considerable research into the effects of introduced rats on Least Auklets at Kiska (Major & Jones 2005, Major *et al.* 2006, 2007), but there is little information on rat predation of Crested Auklets for several reasons. Firstly, Crested Auklets tend to nest much deeper in talus slopes and lava formations than Least Auklets (Bédard 1969), making active nests much harder to find and monitor. Secondly, Least Auklets outnumber Crested Auklets by a factor of 5–10 \times at the Sirius Point colony (Day *et al.* 1979, Byrd *et al.* 2005, Jones & Hart 2006), so Crested Auklet nest crevices were inherently less likely to be sampled. The sample of crevices selected for monitoring during 2001–2010 (on three plots, Jones *et al.* 2001, Major *et al.* 2006) included a more or less random sample

of crevices (i.e., no effort was made to obtain equal numbers of Least and Crested Auklets crevices for monitoring) and therefore has generally included few Crested Auklets.

Rats at Sirius Point have a diet dominated by terrestrial invertebrates, but adults and chicks of both auklet species constitute a significant proportion based on stable-isotope modelling (Major *et al.* 2007). Inferences regarding the predation of adult Least Auklets early in the breeding season (May) have been made from the contents of rat caches found mainly in 2001 and 2002 (Major & Jones 2005). Crested Auklet eggs, but rarely adults, were found frequently in these caches (see a summary in Table A3, available in the Appendix on the Web site). We believe the low number of Crested Auklet adults in caches was a result of the low proportion of Crested Auklets at the Sirius Point colony, their more aggressive nature (Jones 1993) and their relatively high body mass (260 g), which would make them difficult for a rat to drag from a crevice to a cache site. In general, rat caching of auklets is an ephemeral phenomenon, occurring in early spring, and reflects only a small indicator of rat predation on auklets at Sirius Point. The small number of depredated Crested Auklet eggs compared to those of Least Auklets likely is more reflective of their relative abundance.

The evidence in this study, although limited and circumstantial, indicates that there might be a biologically significant effect of rat predation on Crested Auklets at Sirius Point. Kiska Island represents an important breeding colony for this species in the Aleutian Islands, and its persistence may be in doubt. Further study at Sirius Point with an emphasis on Crested Auklets is needed to confirm these conclusions. We urgently need to know how frequently rat outbreaks (such as 2001–2002) occur at Kiska and to quantify the exact relationship between rat abundance and distribution on the one hand and Crested Auklet demography on the other. Such information will help to determine whether rat control or eradication is necessary for conservation of this important colony.

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APPENDIX (ONLINE ONLY)

Appendix 1 – Details of survival analysis

Because our technique captures both breeding and non-breeding individuals, some individuals are never seen again after marking (Jones *et al.* 2002, Jones *et al.* 2007). These transient “prospectors” that we marked on the plot but had no fidelity to it result in a lower estimate of survival on the first occasion after marking (Pradel *et al.* 1997, Prévot-Julliard *et al.* 1998, Bertram *et al.* 2000, Jones *et al.* 2007). To account for this permanent emigration, we included a transient term that modelled survival estimates for the period following capture independently of estimates in subsequent years. This results in the first estimate of survival being the product of both survival and permanent emigration from the study plot (Pradel *et al.* 1997). Marked individuals’ breeding status each year was not known. We defined a global model that included a transient term and both survival and resighting probabilities varying with time.

We tested the goodness-of-fit of the global model to the data using 100 parametric bootstraps (Jones *et al.* 2002, Jones *et al.* 2007). From these bootstraps, we obtained the mean model deviance and mean overdispersion, or extra-binomial variation. This variation arises when assumptions of the model are not met, such as variation in the recapture rates of individuals (Burnham & Anderson 2002). The observed deviance and \hat{c} (which measures extra-binomial variation) were divided by the mean values from the bootstraps and the higher of the two results was taken as an estimate of overall overdispersion, \hat{c} . We restricted our candidate

models to the global model, plus a series of reduced parameter models. We did not construct every reduced parameter model, many of which would have poor fit, but rather we used the approach of Lebreton et al. (1992) by first modelling recapture rates to determine the best structure for recapture rates and then modelling survival rates.

Table A1. Comparison of capture-mark-recapture/resight models from program MARK for Crested Auklets at Sirius Point, Kiska Island, Alaska from 2001-2009, where ϕ is survival, p is the encounter probability and t is time. The term “Year1” estimates survival separately for the year immediately following marking. $p(\text{grouped})$ groups years with similar resight probability to reduce model parameterization (see Table 2). All models were adjusted for $\hat{c} = 1.146$.

Model	QAIC _c	ΔQAIC _c	Akaike Weight	Model Likelihood	No. Parameters	Deviance
A $\{\phi_{(\text{Year}1+t)} p_{(\text{grouped})}\}$	340.595	0.00	0.965	1.000	9	51.132
B $\{\phi_{(\text{Year}1+t)} p_{(t)}\}$	347.261	6.67	0.034	0.036	13	49.137
C $\{\phi_{(.)} p_{(t)}\}$	360.592	20.00	< 0.001	< 0.001	10	68.987
D $\{\phi_{(t)} p_{(t)}\}$	360.770	20.17	< 0.001	< 0.001	17	53.734
E $\{\phi_{(t)} p_{(.)}\}$	382.016	41.42	< 0.001	< 0.001	10	90.411
F $\{\phi_{(.)} p_{(.)}\}$	384.689	44.09	< 0.001	< 0.001	2	109.814

Table A2. The number of Crested Auklets marked and resighted during our study at Kiska Island, 2001-2010. Resighted birds do not include those marked in the same year. There was reduced resighting effort in 2005, and therefore a lower probability of detection (Table 2).

Year	Newly banded adults	Total birds resighted
2001	23	-
2002	1	17
2003	6	18
2004	0	20
2005	0	9
2006	0	18
2007	23	13
2008	41	28
2009	26	54
2010	7	60
Total	127	237

Table A3. A summary of Crested Auklet adults and eggs found depredated by rats or in rat caches at Sirius Point. There was one brief visit in 1996 and visits encompassing the entire breeding season in 2001-2010. Dead adults that had been cached or partially eaten by rats were assumed to be the result of direct predation rather than scavenging (see text).

Date	Details	Source
23 August 1996	1 egg in rat cache	(Williams 1996)
23 August 1996	4 adults found separately	(Williams 1996)
04 June 2002	4 eggs in a rat cache	(Major & Jones 2002)
17 July 2002	1 broken egg with bite marks	(Major & Jones 2002)
01 August 2003	1 depredated adult	(Major & Jones 2003)
08 June 2004	1 depredated egg in productivity crevice	(Jones <i>et al.</i> 2004a)
26 June 2004	1 depredated egg	(Jones <i>et al.</i> 2004a)
16 June 2006	4 eggs in a rat cache	(Eggleston & Jones 2006)
29 May 2007	1 egg in rat cache	(Bond & Jones 2007)
15 July 2008	1 depredated egg	(Bond & Jones 2008)
19 July 2008	1 depredated egg	(Bond & Jones 2008)
31 May 2009	1 depredated egg	(Bond & Jones 2009)
06 June 2009	1 depredated egg	(Bond & Jones 2009)
11 June 2009	2 eggs in rat cache	(Bond & Jones 2009)
06 July 2009	2 depredated eggs	(Bond & Jones 2009)
13 July 2009	1 depredated egg	(Bond & Jones 2009)

29 July 2009	1 depredated adult	(Bond & Jones 2009)
02 June 2010	1 depredated egg, 3 eggs in rat cache	(Bond <i>et al.</i> 2010)
07 June 2010	3 depredated eggs	(Bond <i>et al.</i> 2010)
11 June 2010	3 depredated eggs	(Bond <i>et al.</i> 2010)
13 June 2010	1 depredated egg	(Bond <i>et al.</i> 2010)
