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Research Article

Habitat Modification as a Means of Restoring Crested Auklet Colonies

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ABSTRACT Seabirds that forage in dense groups can be especially vulnerable to anthropogenic threats at sea. To mitigate these threats to populations, nesting habitat restoration may be a viable option by reducing negative density dependence. Accordingly, we undertook a before-after control-impact (BACI) experiment to test whether habitat modification could be an effective means of restoring nesting habitat of crested auklets (*Aethia cristatella*) breeding on Gareloi Island, Alaska, USA. Despite supporting large numbers of crevice-nesting auklets, many lava flows at Gareloi Island are in a stage of late vegetative succession that may prevent birds from accessing subterranean nesting habitat. We hypothesized that crested auklet density is highest in unvegetated blocky and porous lava, and predicted that removing vegetation from the surface would allow new recruits to secure previously unavailable nesting sites. In 2009 and 2010, we delineated 34 200-m^2 plots throughout the southeast colony at Gareloi, and color marked a subset of crested auklets landing in each plot to measure movement and abundance. We removed vegetative overgrowth and peat from half of each plot at the end of the 2009 (4 plots) and 2010 (30 plots) breeding seasons. Before and after vegetation removal, we counted the number of active nesting sites and calculated the ratio of banded to un-banded breeders on the surface of each plot half. Overall, active nesting sites, number of individuals on the surface, and number of breeders landing did not increase after vegetation removal. However, among banded individuals that moved among plot halves, birds were 1.7 times more likely to move to a de-vegetated plot half. Based on our experimental results, we found no evidence that vegetation removal increased crested auklet numbers at Gareloi Island, and thus in the short term this may not be a viable option for increasing crested auklet abundance. © 2016 The Wildlife Society.

KEY WORDS abundance, *Aethia cristatella*, Alaska, crested auklet, Gareloi Island, habitat modification, nesting density.

Globally, seabird populations face numerous threats including introduced predators on breeding islands, climate change, fisheries interactions, and oil spills (Ford et al. 1987, Furness 2003, Hipfner 2008, Jones et al. 2008). Mitigating anthropogenic impacts on seabirds is an important aspect of population management and conservation (Jones and Kress 2012, Russell and Holmes 2015). The designation of Important Bird Areas (IBAs) and protected areas, and the eradication of introduced predators protect existing breeding populations; active restoration programs, including re-colonization programs (e.g., translocation programs), have become increasingly important for extirpated or damaged populations (Jones and Kress 2012).

Population size in seabirds can be partly limited by the availability of breeding habitat, with areas of high suitability being occupied before those of lesser suitability (Fretwell and Lucas 1970, Fretwell 1972, Pulliam and Danielson 1991). Increased density of breeders may reduce an area's suitability because of negative density dependence. Consequently, as a population increases, sites of progressively lower suitability are occupied, reducing the per capita growth rate because of the fitness consequences of occupying sites of low suitability (Rodenhouse et al. 1997). Furthermore, seabirds alter the flow of nutrients through island ecosystems via inputs of marine nutrients, and change vegetative structure by burrowing and trampling (Mulder and Keall 2001, Croll et al. 2005, Fukami et al. 2006). Marine nutrient inputs deposited by seabirds can enhance nutrient composition and vegetative growth (Anderson and Polis 1999), which may in turn decrease or eliminate access to nesting sites (Jones and Hart 2006). Given current seabird population declines resulting from anthropogenic impacts, vegetative overgrowth

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at some important seabird colonies could have population-level effects. Removing vegetative overgrowth at some otherwise healthy seabird colonies may be an effective method to enhance breeding populations after catastrophic events (e.g., an oil spill) by exposing unoccupied nesting habitat.

Crested auklets (*Aethia cristatella*) are small, socially monogamous seabirds that breed in large colonies in the Bering and Okhotsk seas (Jones 1993*a*). They are an abundant seabird with high adult survival (~90%) and an average reproductive success of 0.64 chicks fledged/year (Jones 1993*a*, 2009; Gaston and Jones 1998; Fraser et al. 1999; Dragoo et al. 2016). Crested auklets spend considerable time socializing on the surface of their colonies, frequenting specific areas where intra-specific interactions occur (Jones 1993*a*, Zubakin et al. 2010). There are several million crested auklets nesting in the Aleutian Islands, Alaska, USA, with nearly 90% nesting on Buldir and Gareloi islands (Byrd et al. 2005). Thus, any large localized event (e.g., oil spill) near these colonies or at wintering areas for these birds has the potential to drastically reduce the Aleutian Islands' population of crested auklets.

In the Aleutian Islands, auklets nest in crevices produced by coastal erosion (e.g., talus slopes, beaches) and in blocky and porous lava flows (Jones 1993*a*). Crested auklets do not use earthen burrows (Jones 1993*a*); therefore, nesting density is limited by access to suitable naturally occurring rock crevices. Re-vegetation of exposed rock may occur within decades of a lava flow or rockslide, covering sites and eventually rendering them unsuitable for auklet nesting activity by blocking access to crevices (Roby and Brink 1986, Jones et al. 2001, Jones and Hart 2006). At Kiska Island, Alaska, Jones et al. (2001) reported that auklet nesting density was low (or zero) in previously occupied now grassy areas at the auklet colony site at Sirius Point. Complete vegetation cover in areas occupied by auklets in 1986 had led to their abandonment by 2001 because no nesting sites were available (Jones et al. 2001). The Aleutian Islands lie at the southern limit of the breeding range of crested auklets where a mild, wet climate facilitates rapid plant growth that, based on lava flow age and changes in auklet nesting density, can cover young lava flows with dense grasses, mosses, and peat within 100–150 years (I. L. Jones, Memorial University of Newfoundland, unpublished data). At Gareloi Island, numerous auklets nest in beach boulders and along stream beds, substrates that are infrequently or not used at other colonies (Jones and Hart 2006). Thus, we posited that nesting habitat is limiting at Gareloi Island and that if vegetation removal exposed formerly inaccessible crevices, we would see increases in crested auklet surface attendance and nesting density.

In December 2004, an oil spill at Unalaska Island (~800 km east of Gareloi Island) resulted in the death of marine animals, including crested auklets (Morkill 2006). The origin(s) of the birds killed at Unalaska Island remain unknown, but recent studies using geolocation tags at 2 islands in the western Aleutians, including Gareloi Island in 2013 and 2014, reveal that birds from the western Aleutians overwinter in the general spill area (K. F. Robbins, Memorial University of Newfoundland, unpublished data). We experimentally tested whether habitat modification via vegetation removal could be an effective means of increasing crested auklet numbers to mitigate the impacts of this oil spill. Our objectives were to investigate whether habitat modification through vegetation removal would allow individuals previously unable to secure a nesting site to settle and breed, contributing new breeding individuals to the population. We hypothesized that population size may be limited by the availability of unvegetated lava flows and that by experimentally exposing unoccupied nesting sites through removal of vegetation, we would see an increased number of crested auklets socializing on the surface of the modified habitat versus the control habitat, an increased number of breeders landing on the surface of modified habitat versus the control habitat, increased nesting density in modified habitat versus control habitat, and a greater proportion of individuals moving from control habitat to modified habitat.

STUDY AREA

Gareloi Island (51°45′N 178°45′W, Fig. 1) is a small (6,720 ha), uninhabited island that is part of the Alaska Maritime National Wildlife Refuge (AMNWR), USA, and is the northernmost of the Delarof Island group in the central Aleutian archipelago. Gareloi Island is dominated by Mount Gareloi, a 1,573-m stratovolcano with 2 summits that last erupted in the 1980s (Miller et al. 1998, Coombs et al. 2008). Gareloi Island is treeless and characterized by tall grasses and ferns in low-lying areas, alpine heaths and meadows in higher inland areas, and sparse to no vegetation at higher elevations (Hultén 1960). Gareloi Island has no resident mammals but a relatively diverse avian community (≥20 breeding species) including 1 of only 9 least (*Aethia pusilla*) and crested auklet colonies in the Aleutian Islands (Byrd et al 2005, Jones and Hart 2006). In 2006, there were an estimated 1.2 million breeding crested auklets and 1.2 million breeding least auklets at Gareloi Island distributed across 2 major colonies in the porous twentieth-century-aged

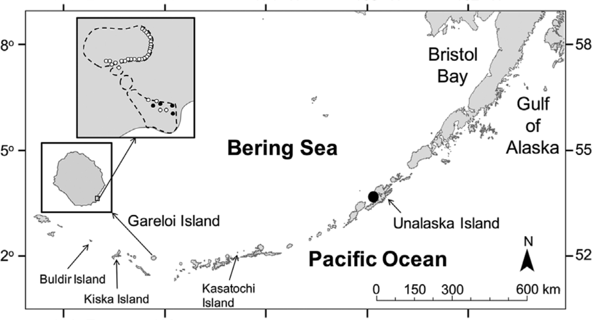

Figure 1. Aleutian Islands, Alaska, USA, indicating the location of Gareloi, Unalaska, and other islands, the crested auklet experimental area with the Southeast Colony outline shown as a dashed line, the 34 experimental plots (solid black dots are the 4 plots delineated in 2009, and white dots are the 30 plots delineated in 2010), and the location of the Selendang Ayu oil spill of December 2004 (large black dot).

lava flows and in beach boulders along all Gareloi shorelines (Jones and Hart 2006). Least and crested auklets breed in mixed species colonies with crested auklets occupying larger crevices than least auklets (least auklets will nest in larger crevices in the absence of crested auklets; Bédard 1969). We examined the southeast colony where approximately 460,350 pairs of crested auklets nest (Fig. 1; Jones and Hart 2006). The auklet colony at Gareloi is likely the largest auklet colony in the Aleutians (Byrd et al. 2005, Jones and Hart 2006) but is situated on lava flows that are at the final successional stages before becoming meadows, which are not suitable for nesting auklets (Jones and Hart 2006).

METHODS

Field Methods

In 2009, we initiated a before-after control-impact (BACI; Green 1979, Stewart-Oaten et al. 1986) experiment to test whether removal of vegetative overgrowth and peat from parts of an auklet breeding colony site would increase nesting opportunities for crested auklets. We evaluated abundance, nesting density, and movement before and after vegetation removal on multiple impact and control plots 1 year before and 3 years after impact. We used a BACI design because it allowed us to quantitatively evaluate whether our experimental manipulation (i.e., vegetation removal) was responsible for changes in our dependent variables (i.e., abundance and nesting density). When using a BACI design, the most important variable is the interaction between period (i.e., before-after) and site (i.e., control-impact), where a significant interaction indicates that changes before and after impact are statistically different at the impact and control sites. Our research was carried out during incubation and chick-rearing in 2009–2011 and 2013 (Jun to late-Jul; Appendix A) and was approved by the Institutional Animal Care Committee at Memorial University (protocol no.: 09-20-IJ, 10-01-IJ, 11-01-IJ, and 13-01-IJ). All banding was carried out under banding permit #22181 (Master Permit to I. L. Jones).

We delineated 4 200-m^2 (10 m × 20 m) plots in the southeast auklet colony in 2009 (Fig. 1). For inclusion in our experiment, we considered only plots with 100% vegetative cover, low-to-moderate crested auklet nesting density (<100 occupied crevices/100 m^2; Jones et al. 2001; Jones and Hart 2006), and access from the beach to enable landing of equipment and personnel for vegetation removal. In addition, we required both plot halves to have similar substrate characteristics, percent vegetation cover, blocking of surface entrances, blocking of subterranean interstices, and surface and nesting density of crested auklets. We divided each plot into plot halves, resulting in paired 10-m × 10-m modified and unmodified (control) plot halves. We captured adult crested auklets in late June and early July 2009 using noose carpets (Jones et al. 2000) placed in areas frequently used for socializing within each of the 8 plot halves. We color marked each captured adult crested auklet with a unique combination of 3 Darvik color bands. Prior to release, we recorded culmen length and bill depth to discriminate the sex of individuals (Jones 1993*b*), and noted the presence or absence of a brood patch to determine breeding status. We used resighting information (see below) from all years of our study to determine plot association for each banded bird.

Early in the 2010 auklet breeding season, we delineated an additional 30 200-m^2 plots in areas of the southeast colony where crested auklet nesting density was lower (Fig. 1). In these plots, we used the same criteria as in 2009 but assessed crested auklet nesting density in the field as opposed to using the Jones and Hart (2006) report, ensuring plots were located in areas of low-to-moderate crested auklet nesting density. We did not color mark crested auklets on these plots nor did we monitor these plots for surface activity, but we assessed nesting density in 2010, 2011, and 2013. In all cases, we denoted treatment as modified (m) or control (c). We completed all surveys described below for 1 auklet breeding season prior to modification, and 2 ($n = 30$; 2,010 plots) or 3 ($n = 4$; 2,009 plots) breeding seasons following vegetation and peat removal (Appendix A).

We removed vegetation and peat from half of each plot after all auklets departed the colony during 4–20 August 2009 (4 plots) and 2010 (30 plots). In each year, a group of 6–10 contractors working in groups of 2–4 individuals/plot used shovels and picks to remove all surface vegetation from each plot. In many cases, our crews were able to tip grassy hummocks off underlying rocks and carry them off the colony in one piece, leaving the underlying rock completely free of all vegetation and peat. Crews carried removed vegetation off the colony and deposited it in nearby areas free of nesting auklets. We considered a plot to have all of its vegetation removed when the underlying lava rock was visible and free of overlying vegetation, sediment, and debris.

In 2009, 2010, 2011, and 2013, we conducted surface counts of all crested auklets using the surface of the 8 plot halves established in 2009. We conducted daily counts between 1000 and 1600 Hawaii-Aleutian Daylight Time (HADT) from 1 July to 31 July, when adult auklets are most active on the surface (Appendix A). We excluded days with high winds and heavy rain because colony attendance and surface social behaviors are reduced. At the beginning of a series of 10-minute intervals, we completed a systematic count of all banded and un-banded crested auklets from fixed observer locations using binoculars. We completed counts in 1 continuous sweep of the plot taking no longer than 1 minute and did not include individuals whose legs were not visible to the observer. One observer completed daily counts on 1 plot half each day; observers rotated among plot halves so that each plot half had an approximate equal number of daily counts completed by each observer.

Breeding crested auklets transport meals for chicks from the ocean to the colony in a throat pouch and are readily identifiable because of the distended appearance of their throat that is often paired with an up-and-down swallowing motion when standing on the colony surface. Starting in early July, we counted all banded and un-banded birds arriving on each of our 8 plot halves established in 2009 with a chick meal within the daytime activity period (Appendix A). In 2009, we conducted continuous 3-hour counts between 1000 and 1300 HADT. In 2010, 2011, and 2013, we performed counts in 30-minute on and off intervals between 1000 and 1500 HADT to ensure the counts were not skewed by observer fatigue.

During May through July 2009, 2010, 2011, and 2013, we systematically searched our plots to locate and map all active least and crested auklet nesting crevices visible from the surface ($n = 4$ plots in 2009 and $n = 34$ plots in 2010–2011 and 2013); we did not mark active nests. We defined a nesting crevice as a crevice containing an incubating adult or an egg and we did not include empty crevices. Because of differences in survey effort among observers and between years, we were unable to compare counts of active nests within our plot halves. Instead, we calculated the proportion of active crested auklet crevices in any plot half as the number of active crested auklet crevices located, divided by the number of active least and crested auklet crevices located within that plot half. In this way, our analysis evaluated whether a proportional difference in least or crested auklet nesting density occurred after vegetation removal and whether those proportional changes were consistent between control and modified plot halves. For clarity, we present nest counts and proportions for each species (Tables S1 and S2; available online in Supporting Information). Based on qualitative direct observations, we assumed that nesting habitat was homogeneous and therefore the likelihood of detecting occupied crevices visible from the surface was equal among plots. To account for differences in initial density of crested auklets among plots, we divided the 34 plots into high (>4 nests/m^2, $n = 4$), medium (1–4 nest/m^2, $n = 11$), and low (<1 nest/m^2, $n = 19$) density during the first pre-vegetation removal survey.

To assess the amount of movement among plots during the daily observation periods in June and July 2009–2011 and 2013, we recorded the color band combination of all re-sighted birds. Later in the season, we also recorded whether the banded individual was observed carrying a chick meal. We excluded all incomplete and incorrect band combinations from all analyses. Using this information, we identified the plot half frequented by each color marked individual in each year of our study. In the movement analysis, we included only birds that could be assigned to one plot half (i.e., in any year >50% of observations were from one plot half) and individuals that were observed in >1 year. We tallied birds that returned to the same plot half (e.g., plot A_c to A_c), moved from one plot half to another (e.g., plot A_c to A_m), and those that switched to an entirely different plot among years (e.g., plot A_c to C_c), noting whether the individual switched to the control or modified half of the new plot.

Mark-Resight Analysis

We estimated crested auklet surface and breeder abundance on each plot half in each of the 4 years of our study using our surface and breeder count data (see above) in a zero-truncated Poisson-log normal mark-resight model with robust design and a sin link in Program MARK (McClintock 2014). We used the Poisson-log normal model because our sampling design allowed for individuals to be sighted more than once during any one observation period (i.e., sampling with replacement) and the number of marked individuals on each plot was unknown after the first year. Program MARK uses an information theoretic approach to rank candidate models and derive estimates of abundance, survival, and recapture rate. Following this approach, we considered all combinations of the parameters: modified versus control plot half, year, and the interaction term plot half × year, resulting in 64 candidate models. We present the top 5 candidate models and the derived estimates of abundance from the top candidate model for both surface and breeder counts. We used these abundance estimates in our BACI comparisons (see below).

Statistical Analyses

We conducted statistical analyses of BACI comparisons using the R Studio environment (R version 3.2.4, www.r-project.org, accessed 3 Apr 2016). Our fixed effects included period (before or after impact), treatment (control or modified), and the interaction term period × treatment. We included the terms year, plot, and the interaction term year × plot as random factors in all models including the null. We used a linear mixed model (R package lme4; Bates et al. 2015) fit by maximum likelihood to evaluate whether vegetation removal 1) increased abundance of crested auklets using the surface of the colony and 2) increased abundance of breeders attending a plot. We used a generalized linear mixed model (R package lme4) with a binomial distribution and logit link function to evaluate whether vegetation removal 3) increased nesting density (model weighted by no. of nests observed in each plot). We defined plot as A, B, C, or D in the surface and breeder abundance analyses, and as high, medium, or low density in our nesting density analysis. We used a second generalized linear mixed model with a binomial distribution and logit link function to assess whether 4) crested auklet movement among plots was related to the treatment of their original plot half (i.e., whether an individual moved to a modified plot half, yes or no). In this model, we included treatment prior to movement (control or modified) as a fixed effect and initial plot half as a random effect (A_m, A_c, B_m, B_c, C_m, C_c, D_m, D_c).

We used an information-theoretic approach and considered 5 and 2 (for movement) a priori candidate models composed of the parameters of interest and an intercept only null model for all analyses. We ranked our models using Akaike's Information Criterion for small sample sizes (AIC$_c$), and used AIC$_c$ weights (w_i) to evaluate model likelihood (Burnham and Anderson 2002). When the best-supported model received a weight less than 0.9, we used model averaging to generate parameter estimates and unconditional standard errors (Johnson and Omland 2004), which we used with parameter likelihoods to indicate the direction and strength of each covariate. Summary data are presented as means ± 95% confidence intervals.

RESULTS

In 2009, we color marked 614 crested auklets; of these, 6 band combinations were inadvertently used twice and 100 were not resighted after banding, resulting in 508 unique

Table 1. Top 5 candidate models describing crested auklet surface and breeder abundance on 8 plot halves at Gareloi Island, Alaska, USA, during July 2009–2011 and 2013, where α represents recapture rate, σ heterogeneity, υ abundance, ϕ survival, γ” emigration, and γ’ immigration. We modeled each parameter as constant (.) or varying by group (p; plot half), time (t; year), or an interaction of terms. We present number of parameters (*K*), change in corrected Akaike’s Information Criterion (ΔAIC_c), and model weights (w_i).

Response	Model	*K*	ΔAIC_c	w_i
Surface abundance	α(p×t) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(t)	71	0.00	1.00
	α(p×t) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(.)	70	24.23	0.00
	α(p×t) σ(.) υ(p×t) ϕ(.) γ”(.) γ’(t)	69	27.92	0.00
	α(t) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(t)	43	82.45	0.00
	α(p×t) σ(.) υ(p×t) ϕ(.) γ”(.) γ’(.)	68	91.01	0.00
Breeder abundance	α(t) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(t)	43	0.00	0.95
	α(t) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(.)	42	6.10	0.05
	α(t) σ(.) υ(p×t) ϕ(.) γ”(.) γ’(t)	41	24.16	0.00
	α(p×t) σ(.) υ(p×t) ϕ(.) γ”(.) γ’(t)	67	47.84	0.00
	α(.) σ(.) υ(p×t) ϕ(.) γ”(t) γ’(.)	39	55.86	0.00

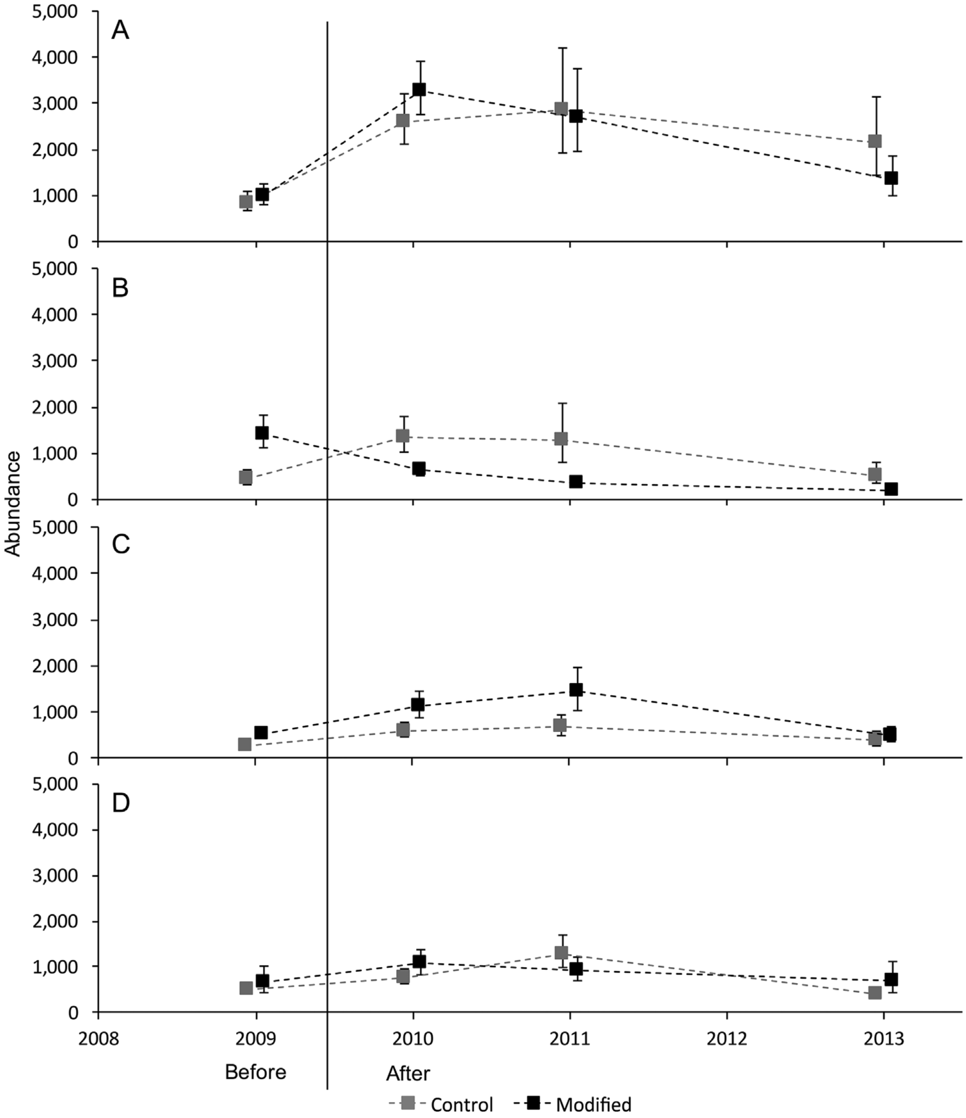

Figure 2. Summary of abundance estimates from our mark-resight analysis of crested auklet surface activity for each of the 4 plots (A, B, C, and D) and plot halves (control shown as gray squares and modified shown as black squares) before and after vegetation removal at Gareloi Island, Alaska, USA, in 2009–2013. We derived estimates from the top candidate model describing crested auklet surface abundance, where abundance was a function of plot half and year for both abundance and recapture rate, using a zero-truncated mark-resight model in Program MARK with a robust design and a sin link function. Data are shown as means with 95% confidence intervals with jitter to minimize overlap between points.

band combinations available to be resighted. Of these, 68 were male, 348 female, and 98 of unknown sex (Table S3). On average, 56 ± 9 (range = 37–78) crested auklets were banded on each plot half (Table S3).

Mark-Resight Analyses

Over the 4 years of our study, we completed 4,851 ($\bar{x} = 24 \pm 0.56$ counts/day) surface counts of banded and un-banded crested auklets. The number of counts performed on each plot half varied little among years ($\bar{x} = 606 \pm 30$, range = 537–661), as did the proportion of banded birds observed on each of the 8 plot halves ($\bar{x} = 1.4 \pm 0.4\%$, range = 2.7–0.7%). Of the 64 candidate models included in our mark-resight analysis to estimate abundance of crested auklets using the surface of each plot half, the top candidate model received all of the AIC_c weight (w_i) and included the terms plot half and year for recapture rate and abundance (Table 1).

In 2009, before vegetation removal, we completed 28 ($\bar{x} = 3.50 \pm 0.37$/plot half) 3-hour long counts of crested auklets landing on the plot surface with a chick meal. In 2010, 2011, and 2013, after vegetation removal, we completed 639 ($\bar{x} = 80 \pm 10$/plot half) 30-minute breeder counts on each plot half over 150 days ($\bar{x} = 50$ days/year or 6 days/plot half/year). In all cases, approximately 4–5% of the number of adult crested auklets landing on the surface were carrying a chick meal (2009: 4.7 ± 1.2% [range = 0.0–15.0%]; and 2010–2011 and 2013: 5.0 ± 0.9% [range = 0.0–33.0%]). Of the 64 candidate models used to estimate breeding population size of crested auklets on each plot half, the top candidate model received 95% of the AIC_c weight (w_i) and included the recapture rate term year and the abundance terms plot half and year (Table 1).

BACI Comparison

Estimates of surface and breeder abundance predicted from our mark-resight model and 95% confidence intervals showed variability among plot halves and year, but showed no step-wise changes before and after vegetation removal or between control and modified plot halves (Figs. 2 and 3). Our statistical analysis supported this trend; where among

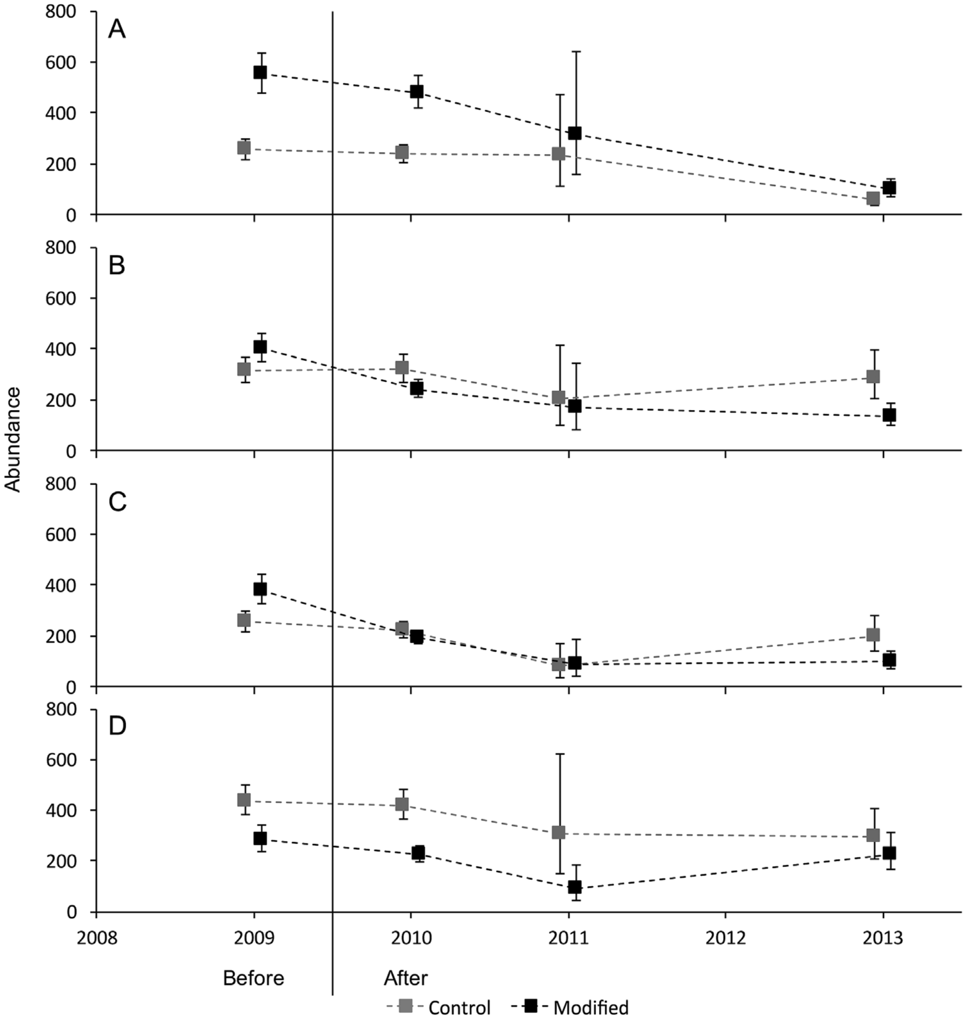

Figure 3. Summary of abundance estimates from our mark-resight analysis of crested auklet breeders landing on the surface of each of the 4 plots (A, B, C, and D) and plot halves (control shown as gray and modified shown black) before and after vegetation removal at Gareloi Island, Alaska, USA, in 2009–2013. We derived estimates from the top candidate model describing crested auklet breeder abundance, where abundance was a function of year for recapture rate and plot half and year for abundance, using a zero-truncated mark-resight model in Program MARK with a robust design and a sin link function. Data are shown as means with 95% confidence intervals with jitter to minimize overlap between points.

Table 2. Candidate model sets describing the relationship between vegetation removal and crested auklet surface abundance ($n = 32$), breeder abundance ($n = 32$), nesting density ($n = 200$), and movement ($n = 69$). Period was before or after modification, plot referred to the 42,009 plots for abundance analyses and density category assigned to each plot for density analysis (where high density plots were those that contained >4 nests/m^2, medium density <4 and >1 nest/m^2, and low density <1 nest/m^2), and treatment referred to the control versus modified plot halves. We present number of parameters (K), change in corrected Akaike's Information Criterion (ΔAIC_c), and model weights (w_i).

Response	Model	K	ΔAIC_c	w_i
Surface abundance[a]	Null	5	0.00	0.53
	Period	6	1.45	0.26
	Treatment	6	2.85	0.13
	Period + treatment	7	4.56	0.05
	Period + treatment + period × treatment	8	6.15	0.02
Breeder abundance[a]	Null	5	0.00	0.43
	Period	6	0.25	0.37
	Treatment	6	3.05	0.09
	Period + treatment	7	3.56	0.07
	Period + treatment + period × treatment	8	4.95	0.04
Nesting density[a]	Period + treatment + period × treatment	8	0.00	0.76
	Treatment	6	3.28	0.15
	Period + treatment	7	4.23	0.09
	Null	5	16.16	0.00
	Period	6	16.28	0.00
Movement[b]	Treatment	4	0.00	0.96
	Null	3	6.14	0.04

[a] All models, including the null, included the random terms year, plot, and the interaction term year × plot.

[b] All models, including the null, included the random term plot half (the initial plot assigned to each individual): A_m, A_c, B_m, B_c, C_m, C_c, D_m, or D_c.

our 5 candidate models, the full BACI model (i.e., the only model that included the interaction term period × treatment) received virtually no support (2% surface abundance and 4% for breeder abundance; Table 2). The null model was the top supported model for surface and breeder abundance analyses, receiving 53% and 43% of the total weight among models, respectively (Table 2). The second best supported models in both cases included the term period; weighted parameter estimates suggested that surface abundance was lower and breeder abundance higher before vegetation removal (Table 3). However, these effects are weak because unconditional standard errors bound zero (Table 3).

The number of least and crested auklet nests observed on each of the 68 plot halves varied between 0 and 45 for least auklets and 0 and 109 for crested auklets (Tables S1 and S2). We noted some evidence of a step-wise increase in the proportion of nests that were crested auklet nests in medium- and low-density control plot halves after vegetation removal (Fig. 4). Our analysis supported this trend; the full BACI model received 76% of the weight among our 5 candidate models (Table 2). Weighted parameter estimates suggest that crested auklet nesting density was higher on control plot halves after vegetation removal (Table 3).

In 2009–2011 and 2013, we completed 135–655 hours of resighting per year during the morning activity period. Effort on each of the 8 plot halves was consistent (162 ± 5 hours; range: 151–170 hours). Overall, we were able to assign 318 of the 508 unique band combinations to a plot half in multiple years. The majority (78%) of these birds did not move from their original assigned plot half, but of those that did, almost half (43%) moved from a control plot half to a modified plot half, this was true with all birds together and when assessing males and females separately (Table 4). In our analysis, evaluating whether movement to a modified plot was related to treatment of initial plot half (control or modified), the top supported model received 96% of the total weight among models and included the term treatment (Table 2). Parameter estimates revealed that among individuals that changed sub-plots,

Table 3. Summed quasi-Akaike weights ($\sum w_i$), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted estimates calculated from candidate models describing the relationship between vegetation removal and crested auklet surface abundance, breeder abundance, nesting density, and movement at Garleoi Island, Alaska, USA, during 2009–2013.

Parameter[a]	$\sum w_i$	Weighted parameter estimate	SE_u
Surface abundance			
Intercept	1.00	1,125.68	341.84
Period: before	0.34	−174.45	280.75
Treatment: modified	0.21	9.86	38.36
Period × treatment	0.02	10.72	23.21
Breeder abundance			
Intercept	1.00	243.60	43.17
Period: before	0.48	62.90	79.23
Treatment: modified	0.20	−0.36	7.51
Period × treatment	0.04	4.07	8.68
Nesting density			
Intercept	1.00	1.01	0.13
Period: before	0.85	−0.01	0.13
Treatment: modified	1.00	−0.40	0.11
Period × treatment	0.76	0.30	0.21
Movement			
Intercept	1.00	1.32	0.40
Treatment: control[b]	0.96	1.65	0.54

[a] We set categorical variables period: before and treatment: control to zero in all models.

[b] We set categorical variable treatment: modified to zero.

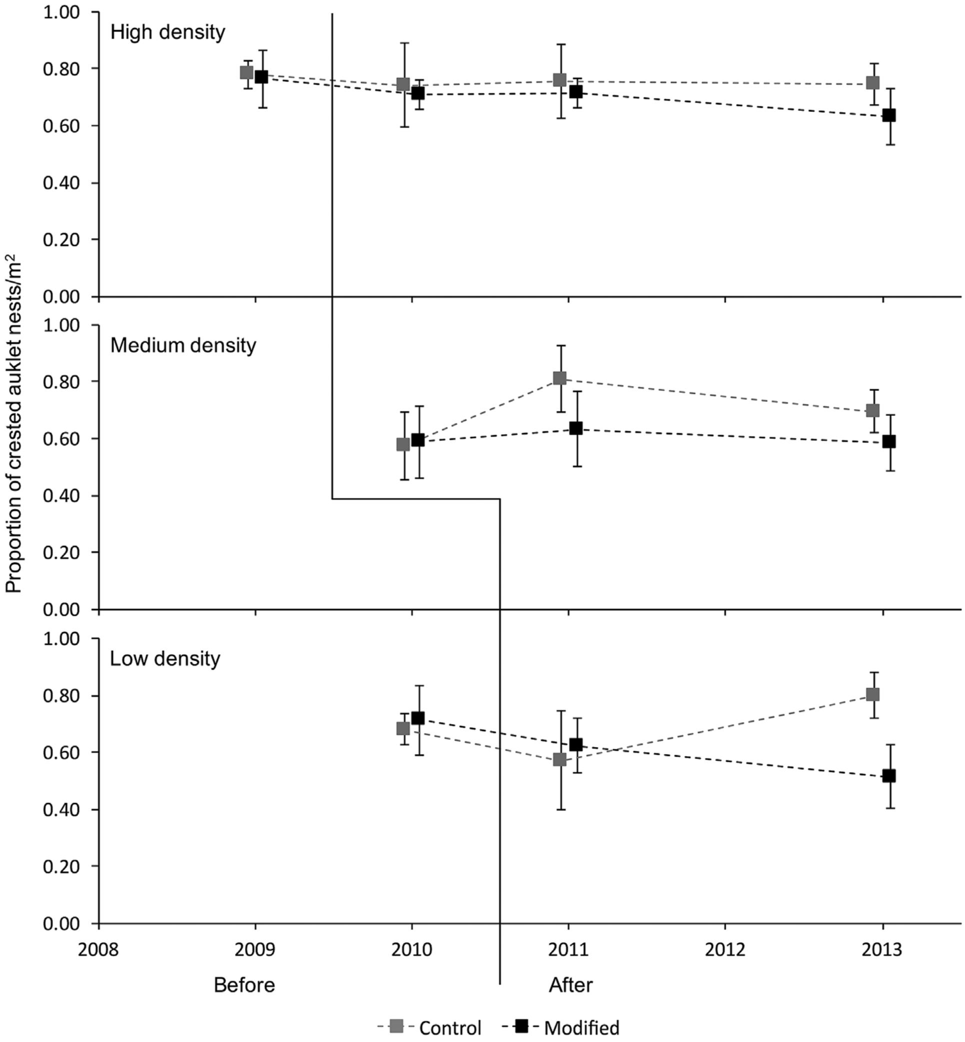

Figure 4. Comparison of the proportion of auklet nests that were crested auklet nests (i.e., no. of crested auklet nests divided by no. least and crested auklet nests) before and after vegetation removal on control (gray squares) and modified (black squares) plot halves in the high ($n = 4$), medium ($n = 11$), and low ($n = 19$) density plots at Gareloi Island in 2009–2013. Data are shown as means with 95% confidence intervals with jitter to minimize overlap between points.

those who were originally assigned to a control plot half moved to a modified sub-plot 1.65 times more often than those who were originally assigned to a modified plot half (Table 3).

Table 4. Summary of movement by crested auklets at 8 plot halves on Gareloi Island, Alaska, USA, in 2009–2013. Numbers in parentheses represent movement within a plot (e.g., A_c to A_m) followed by movement between plots (e.g., A_c to B_m).

	Final plot half			
Original plot half	**No movement**	**Control**	**Modified**	**Total**
Control				
All	117	8 (0, 8)	30 (15, 15)	155
Female	77	6 (0, 6)	20 (11, 9)	103
Male	12	0 (0, 0)	4 (2, 2)	16
Modified				
All	132	18 (3, 15)	13 (0, 13)	163
Female	93	14 (2, 12)	7 (0, 7)	114
Male	18	1 (0, 1)	4 (0, 4)	23
Total				
All	249	26 (3, 23)	43 (15, 28)	318
Female	170	20 (2, 18)	27 (11, 16)	217
Male	30	1 (0, 1)	8 (2, 6)	39

DISCUSSION

We found little evidence to support our hypothesis that vegetation removal would increase the number of nesting crested auklets; it was supported by our movement data only. Our results showed no increase in surface or breeder abundance, or nesting density after vegetation removal, at least not on the time scale of this study. However, as predicted, we found crested auklets moved more frequently from control to modified plots, suggesting that vegetation removal influenced movement within the colony.

Detecting no change in abundance and a decrease in nesting density was surprising and leads to many questions related to crested auklet habitat suitability and whether our current knowledge is limited. To date, there is 1 published paper evaluating auklet habitat use (Roby and Brink 1986) and 1 report providing evidence that auklet habitat suitability is reduced (to zero) when a former nesting area is covered in dense vegetation (Jones et al. 2001). Although many auklet colonies occur on unvegetated lava, some of the largest Aleutian colonies occur within highly vegetated areas (e.g., colonies at Kiska, Semisopochnoi, and Gareloi islands;

Byrd et al. 2005). However, in all cases, colonies are present on active volcanos and lava flows <150 years old (Miller et al. 1998). Thus, habitat suitability may be more dependent on volcanic activity and continuous habitat renewal, rather than the presence of vegetation.

Recent work at Kasatochi Island, Alaska, where a 2008 volcanic eruption covered the former auklet colony in tephra (Williams et al. 2010), located a new least and crested auklet colony on an unvegetated talus slope (G. S. Drew, U.S. Geological Survey, personal communication). Unlike the former colony, where surface counts of least and crested auklets were almost equal (Byrd et al. 2005), the new colony was dominated by least auklets (G. S. Drew, personal communication). During our work at Gareloi Island, we noticed a substantial increase in the number of least auklets socializing on the surface of the modified plot halves. Unfortunately, we did not quantitatively assess least auklets and cannot test a hypothesis related to whether habitat modification increased their abundance; however, this is a potential new avenue for auklet research.

Least and crested auklets often nest in mixed species colonies (Jones 1993*a*), where crested auklets are aggressive toward the smaller least auklet and can displace them from nesting crevices and specific rocks used for socialization (Knudtson and Byrd 1982). From our observations, least auklets are better camouflaged on unvegetated areas; they also lack fluorescence found in crested auklets (Wails et al. 2017), which could affect vulnerability to avian predators, such as the glaucous-winged gull (*Larus glaucescens*) while socializing at the colony. Thus, it may be that least auklets are those most likely to rapidly colonize unvegetated, blocky, porous lava, with crested auklets arriving somewhat later, perhaps attracted to the location by the actions of least auklets. If this is the case, it may be that the timeframe of our study was not adequate to detect a change in crested auklet numbers and that future studies conducted over a longer timeframe may in fact support our predictions. Our study was a first attempt to identify an effective method to mitigate anthropogenic mortality of auklets by increasing access to nesting habitat. Our results indicate that the removal of vegetation alone was not adequate and that further research into habitat preferences, annual movements, and dispersal among colonies are required to best manage auklet populations.

MANAGEMENT IMPLICATIONS

Our study revealed that habitat modification through vegetation removal is not an effective short-term method to enhance crested auklet populations. We recommend that future studies investigate the long-term benefits of habitat modification to both least and crested auklets.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix A

Summary of 4 survey types, dates, times, and survey intervals used at Gareloi Island, Alaska, USA, in 2009, 2010, 2011, and 2013 to assess crested auklet abundance and movement in relation to vegetation removal.

Year	Dates surveyed	Daily survey times	Survey interval (min)
Surface counts			
2009	5 Jul–17 Jul	1,000–1,600	10
2010	2 Jul–31 Jul	1,100–1,500	10
2011	1 Jul–26 Jul	1,100–1,500	10
2013	5 Jul–29 Jul	1,030–1,500	10
Breeding population			
2009	8 Jul–17 Jul	1,000–1,300	180
2010	2 Jul–1 Aug	1,100–1,500	30
2011	30 Jun–26 Jul	1,100–1,500	30
2013	1 Jul–29 Jul	1,030–1,500	30
Nesting abundance			
2009	5 Jul–14 Jul		
2010	14 Jun–21 Jun		
2011	14 Jun–29 Jun		
2013	29 May–12 Jun		
Resighting and movement of marked birds			
2009	2 Jul–30 Jul	1,000–1,600	Continuous
2010	8 Jun–1 Aug	1,100–1,500	Continuous
2011	14 Jun–26 Jul	1,100–1,500	Continuous
2013	29 May–29 Jul	1,030–1,500	Continuous