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EXAMINING PATTERNS IN NOCTURNAL SEABIRD ACTIVITY AND RECOVERY ACROSS THE WESTERN ALEUTIAN ISLANDS, ALASKA, USING AUTOMATED ACOUSTIC RECORDING

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Abstract.—Populations of nocturnal burrow-nesting seabirds are notoriously difficult to measure because of their cryptic behavior at remote breeding sites. However, there is an urgent need to identify factors that influence recovery of these populations, because of the increasing number of introduced-predator eradication projects whose ultimate goal is to facilitate seabird and, thus, ecosystem recovery. We asked whether the relative status of nocturnal burrow-nesting seabirds across the Aleutian Islands, Alaska—inferred from levels of vocal activity collected with automated acoustic recording devices—can be explained in terms of ecological factors such as time since eradication, island size, and distance to source population. We deployed a total of 19 acoustic recorders on six islands during 2008–2010. Overall nocturnal call activity (mean number of calls night^{-1} ± SE) was high (493 ± 287) where predators were never introduced, low (0.3 ± 0.1) where introduced rats were present, and intermediate (29 ± 18) where introduced predators have been eradicated. Using an information-theoretic approach, we found support for multiple factors as an explanation for the call activity of Leach's Storm-Petrels (*Oceanodroma leucorhoa*), Fork-tailed Storm-Petrels (*O. furcata*), and Ancient Murrelets (*Synthliboramphus antiquus*). Specifically, we conclude that although recovery of nocturnal burrow-nesting seabird populations in the Aleutians is not straightforward, the presence of nearby "predator refugia" may maximize the probability of seabird recovery and can be used when prioritizing islands for eradication programs. *Received 16 July 2012, accepted 10 February 2013.*

Key words: acoustic monitoring, introduced predators, island restoration, nocturnal seabirds, population recovery.

Examen des tendances de l'activité nocturne et du rétablissement des oiseaux de mer sur les îles Aléoutiennes de l'Ouest, en Alaska, à l'aide d'enregistrements acoustiques automatisés

Résumé.—Les populations des oiseaux de mer nocturnes nichant dans des terriers sont très difficiles à évaluer en raison de leur comportement cryptique dans les sites de reproduction en région éloignée. Néanmoins, il est urgent d'identifier les facteurs qui influencent le rétablissement de ces populations en raison du nombre grandissant de projets d'éradication des prédateurs introduits, dont le but ultime est de favoriser le rétablissement des oiseaux de mer et, par conséquent, de l'écosystème. Nous nous sommes demandé si le statut relatif des oiseaux de mer nocturnes nichant dans des terriers sur les îles Aléoutiennes, en Alaska – inféré à partir de niveaux d'activité vocale recueillis avec des enregistreurs acoustiques automatisés – peut être expliqué en termes de facteurs écologiques tels que le temps écoulé depuis l'éradication, la taille de l'île et la distance par rapport à la population source. Nous avons déployé un total de 19 enregistreurs acoustiques sur six îles au cours de 2008–2010. L'activité vocale nocturne globale (nombre moyen de cris nuit^{-1} ± SE) était élevée (493 ± 287) aux endroits où les prédateurs n'ont jamais été introduits, faible (0.3 ± 0.1) où des rats introduits étaient présents et intermédiaire (29 ± 18) où les prédateurs introduits ont été éradiqués. En utilisant une approche théorique de l'information, nous avons trouvé des éléments étayant l'hypothèse de multiples facteurs pour expliquer l'activité vocale de *Oceanodroma leucorhoa*, *O. furcata* et *Synthliboramphus antiquus*. Plus spécifiquement, nous concluons que malgré que le rétablissement des populations d'oiseaux de mer nocturnes nichant dans des terriers sur les îles Aléoutiennes ne soit pas simple, la présence de refuges contre les prédateurs à proximité peut maximiser la probabilité de rétablissement des oiseaux de mer et être utilisée lors de l'identification des îles prioritaires pour les programmes d'éradication.

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INCREASED EFFICIENCY IN conservation efforts has precipitated large-scale restoration of avian habitat after anthropogenic disturbance (Gårdmark et al. 2003). Thus, understanding factors that limit or facilitate recovery has become a new conservation priority. Measuring avifaunal population recovery on oceanic islands after the eradication of alien predators has been a growing concern as island restoration projects proceed worldwide (Towns et al. 2006). Avifaunal extinctions and population declines have occurred disproportionately on oceanic islands because of the unique and vulnerable nature of island ecosystems (Atkinson 1989). Introduced mammals such as Domestic Cats (*Felis catus*) and rats (*Rattus* spp.) are the primary mechanism of avian, notably seabird, population decline (Nogales et al. 2004, Jones et al. 2008). In many cases, seabirds affected by invasive predators have benefited from eradication (e.g., Whitworth et al. 2005, Lock 2006, Smith et al. 2006). However, the species- and site-specific patterns by which seabirds recolonize and recover have gone largely unstudied. There is now a need to invest in establishing criteria to measure restoration success by quantifying the process of population recovery (Lavers et al. 2010).

The Aleutian Islands, Alaska, have suffered extensive ecological damage from the introduction of Arctic Foxes (*Vulpes lagopus*) for the fur trade and from accidental introduction of Norway Rats (*R. norvegicus*) during military occupation in World War II (Bailey 1993, Ebbert 2000, Major and Jones 2005). A drastic decrease or total exclusion of seabird populations on Aleutian Islands used as fox farms was noted as early as 1937 (Murie 1959). Although all species were affected, it is likely that small, nocturnal, burrow-nesting seabirds such as Leach's Storm-Petrels (*Oceanodroma leucorhoa*), Fork-tailed Storm-Petrels (*O. furcata*), Ancient Murrelets (*Synthliboramphus antiquus*), and Cassin's Auklets (*Ptychoramphus aleuticus*) were the first to disappear after fox and rat introductions (Bailey 1993). A fox-eradication program began in 1949 as the extent of ecological devastation in the Aleutians was realized, and efforts accelerated after consolidation of the Alaska Maritime National Wildlife Refuge (AMNWR) in 1980 (Ebbert 2000). The first successful rat eradication in the Aleutians occurred at Rat Island in 2008 (Buckelew et al. 2011). After more than six decades of restoration, the Aleutians now represent a patchwork of islands with, without, and at different stages of recovery from introduced predators (Ebbert and Byrd 2002). Although not documented quantitatively, evidence suggests an increase in avian populations after predator removal (e.g., Black Oystercatcher [*Haematopus bachmani*] and Pigeon Guillemot [*Cepphus columba*]; Byrd et al. 1994, 1997). Nevertheless, evidence is scarce, and there are few post-eradication surveys of nocturnal burrow-nesting populations.

The Aleutians provide an ideal opportunity for a large-scale study investigating the recovery of seabirds because of their homogeneous floral, faunal, and weather patterns and lack of human disturbance (Croll et al. 2005). However, monitoring seabirds throughout the Aleutian chain also poses challenges. Sites are logistically difficult and expensive to reach, and seabird species most affected by introduced foxes and rats live in burrows and are active above ground only at night. Measuring populations of nocturnal burrow-nesting seabirds at Aleutian breeding sites, although important, is not feasible using conventional techniques.

We used vocal activity collected with automated acoustic recording devices to infer the status of nocturnal burrow-nesting seabirds at selected Aleutian Islands. Bird vocalizations are often the most efficient means for detecting the presence and relative abundance of cryptic species, particularly nocturnal species that have conspicuous nighttime vocalizations (Brandes 2008, Robb et al. 2008). Calls are easily quantified and, for all nocturnal Aleutian species, have been described and linked to behavior (Simons 1981, Taoka et al. 1988, Jones et al. 1989, Seneviratne et al. 2009). Previously, we tested the feasibility of this approach in detail, considering device placement and the detection, identification, and measurement of nocturnal seabird calls in the harsh weather of the Aleutians (Buxton and Jones 2012b).

The objectives of our study were to (1) use recorded vocalizations to quantify the activity of nocturnal burrow-nesting seabirds at six western Aleutian islands with different introduced-predator histories; (2) evaluate patterns of call activity and, thus, the relative status of nocturnal seabirds on four islands where alien predators have been eradicated for different lengths of time; (3) use an information-theoretic approach to determine whether ecological factors related to population recovery after eradication can explain call activity on different islands; and (4) derive, from the combined results, recommendations for Aleutian Island seabird restoration and population monitoring that would be broadly applicable to island bird conservation.

METHODS

Study sites.—We deployed 16 acoustic recorders across six western Aleutian Islands: three islands in 2008 (Amatignak, Little Sitkin, and Buldir), five in 2009 (Amatignak, Nizki–Alaid, Kasatochi, Kiska, and Buldir), and one in 2010 (Kiska; Fig. 1 and Table 1). Recording sites on each island had typical Aleutian habitat: treeless,

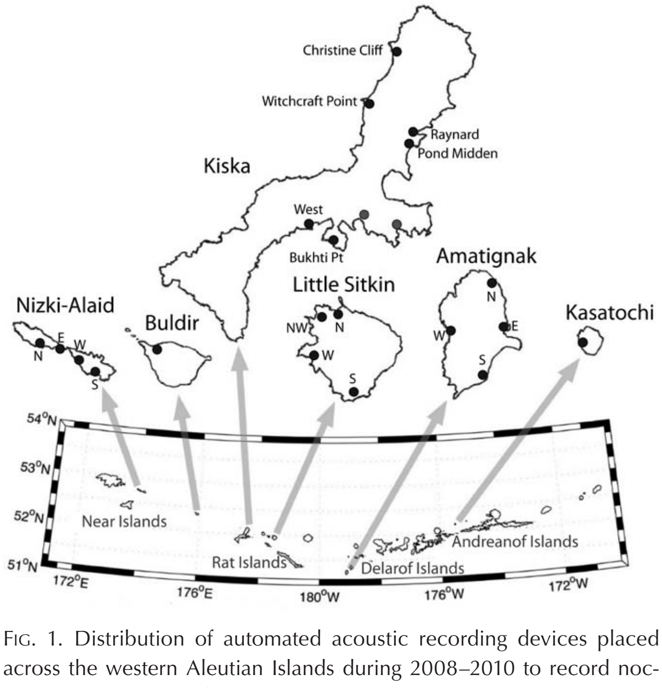

FIG. 1. Distribution of automated acoustic recording devices placed across the western Aleutian Islands during 2008–2010 to record nocturnal vocalizations of seabirds. Acoustic device (song meter) locations are indicated by black dots. Gray dots on Kiska indicate song meters that were placed but malfunctioned.

Table 1. Dates, locations, and recording durations of automated acoustic recording devices placed in the western Aleutian Islands, Alaska, 2008–2010, to record nocturnal vocalizations of seabirds.

Island	Site	Position (WGS 84)	Year	Recording start	Recording end	Device nights	Recording hours
Kasatochi	Troll Talus	52.169°N, 175.524°W	2009	16 June 2009	11 August 2009	56	98
Amatignak	North	51.293°N, 179.090°W	2008	27 June 2008	29 July 2008	32	96
			2009	4 June 2009	3 August 2009	60	180
	East	51.264°N 179.074°W	2008	17 June 2008	4 August 2008	48	144
			2009	28 May 2009	4 August 2009	68	204
	South	51.230°N, 179.010°W	2008	16 June 2008	18 July 2008	32	96
			2009	30 May 2009	1 August 2009	63	189
	West	51.262°N, 179.134°W	2008	15 June 2008	26 July 2008	41	123
			2009	31 May 2009	4 August 2009	65	195
Little Sitkin	North	51.975°N, 178.457°E	2008	18 July 2008	31 July 2008	13	39
	North–West	51.955°N, 178.452°E	2008	2 July 2008	2 August 2008	31	93
	South	51.904°N, 178.538°E	2008	10 July 2008	1 August 2008	22	66
	West	51.932°N, 178.453°E	2008	19 July 2008	2 August 2008	14	42
Nizki–Alaid	West	52.748°N, 173.950°E	2009	31 May 2009	31 July 2009	61	107
	North	52.750°N, 173.898°E	2009	31 May 2009	31 July 2009	61	107
	South	52.750°N, 173.928°E	2009	31 May 2009	31 July 2009	61	107
	East	52.733°N, 173.967°E	2009	31 May 2009	31 July 2009	61	107
Kiska	Bukhti Point	51.919°N, 177.461°E	2009	22 June 2009	25 July 2009	33	115
	West	51.940°N, 177.430°E	2009	2 July 2009	2 August 2009	31	109
	Christine Cliff	52.087°N, 177.552°E	2010	30 June 2010	3 August 2010	35	61
	Witchcraft Point	52.049°N, 177.501°E	2010	26 June 2010	2 August 2010	38	67
	High Talus	52.025°N, 177.560°E	2010	25 June 2010	19 July 2010	24	42
	Raynard Cove	52.018°N, 177.587°E	2010	2 July 2010	1 August 2010	30	53
	Pond Midden	51.007°N, 177.580°E	2010	1 July 2010	31 July 2010	31	54
Buldir	North Bight	52.372°N, 175.894°E	2008	29 May 2008	27 July 2008	59	177
			2009	7 June 2009	30 July 2009	53	159

sub-Arctic grassland tundra, with a relatively uniform geological, climatological, and marine environment (Croll et al. 2005).

Little Sitkin, Amatignak, Kasatochi, and Nizki–Alaid islands were selected to represent a range of time durations since eradication of introduced Arctic foxes (8–33 years). Four recording devices were placed as close as possible to the cardinal points of Amatignak and Little Sitkin. Two devices were placed at the southeast corner of Nizki ("N" and "E"; Fig. 1 and Table 1) and two on the southwest corner of Alaid ("S" and "W"; Fig. 1 and Table 1). These islands are joined by a sandbar at low tide and, thus, are considered here as one island, "Nizki–Alaid" (Byrd et al. 1994). The size of historical seabird populations on these three islands prior to fox introduction is unknown (Murie 1959). However, Aleut midden sites throughout the western Aleutians contain skeletal remains of seabirds that presumably bred locally (Lefèvre et al. 1997, Causey et al. 2005), which suggests that nocturnal seabird abundance was high on all islands prior to fox and rat introductions. One recording device was placed at Kasatochi Island (Troll Talus; Table 1), which erupted in August 2008, temporarily destroying seabird breeding habitat on the island (Williams et al. 2010). Before the eruption, Kasatochi supported large populations of storm-petrels (Williams et al. 2010).

For control purposes, we placed one recording device at Buldir, an island never invaded by alien predators, and six at Kiska, where introduced Norway Rats are still present (Table 1). Buldir supports dense colonies of 21 seabird species (Byrd and Day 1986), whereas nocturnal seabirds are presumed to be rare or absent at Kiska.

Study species.—We measured call activity of Leach's and Fork-tailed storm-petrels, Cassin's Auklets, and Ancient Murrelets, which breed in large numbers in the Aleutian Islands, have conspicuous nighttime vocalizations, and forage and nest in similar habitat (Manuwal and Thoresen 1993, Huntington et al. 1996, Boersma and Silva 2001, Gaston and Shoji 2010).

For each species, we noted two to four call types: calls given by both sexes and all life stages in a variety of situations (Leach's Storm-Petrel "chuckle," Fork-tailed Storm-Petrel "flight call," Ancient Murrelet "chirrup," and Cassin's Auklet "*kreer-er* call"); calls associated with mate advertising and pair formation (Leach's Storm-Petrel "purr," Fork-tailed Storm-Petrel "three-syllable male calls," Ancient Murrelet "song," and Cassin's Auklet "*kut-reearh call*"); calls used during burrow defense (Leach's Storm-Petrel "screech"); and chick calls (Leach's Storm-Petrel and Ancient Murrelet) (Simons 1981, Taoka et al.

1988, Jones et al. 1989, Naugler and Smith 1992, Seneviratne et al. 2009).

Acoustic recorders.—We used digital automated acoustic recorders called "song meters" (Wildlife Acoustics, model SM1), described in detail in Buxton and Jones (2012b). Briefly, song meters were set to record for the entire breeding season (around May to August; Table 1), gain on both microphones was set to +42.0 dB, and sample rate was set to 16 kHz, capturing maximum call frequency of 8 kHz for all study species. These devices can detect calls from ≤50 m, depending on background noise and call properties (Agranat 2009, R. T. Buxton pers. obs.). Song meters placed on Amatignak, Little Sitkin, Kiska, and Buldir were programmed to record in 15-min on–off increments from dusk (0030 hours Hawaii–Aleutian Standard Time) to dawn (0615 hours). Song meters placed on Nizki–Alaid and Kasatochi, where we were unable to regularly change batteries, were programmed to record in 15-min increments from 0130 to 0430 hours, peak nocturnal seabird activity (Buxton and Jones 2012b). Song meters were placed in suitable nocturnal burrow-nesting habitat, with some wind and wave noise shelter adjacent to sheltering slopes or cliffs (Buxton and Jones 2012b).

Measuring call activity.—We quantified call activity by counting the number of calls per night at each site using a combination of automated methods and visual scanning of spectrograms in SONG SCOPE, version 2.3 (Wildlife Acoustics, Concord, Massachusetts). We automatically counted calls in recordings with an average of <500 calls night^{-1} by building call-recognition models in SONG SCOPE. Details of recognition-model construction are available in Buxton and Jones (2012b). Briefly, recognition models were built for each species' calls using loud and clear calls from our recordings and other high-quality recordings as "training data" (an assortment of calls that "train" a model to identify specific calls of interest within recordings). Recognition model parameters (frequency range, sample rate, etc.) were set to maximize signal-to-noise ratio within recordings with low to moderate background noise. Once generated, recognition models scanned all recordings to identify calls of each different species. To filter false positives (wind noise or calls of other species), identified sounds were reviewed in corresponding spectrograms to ensure that they were the call of interest.

Recognition models and visual scanning were unable to count the exact number of calls in recordings where activity was >500 calls night^{-1}. Instead, we calculated a call-count index based on the amount of spectrogram covered in calls versus no calls. First, we calculated the total number of calls that would be present over a 15-min recording period if calls were constant by multiplying the average call duration for each species by 15 min. This resulted in a total of 900 Leach's Storm-Petrel calls (60 s × 15 min/1 s), 750 Fork-tailed Storm-Petrel calls (60 s × 15 min/1.2 s), and 1,800 Ancient Murrelet calls (60 s × 15 min/0.5 s). Using the default settings in SONG SCOPE, we scanned each 15-min spectrogram visually for periods with no calls (i.e., silence). These periods of silence were then subtracted from constant call totals. Because of extreme call activity and time constraints, only 20 randomly selected nights were measured at Buldir and Kasatochi. Although this represents a coarse underestimation of activity, the number of calls calculated is many orders of magnitude above that on other islands and, thus, is suitable for our comparative purposes.

We compared the presence or absence of different call types and average number of calls per night between sites and islands, using vocal activity as an index of relative status for each species (Tables S2–S5, available with the online version of this article; see Acknowledgments). Although call rate does not give an accurate count of individuals or population (Gaston et al. 1988), it can indicate activity levels and, with some caution (see below), can be used to infer relative status and abundance (Jones et al. 1990, Keitt 2005, Buxton and Jones 2012b).

Variables affecting call rates.—We compared mean nightly call activity of the most common species and call types (Leach's Storm-Petrel chuckle, Fork-tailed Storm-Petrel flight call, and Ancient Murrelet chirrup) to four hypothetical explanatory factors related to recovery after Arctic Fox eradication.

First we controlled for two environmental factors that affect call activity on a nightly basis: (1) proportion of the moon visible, from 0 = new moon to 1 = full moon (from U.S. Naval Observatory), because most nocturnal seabirds are less active on moonlit nights (Watanuki 1986); and (2) wind speed (from National Oceanic and Atmospheric Administration weather buoy no. 46071 at 51.16°N, 179.00°E; and no. 46070 at 55.00°N, 175.28°E), known to affect colony attendance at a large scale (Major 2011) and, on a small scale, to decrease the number of calls identified by an acoustic monitoring device (Buxton and Jones 2012b). We also included the number of flight calls of the two heterospecific nocturnal seabirds. Evidence suggests that colonial seabirds are attracted to cues provided by conspecifics and by heterospecifics with overlapping habitat requirements, a phenomenon called "social attraction" (Kress 1997, Nocera et al. 2006). Thus, higher levels of vocal activity may facilitate more activity in heterospecifics. On the other hand, high levels of overlapping heterospecific calls can obscure other calls, making them more likely to be underestimated (Buxton and Jones 2012b).

Two variables were included that we assumed would affect nocturnal seabird population recovery and, thus, levels of call activity, on a site-level scale: (1) the presence of refugia from predators within 500 m of the song-meter site: 0 = no refugia, 1 = talus, 2 = steep cliffs, 3 = offshore islets only, and 4 = cliffs and offshore islets; and (2) distance to the nearest large predator-free source colony calculated in Google Earth 6.2 (Buldir and Koniuji islands; Byrd et al. 2005). It has been proposed that seabirds can escape predation by breeding in habitat inhospitable to predators, such as steep cliffs (Drummond and Leonard 2010, Russell 2011). We hypothesize that faster recovery (and, thus, higher call activity) would occur at sites with nearby refugia and/or predator-free source populations.

Finally, we included two island-level recovery-related factors. The first was the number of years since predator eradication: zero for Kiska, 9 for Little Sitkin, 18 for Amatignak, 25 for Kasatochi, 34 for Nizki–Alaid, and 1,000 for Buldir. Buldir has never had introduced predators but is a recent volcanic island (Coats 1953) that would have been available to storm-petrel colonization after the last major volcanic eruption ≥1,000 years ago (we found that the results did not change if we altered 1,000 by ±500). The second factor was island size in hectares (AMNWR unpubl. data), to control for the fact that seabirds are generally more dense and abundant on small islands (Estades 2001).

Statistical analysis.—All statistical tests were performed in R, version 2.14.2, using the library "glmmadmb" (R Development Core Team, Vienna). To test whether flight-call activity differed among islands, we compared effect sizes using confidence intervals calculated from a negative binomial generalized linear mixed model (GLMM; Nakagawa and Cuthill 2007). A separate GLMM was run for each species' flight call, with island as a categorical explanatory variable, site as a random variable, a log link, and Laplace approximation. Because of low incidence across islands and sites, Cassin's Auklet flight calls and other call types of all species (mate-attracting calls, territorial calls, etc.) were excluded from further analysis.

To assess whether ecological factors related to the eradication of introduced predators could explain call activity on different islands, we considered 15 *a priori* candidate negative-binomial GLMMs (Table S1). Models were corrected for zero inflation and had log links and Laplace approximations. Negative-binomial GLMMs, including a categorical random factor (site nested within island), were used to control for unaccounted variation between sites and islands and overdispersion. Each model was composed of biologically relevant combinations of 11 variables in three separate analyses (calls night^{-1} for Leach's and Fork-tailed storm-petrels and Ancient Murrelets). We used only Amatignak recording data from 2009, because we found no significant difference between years and obtained more data in 2009. Zero-inflated negative binomial GLMMs would not allow for continuous random factors; thus, Julian date was included as a continuous fixed effect in the global model (Table S1). We did not include interaction terms, because the mixed models would be overparameterized (Ginzburg and Jensen 2004).

We used an information-theoretic approach to rank our candidate models using Akaike's information criterion for small sample sizes (AIC$_c$); DAIC$_c$ and AIC$_c$ weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002). We did not correct for overdispersion, which was accounted for using the "zero inflation" function in negative binomial mixed models. When the best-supported model received a weight <0.9, we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inferences from our data set (Johnson and Omland 2004).

Results

Recordings.—We obtained a total of 2,788 recording hours on 1,099 nights (Table 1). We detected a total of 100,953 Leach's Storm-Petrel calls; 90,911 Fork-tailed Storm-Petrel calls; 13,269 Ancient Murrelet calls; and 717 Cassin's Auklet calls (including only 20 nights of analysis of call activity from Buldir and Kasatochi islands). Of these total calls, 448 were recorded on Kiska; 2,204 on Little Sitkin; 4,022 on Nizki–Alaid; 34,263 on Kasatochi (20 nights of data only); 42,276 on Amatignak (average between 2008 and 2009); and 94,036 on Buldir (20 nights of data only).

Call activity.—High activity was detected for all nocturnal seabird species at Buldir, and virtually no activity was detected at rat-infested Kiska (Fig. 2). For all species, flight-call activity was about 9× higher at Buldir versus Kiska (Tables S2–S4), and we detected no mate-attracting or territorial calls at Kiska (Fig. 2). Flight-call activity of all species was only slightly higher on Little Sitkin (foxes removed in 2000) versus Kiska, with confidence intervals bounding zero for Ancient Murrelet chirrup calls, indicating no difference in activity between these islands (Tables S2–S4). We did not record any territorial calls or mate-attracting calls on Little Sitkin (except male Fork-tailed Storm-Petrel calls; Fig. 2).

Flight-call activity of all species was about 5× higher at Amatignak (foxes removed in 1991) than at Little Sitkin (Tables S2–S4). Mate-attracting calls and territorial calls were also numerous (Fig. 2), and Leach's Storm-Petrel chicks' begging calls were recorded at the western site, where flight-call activity was greatest.

Fork-tailed Storm-Petrel and Ancient Murrelet flight-call activity was about 2× higher at Kasatochi (foxes removed in 1984) than at Amatignak and did not differ with activity levels at Buldir (Tables S3–S4). Mate-attracting calls were also numerous, but no chick calls were recorded. Leach's Storm-Petrel call activity did not differ between Kasatochi and Kiska (overlapping effect sizes;

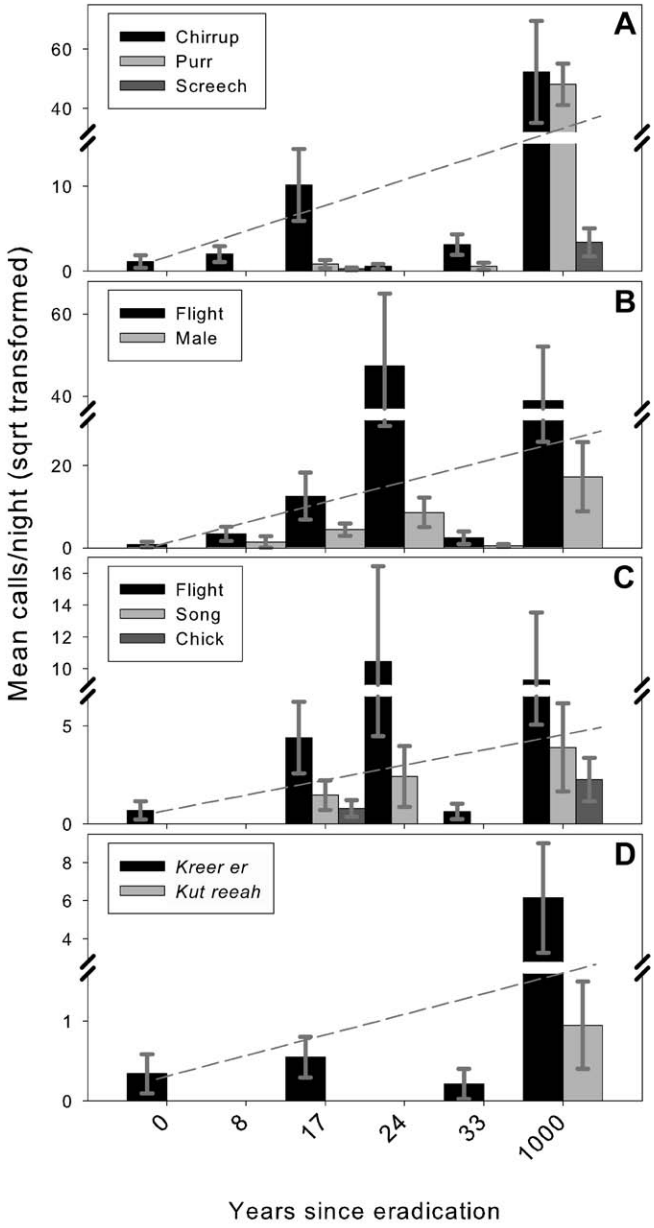

Fig. 2. Vocal activity of (A) Leach's Storm-Petrels,(B) Fork-tailed Storm-Petrels, (C) Ancient Murrelets, and (D) Cassin's Auklets detected at six western Aleutian Islands during 2008–2010. Each island had a different amount of time since predators were eradicated (0–1,000 years). Dashed lines indicate the positive relationship between times since eradication for each call type.

TABLE 2. Top five candidate models describing call activity (calls per night) of three species of nocturnal seabirds on six islands in relation to the number of years since the eradication of introduced predators (YearsPred), island size (IS), presence of refugia (Ref), moon phase (Moon), wind speed (WS), distance to the nearest large source population (DistS), Leach's Storm-Petrel chuckle calls (LESP), Fork-tailed Storm-Petrel flight calls (FTSP), Ancient Murrelet chirrup calls (ANMU), and Julian date (JD) during 2008–2010 ($n = 704$). All models included the random term "island nested within site" (island/site).

Candidate model	K	AIC$_c$	ΔAIC$_c$	Akaike weight
Leach's Storm-Petrel				
YearsPred + IS + Ref + Moon + WS + DistS + FTSP + ANMU + JD + (1 | island/site)	15	4,303.2	0.0	0.8
IS + Ref + Moon + WS + DistS + FTSP + ANMU + JD + (1 | island/site)	14	4,306.4	3.2	0.2
YearsPred + IS + Ref + DistS + JD + (1 | island/site)	11	4,309.0	5.8	0.0
YearsPred + IS + Ref + Moon + WS + DistS + FTSP + ANMU + (1 | island/site)	14	4,323.3	20.1	0.0
YearsPred + Ref + Moon + DistS + FTSP + ANMU + (1 | island/site)	12	4,324.3	21.0	0.0
Fork-tailed Storm-Petrel				
YearsPred + IS + Ref + DistS + JD + (1 | island/site)	11	3,181.7	0.0	0.5
YearsPred + IS + Ref + Moon + WS + DistS + LESP + ANMU + JD + (1 | island/site)	15	3,182.1	0.5	0.4
Moon + WS + JD + (1 | island/site)	6	3,189.1	7.5	0.0
YearsPred + IS + Ref + Moon + WS + DistS + LESP + ANMU + (1 | island/site)	14	3,194.0	12.4	0.0
YearsPred + Ref + Moon + DistS +LESP + ANMU + (1 | island/site)	12	3,197.5	15.8	0.0
Ancient Murrelet				
YearsPred + IS + Ref + Moon + WS+ DistS + JD + (1 | island/site)	13	1,745.5	0.0	0.9
YearsPred + IS + Ref + Moon + WS + DistS + LESP + FTSP + JD + (1 | island/site)	15	1,749.2	3.7	0.1
YearsPred + IS + Ref + DistS + JD + (1 | island/site)	11	1,754.7	9.2	0.0
IS + Ref + Moon + WS + DistS + LESP + FTSP + JD + (1 | island/site)	14	1,757.1	11.6	0.0
YearsPred + Ref + Moon + DistS +LESP + FTSP + (1 | island/site)	12	1,760.5	15.0	0.0

Table S2). Conversely to this positive relationship between call activity and years since eradication, call activity did not differ between Nizki–Alaid (foxes removed in 1975) and Kiska (Fig. 2).

Variables affecting call rates.—For all three species considered, we found that vocal activity was affected by explanatory variables related to recovery after predator eradication. The best-supported model from our candidate set explaining the mean rate of Leach's Storm-Petrel call activity after the eradication of introduced predators was the global model. This model received 4× more support than the second best-supported model (Table 2). Parameter estimates and standard errors bounded zero for the terms "island size," "wind speed," "Fork-tailed Storm-Petrel flight calls," and "Ancient Murrelet chirrup calls," indicating weak effects. Leach's Storm-Petrel call activity was highest with increasing years since predator eradication, at sites with refugia (except talus refugia, which corresponded to decreased call activity), and when the moon phase was closest to the new moon (Table 3).

The best-supported model from our candidate set explaining Fork-tailed Storm-Petrel call activity included the following variables: years since eradication, island size, refugia, and distance to the nearest source. This model received 1.25× more support

TABLE 3. Summed Akaike weights (*w*) and weighted parameter estimates (*w*PE) ± unconditional standard errors (SEμ) calculated from all candidate models describing call activity of Leach's Storm-Petrels (LESP), Fork-tailed Storm-Petrels (FTSP), and Ancient Murrelets (ANMU) on six islands in the western Aleutians, 2008–2010.

	LESP		FTSP		ANMU	
Parameter	*w*	*w*PE ± SEμ	*w*	*w*PE ± SEμ	*w*	*w*PE ± SEμ
Intercept	1.00	–3.04 ± 1.38	1.000	6.98 ± 3.67	1.00	–1.83 ± 2.73
Years since eradication	0.84	0.04 ± 0.02	0.987	–0.03 ± 0.06	1.00	0.12 ± 0.03
Island size	1.00	–0.001 ± 0.001	0.986	–0.001 ± 0.001	1.00	0.001 ± 0.001
No refugia						
Talus refugia	1.00	–4.55 ± 1.49	0.987	7.85 ± 2.99	1.00	9.55 ± 1.79
Cliff refugia	1.00	2.13 ± 0.49	0.912	4.91 ± 1.90	0.91	2.25 ± 0.82
Offshore islet refugia	1.00	2.81 ± 0.90	0.912	5.08 ± 0.01	0.91	5.77 ± 0.01
Cliffs/offshore islet refugia	1.00	3.19 ± 0.46	0.912	5.84 ± 0.01	0.91	0.82 ± 0.01
Moon phase	0.96	–0.47 ± 0.24	0.451	–0.07 ± 0.01	0.99	–1.11 ± 0.01
Wind speed	0.96	–0.002 ± 0.002	0.451	–0.001 ± 0.001	0.99	–0.008 ± 0.001
Distance to source population	1.00	0.003 ± 0.002	0.987	–0.007 ± 0.001	1.00	0.007 ± 0.001
LESP chuckle			0.438	0.001 ± 0.001	0.14	0.001 ± 0.001
FTSP flight	0.96	0.001 ± 0.001			0.14	0.001 ± 0.001
ANMU chirrup	0.96	0.001 ± 0.002	0.438	–0.001 ± 0.001		
Julian date	1.00	0.001 ± 0.001	0.998	–0.001 ± 0.001	1.00	–0.001 ± 0.001

than the second best-supported model (Table 2). Parameter estimates and standard errors bounded zero for the terms "years since eradication" and "island size," indicating weak effects. Fork-tailed Storm-Petrel call activity was highest at sites with refugia and at increasing distance to the nearest source population (Table 3).

The best-supported model explaining Ancient Murrelet call activity included the terms "years since eradication," "island size," "refugia," "moon phase," "wind speed," and "distance to the nearest source population." This model received 9× more support than the second best-supported model (Table 2). Parameter estimates and standard errors bounded zero for the term "island size." Ancient Murrelet call activity was highest with increasing years since predator eradication, at sites with refugia, when moon phase was closest to the new moon, with decreasing wind speed, and with increasing distance to the nearest source population (Table 3).

For all three species, there was more call activity at sites with at least one type of predator refugium than at sites with none (Table 3). The Leach's Storm-Petrel chuckle was about 3× more numerous at sites with cliffs and offshore islets, the Fork-tailed Storm-Petrel flight call was about 8× more numerous at sites with talus, and the Ancient Murrelet chirrup was about 10× more numerous at sites with talus (Fig. 3).

Discussion

To address a lack of data examining seabird population recovery post-eradication, we investigated patterns of nocturnal burrow-nesting seabird status after the eradication of Arctic Foxes in the western Aleutian Islands. We found that although many factors contribute to seabird recovery, the presence of nearby refugia and, thus, a source population, resulted in higher nocturnal seabird activity and, thus, likely abundance. Using a passive acoustic approach, we were able to circumvent the impracticalities of conventional daytime census techniques. However, this technique represents a coarse scale of information with limitations and may introduce some sampling biases that merit more discussion.

Eradication of introduced foxes in the Aleutians has occurred on >40 islands spanning 210,000 ha (Ebbert and Byrd 2002). These islands are difficult and expensive to reach, and species most affected by fox predation have cryptic breeding sites (Byrd et al. 1983). Because of the ease of acoustic-device placement, the procurement of large amounts of comparable data, and the conspicuous calls of nocturnal seabirds, we found automated acoustic recording to be the most practical method for inferring relative population status and, possibly, abundance on this large scale (Buxton and Jones 2012b). On the other hand, it was not possible to identify and count calls of individuals or directly compare call activity with abundance. Thus, it must be emphasized that our measures were of activity, not population counts (Dawson and Efford 2009, Buxton and Jones 2012b). However, we reason that call activity of our study species is likely related to relative abundance of breeding birds, at least at a coarse scale, for several reasons: call counts have been correlated to numbers of breeding individuals in many other species of birds (Farnsworth et al. 2004, Celis-Murillo et al. 2009) and some seabirds

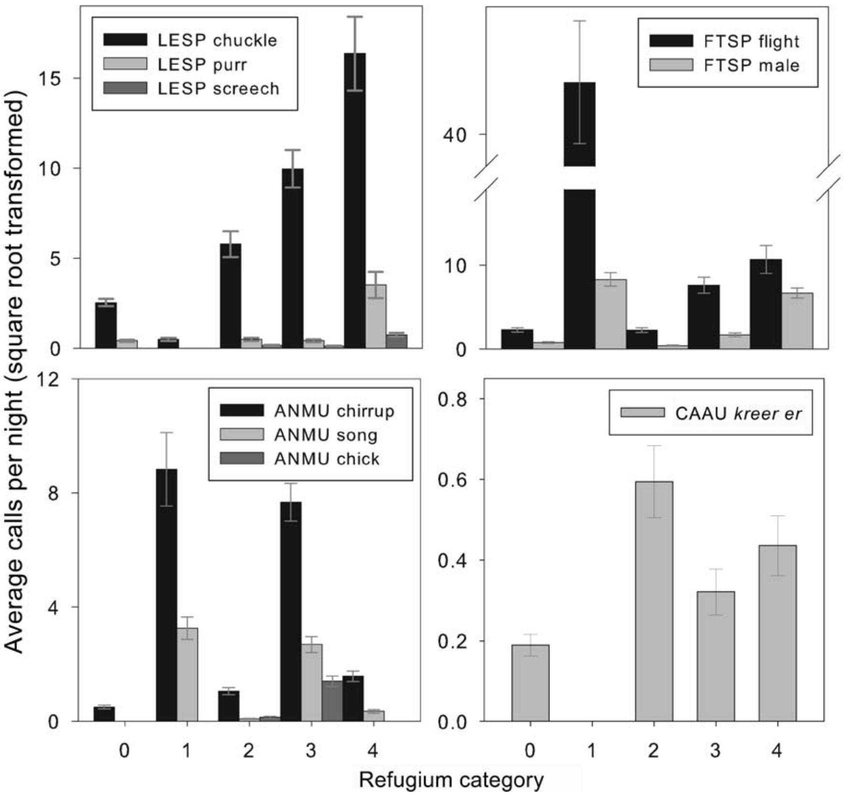

Fig. 3. Summary of the mean number (± SE) and type of calls of each species—Leach's Storm-Petrel (LESP), Fork-tailed Storm-Petrel (FTSP), Ancient Murrelet (ANMU), and Cassin's Auklet (CAAU)—in relation to refugium category: 0 = no predator refugia, 1 = talus, 2 = cliffs, 3 = offshore islets, and 4 = both cliffs and islets.

(A. Borker and M. McKown pers. comm.). At sites with high levels of flight-call activity, we recorded mate-attracting calls, burrow defense calls, and, in some cases, chick calls. By contrast, we recorded no breeding-behavior calls at sites with low flight-call activity. This suggests that high call activity is related to the presence of breeding behavior or even breeding. Furthermore, we found differences of large orders of magnitude in mean call activity between sites (e.g., 0.6 ± 0.3, 70.3 ± 13.4, and 1,092.0 ± 123.6 mean flight-call activity night^{-1} on Kiska, Amatignak, and Buldir, respectively), substantiating a comparison between relative indexes of abundance on a coarse scale.

There were striking differences in call activity between predator-free Buldir and predator-invaded Kiska. Low activity was expected at Kiska, because the island has been occupied for >60 years by Norway Rats, which are well known for their deleterious effects on seabird colonies (Gaston 1994, Jones et al. 2008) and are likely responsible for the current lack of nocturnal seabird activity. We conclude, from low call activity recorded on our song meters, evidence from Byrd et al. (2005), and ground searches (I. L. Jones pers. obs.), that few nocturnal burrow-nesting seabird species currently nest on Kiska.

When we compared call activity among Little Sitkin, Amatignak, and Kasatochi islands (foxes removed in 2000, 1991, and 1984, respectively), a positive pattern emerged among number of years since predator eradication, call activity, and number of different call types. Call activity and diversity were low on Little Sitkin, with vocalization levels similar to Kiska. Conversely, at Amatignak, which had 9 years longer to recover from fox predation, numerous flight calls, mate-advertising burrow calls, territorial calls, and, at some sites, chick calls were recorded. When fox eradication occurred another 7 years back (at Kasatochi), flight-call activity of Fork-tailed Storm-Petrels and Ancient Murrelets was even higher, with vocalization numbers comparable to the non-predator-invaded Buldir. This result is not surprising, given that there is likely a positive relationship between seabird activity and recolonization and time after eradication (Jones 2010). As time passes, increasing numbers of young birds produced at the now predator-free site will have the opportunity to recruit, and immigrants will have more opportunity to prospect and settle (Oro and Ruxton 2001).

On the other hand, Nizki–Alaid, which had foxes removed in 1975, had similar call activity and diversity as Little Sitkin, which had foxes removed 25 years later. This suggests that mechanisms responsible for current nocturnal seabird status are more complicated than simply time since predator eradication. Indeed, seabird recovery at a predator-free island is a product of many factors, such as presence and suitability of breeding habitat, dispersal distance from the nearest colony site, historical escape from predation, and social facilitation (Lavers et al. 2010, Jones and Kress 2012).

Although high levels of mate-advertising calls were recorded at Kasatochi, we detected no chick calls. This is likely because of the previous year's catastrophic volcanic eruption that destroyed breeding habitat (Williams et al. 2010). Breeding and prospecting adults present before the eruption likely survived and returned to Kasatochi but, because of the destruction of nesting habitat, were unable to reproduce.

Our results revealed that among all species, more call activity occurred at sites where refugia were present within 500 m. Evidence suggests that seabirds can breed on sloping talus, steep cliffs, and offshore islet refuges to avoid predation (Birkhead and Nettleship 1995, Drummond and Leonard 2010). After predator eradication, remnant populations in these refugia may provide pioneering individuals to recolonize the island or spread to other habitats. At islands without such refugia, entire populations may be extirpated and recolonization may be delayed until prospectors arrive from distant source populations (Oro et al. 2011). The few signs of activity found at Nizki–Alaid, where no refugia exist, in contrast to the confirmed breeding of Ancient Murrelets on the eastern site of Amatignak, where offshore islet refugia exist, support this hypothesis. Preference of refugium type was species specific: Leach's Storm-Petrels were most numerous at sites with nearby offshore islets and steep cliffs, whereas Fork-tailed Storm-Petrels and Ancient Murrelets were most numerous near rock talus (i.e., Kasatochi pre-eruption). Leach's Storm-Petrels are known to nest only in soil burrows, whereas Fork-tailed Storm-Petrels occasionally use rocky crevices (Harris 1974). This may explain why Fork-tailed Storm-Petrels were so numerous on Kasatochi, where rock talus was abundant, allowing them to take refuge from foxes, whereas Leach's Storm-Petrels were rare. Caution should be taken when comparing flight-call activity close to predator-free refugia, because recording sites may merely represent flyways in transit to actual breeding refugia. However, at all sites where flight-call activity was high, we also recorded mate-attracting calls. Considering that recorders can only pick up calls within 50 m (and no devices were placed within 50 m of a refugium), this suggests that breeding behavior is taking place outside of refugia, within range of the device.

We found that distance from large predator-free source colonies (Buldir and Koniuji; Byrd et al. 2005) was included in the most-parsimonious models for all three species, although the relationship with call activity was weak. None of the nocturnal species tested are known to exhibit strong natal philopatry (Huntington et al. 1996, Boersma and Silva 2001, Gaston and Shoji 2010); thus, individuals can evaluate multiple potential breeding sites prior to settling and breeding. These species should be more likely to recolonize abandoned sites after introduced predator removal, because dispersal rates are higher than in species that exhibit natal philopatry. However, dispersal distance and rate are unknown for many nocturnal burrow-nesting species, as are many aspects of habitat selection, topics that merit more research (Lee et al. 2012).

Habitat selection based on information obtained from conspecifics or ecologically similar heterospecifics may be an important aspect in settlement decisions that affect recovery and recolonization ("social attraction"; Kress 1997, Mönkkönen and Forsman 2002). Our results show that Fork-tailed Storm-Petrel call activity was high at sites where Leach's Storm-Petrel and Ancient Murrelet call activity were also high. This suggests habitat association and/or that the presence of heterospecifics is important as a social cue. The latter hypothesis is supported by previous work that has shown that Leach's Storm-Petrels and Ancient Murrelets are highly attracted to the vocalizations of conspecifics (Major and Jones 2011, Buxton and Jones 2012a). Clearly, further study is required to determine the importance of social facilitation in habitat selection and settlement decisions among these three species.

Any interpretation of nightly call comparisons across seasons must take into account differences between light and weather conditions that may affect activity and actual numbers of calls present at a site. Here again, automated recording devices show their value by allowing simultaneous monitoring at multiple sites, controlling for such environmental variables. Overall, our results revealed that all three species exhibited lower call activity on nights closer to the full moon, similar to published accounts suggesting that individuals are less active on moonlit nights, when they are more vulnerable to predators (Watanuki 1986, Jones et al. 1990). In addition, we found that Ancient Murrelet call activity decreased with increasing wind speeds. Similarly, published accounts suggest that adverse weather conditions make returning to the colony or prospecting more energetically difficult and result in less site visitation under windy or stormy circumstances (Vermeer et al. 1988).

In the present study, we assumed that all three study species occurred historically on all islands included in our analyses. Given current known distributions and habitat requirements for these species across the Aleutian Islands, we consider this assumption justified (Byrd et al. 2005). However, paleoecological investigations at Aleut midden sites may provide the best opportunity to quantify pre-fox and pre-rat distribution of nocturnal seabirds on Aleutian Islands and drive future restoration activities.

In an ever anthropomorphically altered world, understanding factors that limit or facilitate recovery of wildlife has the potential to prioritize future conservation projects and management interventions (Gårdmark et al. 2003). Our results revealed that post-eradication management actions for nocturnal seabirds in the Aleutians should account for the presence of refugia as a source of recruits and an indication that relatively rapid recovery is plausible. For example, at Little Kiska, an island located near Kiska Harbor, a small population of Ancient Murrelets persists (~175 individuals; Byrd et al. 2005). If predation pressure by rats was removed from the larger island of Kiska, this subcolony could provide individuals to recolonize the main island. Thus, eradication work is more likely to result in a rapid recovery of nocturnal seabirds at Kiska than at some other islands without nearby refugia, increasing the short-term conservation potential of eradication work at that island.

We conclude that although the proximity to refugia and years since eradication emerged as important factors in the recovery of nocturnal burrow-nesting seabird populations in the present study, other factors likely contribute to the speed of recovery, and they may have been masked by the inherent sampling biases associated with automated acoustic monitoring. Although eradication of predators is an essential first step in island restoration, it may not directly result in nocturnal seabird recovery. We recommend further song-meter deployments to expand analysis across the Aleutians and tease out details and important factors that affect recovery. In addition, at islands with characteristics unlikely to promote rapid recovery, for example Nizki–Alaid, more extensive management may be required after eradication. In this case, social attraction techniques or translocation could be used to encourage recolonization (Jones and Kress 2012). Finally, we recommend further research into the relationship between call activity and relative abundance of breeding birds, so that acoustic recording can be used in the future as a robust monitoring and census tool for recovering seabird colonies.

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