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Initial Effects of the August 2008 Volcanic Eruption on Breeding Birds and Marine Mammals at Kasatochi Island, Alaska

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Abstract

Kasatochi Island, home to a rich community of largely marine-dependent fauna, erupted with little warning on 7–8 August 2008 and buried the island under up to 30 m of tephra. We visited the island during the summer of 2009 to examine the effects of the eruption on local wildlife. The abundance of sea lions and many seabird species in 2009 was comparable to pre-eruption estimates, suggesting that adult mortality was low for these species. In contrast, shorebirds and passerines formerly breeding on the island were not observed in 2009 and probably perished in the eruption. The largest direct effect of the eruption to individual animals was probably mortality of chicks, with an estimated total 20,000–40,000 young birds lost. Indirect effects on wildlife consisted of loss of foraging habitat for species that relied on former terrestrial, intertidal, or nearshore-subtidal habitat and the near-total destruction of all former nesting habitats for most species. Although several species attempted to breed in 2009, all except Steller's sea lions failed due to lack of suitable breeding sites. The recovery of wildlife at Kasatochi will depend on erosion of the tephra layer blanketing the island to re-expose former breeding habitat.

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Introduction

Kasatochi Island, located within the central Aleutian Islands of Alaska, erupted with little warning on 7–8 August 2008. A small stratovolcano with no prior historical record of eruption, the island was home to a rich community of largely marine fauna, consisting primarily of hundreds of thousands of seabirds and hundreds of marine mammals (Byrd et al., 2005). Following the 2008 eruption, Kasatochi was covered by up to 30 m of tephra that destroyed or covered nearly all the wildlife breeding and foraging habitat on and around the island (Scott et al., 2010 [this issue]).

As one of nine annual ecological monitoring sites in the Alaska Maritime National Wildlife Refuge (AMNWR), Kasatochi was the site of extensive biological surveys prior to the eruption. Basic inventory of wildlife resources at Kasatochi started in the 1980s and included boat-based circumnavigations (e.g., Bailey and Trapp, 1986) and incidental observations of wildlife during efforts to remove introduced arctic foxes (Vulpes lagopus) in the 1980s (e.g., Deines and Willging, 1985). The first study plots for auklets were established in the early 1990s (Thomson and Wraley, 1992), and intensive season-long biological monitoring of seabirds and other biological resources was conducted annually from 1996 until the eruption in August 2008 (summarized in Drummond and Larned, 2007; Buchheit and Ford, 2008). In addition, at-sea bird distributions around Kasatochi were described during ship-board surveys in 1996 and 2003 (Drew et al., 2003; Dragoo, 2007). Combined, these data provide a substantial amount of information on the status of birds and marine mammals at Kasatochi before the eruption.

Our goal was to examine the effects of the volcanic eruption of Kasatochi on breeding bird and marine mammal populations one year after the event and to establish a baseline for quantifying the rate of recovery. Based on a brief helicopter visit and a shipbased offshore survey immediately after the eruption in late August 2008, and supplemented with a series of satellite images during the winter of 2008–2009, initial impressions suggested all wildlife habitat on the island had been completely devastated. To assess the effects of the eruption, we visited Kasatochi in summer 2009 to study the abundance and breeding status of wildlife, evaluate the availability of habitat, and compare conditions to those existing prior to the eruption. Specifically, we addressed the following questions: (1) What were the direct and indirect effects on wildlife diversity, populations, and distribution? (2) Did any pre-eruption wildlife habitat remain? (3) Was any new wildlife habitat created? (4) How would erosion of the overlying mantle of tephra influence the potential for creation of new habitat or recovery of old habitat? (5) If no habitat existed in 2009, how long would wildlife remain in the vicinity of the island?

Study Area and Methods

STUDY AREA AND PRE-ERUPTION CONDITIONS

Located approximately 19 km northwest of the westernmost point of Atka Island, Kasatochi Island (52.17°N, 175.51°W) is a volcanic caldera that, prior to the eruption, encompassed approximately 287 ha and had a diameter of about 2.7 km. Until 2008, there were no reliable reports of the island being eruptive in historic times (Coats, 1950), although steam rose from the caldera and the caldera lake disappeared in 1899 (Jaggar, 1927) and bubbles were seen in the caldera lake in 2005–2007 (Drummond and Rehder, 2005; Drummond, 2006; Drummond and Larned, 2007). Recent work suggests the last major eruption occurred between a few centuries and 1000 years ago (Scott et al., 2010 [this issue]). The rim of the caldera rose to 314 m at its highest point and descended sharply inward to a 0.8-km-wide brackish lake near sea level (Bailey and Trapp, 1986). There were no freshwater streams, ponds, or springs on the island. The southern half of the island consisted mostly of gentle grassy slopes, with a coastline characterized by narrow sand or cobble beaches at the base of dirt cliffs up to 30 m high. The western coast comprised high rocky bluffs rising over boulder beaches, with grassy ravines sloping up from the bluffs to the caldera rim. The northern coastline was dominated by sheer, impassable cliffs interspersed with rock slides and steep vegetated talus slopes.

Kasatochi's diverse terrain provided breeding habitat for a wide range of bird species: auklets (*Aethia* spp.), puffins (*Fratercula* spp.), and storm-petrels (*Oceanodroma* spp.) nested in crevices in talus slopes and rock piles; raptors, murres (*Uria* spp.), and cormorants (*Phalacrocorax* spp.) used cliff ledges; passerines and shorebirds used grassy slopes and beaches. In addition, a Steller's sea lion (*Eumetopias jubatus*) rookery occurred on the northern side of the island, and a small population of harbor seals (*Phoca vitulina*) pupped on beaches and foraged in nearshore waters.

PRE- AND POST-ERUPTION SURVEY METHODS

Pre-eruption data on abundance and breeding status are based primarily on observations collected from 1996 to 2008 as part of the long-term biological monitoring program by AMNWR (Byrd, 2007; Drummond and Larned, 2007). From late May until late August or early September, survey crews annually collected data on population abundance, productivity, adult survival, and diet on a suite of species, including seabirds, shorebirds, raptors, passerines, and marine mammals. Population-survey techniques consisted of a variety of methods, including nearshore circumnavigation surveys by inflatable skiff, land-based counts along transects or on other plots, point-counts, and records of daily wildlife observations (Williams et al., 2002). From these methods, we generated our best estimates of pre-eruption abundance. For many species, accurate island-wide counts did not exist, so we extrapolated from plot counts, based on our knowledge of distribution and the amount of available breeding habitat. For species with apparently stable populations over the past decade, we used data from all years (1996-2008) to generate abundance estimates. For species that had undergone a distinct change in population size over that period (e.g., a steady decline in murres and an increase in sea lions), we used only data from recent years to estimate pre-eruption abundance.

Following a brief post-eruption offshore reconnaissance from the ship M/V Tiglax on 23 August 2008, we conducted the main post-eruption surveys at Kasatochi on 12-15 June and 10-12 August 2009. During six days of land surveys in 2009, we recorded all wildlife observations while walking over the entire coastline several times, climbing to the caldera rim, and visiting sites of former bird nesting colonies and other known centers of wildlife abundance. We also conducted a single nearshore circumnavigation survey on 13 June with a 4.5 m inflatable skiff. From approximately 100 m offshore, two people counted all wildlife on the water or flying within 100 m of either side or 200 m in front of the boat (resulting in a 200-m-wide survey strip). Circumnavigation data were recorded instantaneously on a waterproof, shockproof, hand-held computer (TDS Recon, Tripod Data Systems, Westminster, Colorado) attached to a global positioning system (GPS) unit (Map76CSx, Garmin International, Inc., Olathe, Kansas). Finally, several incidental observations of seabirds were made on 18 July from the M/V Tiglax while transiting past the island about 300 m offshore.

We also recorded activity of colonial seabirds when we were not on the island using two acoustic recording devices (Song Meter model SM-1 with Firmware v1.6.0, Wildlife Acoustics, Inc., Concord, Massachusetts) to document vocalizations. Although no pre-eruption data exist for comparison, the song meters functioned as indicators of post-eruption species presence, particularly for nocturnal species that we could not detect during daytime surveys. We deployed one song meter at Troll Talus (52.16889°N, 175.52423°W), the site of one of the larger nocturnal seabird colonies on the island before the eruption, and the second at Tundering Talus (52.17870°N, 175.52452°W), the location of the former large least and crested auklet (Aethia pusilla and A. cristatella) colony (see Fig. 2 in Scott et al., 2010 [this issue], for pre- and post-eruption colony locations). Both song meters were deployed on 15 June and retrieved on 10 August (56 recording days) and were programmed to record in 15 minute on/off increments during peak activity periods for nocturnal species (0130-0430 h HAST at Troll Talus) and diurnal species (1330-1500 h HAST at Tundering Talus; Drummond and Larned, 2007). Devices detected all ambient sound out to a distance of about 50 m. Data were summarized as the number of calls by species per 15 minute interval during the sampling period. To identify prospecting and mate advertisement behavior we distinguished between flight and male calls of fork-tailed storm-petrels (Oceanodroma furcata; Simons, 1981) and chirrup and song calls of ancient murrelets (Synthliboramphus antiquus; Jones et al., 1989).

In both pre- and post-eruption periods, population estimates were easier to attain and have higher precision for species that were easily counted. These species include those that were present in low numbers with easily observed nest sites (e.g., raptors, shorebirds, cormorants) or that were restricted to one or a few distinct, easily viewed breeding areas (e.g., sea lions concentrated at the northern rookery, glaucous-winged gulls [Larus glaucescens] nested primarily inside the caldera prior to the eruption). Abundance was more difficult to estimate and has greater uncertainty for species that nested in crevices in high concentrations (e.g., auklets), species with nocturnal colony attendance (e.g., storm-petrels), or species distributed across the entire island (e.g., passerines). Estimates for these species are presented as a range, due to both uncertainty and annual variation in pre-eruption abundance. Petersen (2009) found similar problems with accuracies of population estimates on Surtsey Island off Iceland.

We used differences in pre- and post-eruption population estimates and general knowledge of wildlife behavior on the island to approximate percentage of adult mortality during the eruption. We quantified chick mortality based on the proportion of chicks still remaining in nests at the time of the eruption using timing of breeding data in 2008 and dates of first fledging observations from 1996 to 2008 (Buchheit and Ford, 2008). We identified posteruption breeding attempts as any observation of reproductive behavior (mating displays, mate attraction vocalizations, copulation, or nest building activity) or eggs.

Results

SPECIES RICHNESS AND DIVERSITY

In 2009, we recorded 18 bird (murres [*Uria* spp.] were lumped) and two marine mammal species on or just offshore from the island (Table 1). All were prior confirmed breeders at Kasatochi except black-legged kittiwakes (*Rissa tridactyla*), Cassin's auklets (*Ptychoramphus aleuticus*), and orcas (*Orcinus orca*). Most species were recorded only in June; by August, only storm-petrels, bald eagles (*Haliaeetus leucocephalus*), glaucous-winged gulls, and Steller's sea lions were present.

TABLE 1

Detection of birds and marine mammals during post-e	ruption surveys at Kasatochi Island, Alaska, in 2009.

		Direct Observation Song Meter					
	Ju	ne	Aug	gust	June	July	Augus
	on water	on land	on water	on land			
Birds							
Fork-tailed storm-petrel (Oceanodroma furcata)					Х	Х	Х
Leach's storm-petrel (O. leucorhoa)				Х		Х	Х
Red-faced cormorant (Phalacrocorax urile)	Х						
Pelagic cormorant (P. pelagicus)	Х						
Bald eagle (Haliaeetus leucocephalus)		Х					
Peregrine falcon (Falco peregrinus)		Х					
Glaucous-winged gull (Larus glaucescens)	Х	Х		Х	Х	Х	Х
Black-legged kittiwake (Rissa tridactyla)	Х						
Murre spp. (<i>Uria</i> spp.) ^a	Х						
Pigeon guillemot (Cepphus columba)	Х						
Ancient murrelet (Synthliboramphus antiquus)	Х				Х	Х	
Cassin's auklet (Ptychoramphus aleuticus)	Х						
Parakeet auklet (Aethia psittacula)	Х	Х					
Least auklet (A. pusilla)	Х	Х			Х	X^{b}	
Whiskered auklet (A. pygmaea)	Х				Х	Х	
Crested auklet (A. cristatella)	Х	Х			Х	X^{b}	
Horned puffin (Fratercula corniculata)	Х						
Tufted puffin (F. cirrhata)	Х						
Mammals							
Steller's sea lion (Eumetopias jubatus)	Х	Х	Х	Х			
Orca (Orcinus orca)	Х						

^a Common and thick-billed murres were combined due to difficulty distinguishing between species from a distance.

^b The song meter at Tundering Talus failed on 2 July so presence of least and crested auklets on land after that date is unknown, although they were abundant offshore into later July (Drew et al., 2010 [this issue]).

Before the eruption, between 1996 and 2008, 24 bird and two marine mammal species were confirmed as breeding at Kasatochi in at least one year (Table 2). During the 2008 breeding season when the eruption occurred, red-faced cormorants (*Phalacrocorax urile*), common murres (*U. aalge*), and thick-billed murres (*U. lomvia*) were not breeding on the island. A large number of non-breeding species (31 bird species and seven marine mammal species) were also observed on or just around Kasatochi between 1996 and 2008, ranging from accidental vagrants seen only in some years (e.g., brambling [*Fringilla montifringilla*]) to resident non-breeders present annually (e.g., common raven [*Corvus corax*]). Direct comparisons of non-breeding species before and after the eruption are not appropriate due to large differences in observer effort.

SPECIES ACCOUNTS

Diurnal Crevice-Nesting Auklet Species: Crested, Least, and Parakeet Auklets

Crested, least, and, to a lesser extent, parakeet auklets (*A. psittacula*) were the most abundant birds at Kasatochi following the eruption in 2009 (Table 1). We counted 47,336 crested, 27,932 least, and over 1,000 parakeet auklets on the water within 200 m of the coast during the June circumnavigation survey and estimated an additional 200,000 crested and least auklets socializing on the tephra-covered slopes of the former colony. In addition, outside our skiff-based count area we observed several large flocks at sea that could not be accurately counted. On 18 July, auklets were still abundant offshore (Drew et al., 2010 [this issue]), and a few thousand birds were seen swarming just off the northern shore of the island. No auklets were observed on or around Kasatochi

during mid-August surveys, when birds would have begun leaving the colony in a normal year.

Distribution of all three species in nearshore waters in June was concentrated just offshore from talus slopes, cliffs, and rocky beaches where they had nested before the eruption. On land, auklets landed and socialized on the surface of the former colony sites, and vocalizations of both crested and least auklets were recorded on the song meter at the Tundering Talus colony daily until the device malfunctioned on 2 July. Similar to before the eruption, a small number of auklets was seen flying inside the caldera. Large numbers of auklets also explored, landed, and socialized on inland areas that did not have breeding habitat before the eruption, most notably on the southern portion of the island.

Auklets tried to breed at Kasatochi in 2009, copulating on the water and socializing in pairs and larger groups on the water and the surface of the former colony. Almost all former auklet nesting crevices in talus slopes and beach boulders were entirely covered by tephra many meters thick (Fig. 1), and we found hundreds of broken, non-predated auklet eggs out in the open on the barren surface of the former Tundering Talus colony. In addition, four crested auklet eggs were found by divers in small underwater plots immediately offshore (Jewett et al., 2010 [this issue]), suggesting that auklets also were depositing their eggs in the water.

No new nesting habitat was created by the eruption itself, and little former nesting habitat buried in the eruption had been reexposed by the 2009 breeding season. Throughout extensive land surveys in June, we found just three small potential auklet breeding sites. First, along the northern shore of the island, a small rock pile (4 m \times 4 m) formed by a collapsing cliff contained numerous calling birds, including a single crested auklet incubating an egg near numerous broken eggs. Second, at the top of

				-	;	Direc	Direct Effects	Indirect Effects	Effects
	Population	Population Estimates (individuals)		Post-eruption Breeding Status	reeding Status	Adult	Chick/pup	Breeding	Foraging
Status	Pre-eruption ^a	Post-eruption ^b		Attempted ^c	Successful	Mortality (%)	Mortality (%) ^d	Habitat Loss	Habitat Loss
Successful breeders									
Steller's sea lion (Eumetopias jubatus)	500-700	611	(0)	у	у	0	0	n	some
Unsuccessful breeders									
Fork-tailed storm-petrel (Oceanodroma furcata)	1500 - 2000	present	(;)	у	n	0	100	У	ц
Leach's storm-petrel (O. leucorhoa)	10-20	present	(;)	у	n	0	100	У	n
Glaucous-winged gull (Larus glaucescens)	300-400	200-250	(0)	у	n	some	most	some	some
Ancient murrelet (Synthliboramphus antiquus)	25-50	present	(;)	у	n	0	0	У	n
Parakeet auklet (Aethia psittacula)	1000-2000	1000-2000	(0)	у	n	0	40	У	u
Least auklet (A. pusilla)	100,000-250,000	100,000-250,000	(0)	у	u	0	15	у	u
Whiskered auklet (A. pygmaea)	100 - 200	present	(;)	ż	u	0	0	у	п
Crested auklet (A. cristatella)	100,000-200,000	100,000-200,000	(0)	у	n	0	40	У	ц
Did not attempt to breed									
Peregrine falcon (Falco peregrinus)	10–15	2	(-)	u		0	0	У	some
Bald eagle (Haliaeetus leucocephalus)	2-4	4	(0)	n		0	0	У	some
Red-faced cormorant (Phalacrocorax urile)	up to 80	1	(-)	п		0	100	У	some
Pelagic cormorant (P. pelagicus)	up to 60	5	(-)	n		0	100	у	some
Murre spp. (Uria spp.) ^e	30-40	35	(0)	n	I	0	0	У	u
Pigeon guillemot (Cepphus columba)	100 - 200	100-200	(0)	п		0	most	у	some
Horned puffin (Fratercula corniculata)	250 - 500	35	(-)	n		some	100	У	u
Tufted puffin ($F. cirrhata$)	250-500	50	(-)	n		some	100	у	n
Did not return or not recorded									
Black oystercatcher (Haematopus bachmani)	2–6	0	(-)	u		100	100	У	у
Rock sandpiper (Calidris ptilocnemis)	up to 25	0	(-)	п		100	100	У	у
Winter wren (Troglodytes troglodytes)	50 - 100	0	(-)	n		100	100	у	y
Song sparrow (Melospiza melodia)	50 - 100	0	(-)	п		100	100	У	у
Lapland longspur (Calcarius lapponicus)	200-400	0	(-)	n		100	100	У	у
Snow bunting (Plectrophenax nivalis)	2^{-10}	0	(-)	п		100	100	У	у
Gray-crowned rosy finch (Leucosticte griseonucha)	200-400	0	(-)	n		100	100	у	у
Harbor seal (Phoca vitulina)	2^{-10}	0	(-)	n		0	0	У	some

Effects of the August 2008 eruption on historically breeding birds and marine mammals at Kasatochi Island. List includes all historic confirmed breeders at Kasatochi, 1996–2008; most species bred every

TABLE 2

1 eruption estimates.

^c Breeding attempt defined as presence of reproductive behavior (e.g., mating displays, mate attraction vocalizations, copulation, nest building activity) or eggs. For nocturnal species, question marks indicate vocalizing birds were heard throughout breeding season on song meters but breeding attempts could not be confirmed.

^d Estimates of chick mortality are based on the percent of chicks still remaining in nests at the time of eruption from timing of breeding data in 2008 and dates of first fledgling observations, 1996–2008 (Buchheit and Ford, 2008).

^e Includes both common (U. aalge) and thick-billed murres (U. lomvia).



FIGURE 1. Auklets on the colony surface at Kasatochi Island (a) before (June 2004; photo by Brie Drummond) and (b) after the 2008 eruption (June 2009; photo by Gary Drew). Photos taken from approximately the same location.

Tundering Talus, a single crevice showed visible evidence of auklet use (feathers, claw-marks in debris) and contained numerous arthropods normally associated with auklets (Sikes and Slowik, 2010 [this issue]). Finally, at the base of Tundering Talus, wavewashed boulders were explored continuously by prospecting birds. By August, no sites showed evidence of successful breeding, and the small rock pile had been destroyed by erosion.

Nocturnal Crevice- and Burrow-Nesting Seabird Species: Fork-Tailed and Leach's Storm-Petrels, Ancient Murrelets, and Cassin's and Whiskered Auklets

Of nocturnal species that bred at Kasatochi before the eruption, we saw only four ancient murrelets and one Leach's storm-petrel (*O. leucorhoa*) during land-based and circumnavigation surveys. We heard hundreds of whiskered auklets (*A. pygmaea*) calling from offshore on the morning of 12 June but saw none during daytime surveys. Interestingly, just offshore in

June we counted 3573 Cassin's auklets, a nocturnal species that had rarely been seen at Kasatochi prior to the eruption and was not known to breed there.

On the island, all former breeding habitat for nocturnal species (rock crevices or soil for burrowing) was buried under the thick layer of tephra, and no visual evidence of nest digging or egg laying was found. The song meter at the former Troll Talus breeding colony, however, recorded the nocturnal presence of all four species that historically had nested there (fork-tailed and Leach's storm-petrels, ancient murrelets, and whiskered auklets). Fork-tailed storm-petrels were heard most frequently, with 500–1400 flight and male calls recorded nightly between 16 June and 11 August, when the song meter was retrieved. This high level of activity was comparable, and on some nights surpassed, the number of calls heard at the undisturbed storm-petrel colony at Buldir Island in the western Aleutian Islands (R. Buxton, unpublished data). High levels of ancient murrelet chirrup and song calls were also recorded every night until 25 July. Whiskered

auklets calls were recorded until 29 July at lower levels, with the most activity towards the end of each nightly recording period (0400–0415 h HAST). Leach's storm-petrel chuckle calls were recorded only 14 times throughout the season (on 3, 18, 26–29 July and 1 August). No chick calls of any nocturnal species were recorded.

Other Crevice- and Cliff-Nesting Species: Puffins, Cormorants, Pigeon Guillemots, Murres, and Raptors

We saw over 100 pigeon guillemots (*Cepphus columba*) in nearshore waters in June but counted only a few puffins, cormorants, murres, bald eagles, and peregrine falcons (*Falco peregrinus*) on or around the island (Tables 1 and 2). On 18 July, 50 tufted puffins (*Fratercula cirrhata*) were counted on a cliff on the northern side of the island. Much of the former cliff- and crack-nesting habitat was still buried under tephra in 2009, and we found no evidence of nesting attempts for any of these species.

Ground-Nesting Species: Gulls, Shorebirds, and Passerines

We recorded no black oystercatchers (Haematopus bachmani), rock sandpipers (Calidris ptilocnemis), or passerines on any of our post-eruption visits. Glaucous-winged gulls, in contrast, were seen at Kasatochi just two weeks after the eruption, when the island was still steaming. In June 2009, we counted approximately 150 gulls on land and in nearshore waters (Tables 1 and 2), including at least 100 birds on the walls and slopes inside the caldera where they formerly nested. Their distribution was generally similar to that before the eruption, although we also observed many birds loafing and bathing at a new small pond formed on the southern debris fan. As opportunistic foragers, gulls benefited early in the season from easy predation on auklets, preying heavily on disoriented adult birds that no longer had safe nesting crevices and on the eggs they scattered futilely across the island surface. Once the auklets left the island, gull foraging would have been limited, in that the rich intertidal areas they had exploited before the eruption had been destroyed. By August, only 18 gulls were counted around the island.

We encountered four gull nests (containing 0, 0, 2, and 3 eggs) outside of the caldera in June. Nests were constructed of dead *Leymus* grass, seaweed, or dead *Sphagnum* moss, which must have been scrounged from the few pieces of dead vegetation exposed by eroding tephra. In August, all nests were abandoned and covered with erosional debris, and no fledglings were recorded.

Marine Mammals

Just two weeks after the 2008 eruption, over 100 Steller's sea lions were hauled out on newly created sandy beaches on the southern side of the island. Similarly, in 2009, we saw sea lions on land and in nearshore waters in both June and August (Table 1). An aerial survey conducted by National Marine Mammal Laboratory personnel on 4 July 2009 photographed 611 adult and subadult sea lions and 394 pups. Although the former rookery on a sloping rocky outcrop on the northern portion of the island had been completely covered by 30 m of tephra in August 2008, wave action had eroded the coastline by spring, and the rookery site was re-exposed for the 2009 breeding season. We encountered no harbor seals during post-eruption surveys but observed two orcas in June 2009 off the northeastern coast of the island, an area where they had been observed occasionally prior to the eruption.

Discussion

The eruption of Kasatochi volcano in 2008 had significant effects, both direct and indirect, on local marine wildlife. Set in a broader context, however, this disturbance event took place within the volcanically active Aleutian Islands ecosystem and is illustrative of the type of disturbance that wildlife in the region have responded to for millennia (Byrd et al., 1980). Our surveys one year after the eruption suggest that wildlife was affected by and responded to the eruption in different ways based on differences in life-history traits and habitat requirements.

DIRECT EFFECTS

Direct effects of the eruption on wildlife at Kasatochi consisted of mortality to both adults and young. Our posteruption population estimates for most seabird and marine mammal species were similar to those before the eruption (Table 2), suggesting that most adults survived the eruption. Such low adult mortality during the eruption itself was probably due to several factors. First, the eruption took place in August, after or toward the end of the breeding season for most species (Drummond and Larned, 2007), when colony attendance was becoming irregular and most adults were not tied strongly to nests. Second, the eruption occurred during the day, when most nocturnal storm-petrel adults, who were all still attending nest sites, were away from the island on foraging trips. Finally, the eruption consisted of multiple eruptive events, with the first two poor in ash but high in gas emission and later events producing the significant pyroclastic surge and flow material that blanketed the island (Scott et al., 2010 [this issue]). This eruption pattern could have allowed adults that could fly or swim away the time to escape the island before the third, more massive, eruption occurred. There undoubtedly was some minor amount of incidental mortality, in that a small number of birds still attending nests in crevices were likely entombed during the many earthquakes and landslides leading up to the first eruption. In addition, glaucouswinged gulls and horned (Fratercula corniculata) and tufted puffins probably suffered higher mortality than other species, gulls because they nested inside the caldera at the eruption's epicenter, and puffins because they breed later than other seabird species and would have been incubating eggs or brooding small chicks at that time. Indeed, post-eruption population estimates for both puffin species were lower than those before the eruption (Table 2). On the whole, however, direct adult mortality appeared minimal for most seabirds and marine mammals.

Despite relatively few visits to Kasatochi in 2009, our observations probably documented accurately the presence of formerly breeding species that returned to Kasatochi after the eruption due to the small size of the island and our extensive familiarity with pre-eruption species distribution. Post-eruption population estimates, however, may have been inflated by an influx of additional birds in 2009. In many seabird populations, nesting habitat is limited and a large pool of non-breeders exists to fill sites as they become available (e.g., Porter and Coulson, 1987; Klomp and Furness, 1992). If these non-breeders returned to Kasatochi in 2009 and replaced breeding birds that perished in the eruption, we would not have detected a change in population size. In addition, an explosion of food resources can attract predators from surrounding areas (Sherrod et al., 1976). The superabundance of auklet eggs and disoriented birds at Kasatochi in 2009 could have brought in additional gulls from nearby islands. Both effects could have caused us to underestimate adult seabird mortality.

In contrast to seabirds, many land birds almost certainly suffered high adult mortality. We failed to find a single passerine or shorebird during all surveys in 2009, despite large pre-eruption breeding populations (Table 2). This absence suggests these birds may have perished in the eruption, similar to resident song birds in the Mt. St. Helens eruption of 1980 (Andersen and MacMahon, 1986; Manuwal et al., 1987; Crissafulli et al., 2005). At Kasatochi, this mortality probably occurred because passerines and shorebirds, more strongly tied to the terrestrial environment than marine birds and mammals, did not fly away during the eruption. Many of these species were non-migratory (Gibson and Byrd, 2007), and those that do disperse at the end of the season, such as Lapland longspurs (Calcarius lapponicus) and black oystercatchers, still would have been raising young at the time of the eruption (Drummond and Larned, 2007). It is also possible that some surviving or newly prospecting birds visited the island early in the breeding season and quickly departed prior to our arrival after finding no available habitat. Interestingly, although numbers of bald eagles were comparable to those before the eruption, we saw few peregrine falcons at Kasatochi in 2009. The reason for this decline is unclear, as we would expect falcons to escape the eruption, and high fidelity to nest sites (White et al., 1971) and abundant auklet prey in 2009 should have brought the birds back to the island.

Chick mortality was a major direct effect of the Kasatochi eruption for both seabird and land bird species. At the time of the eruption in early August, all storm-petrel, cormorant, and puffin chicks, most pigeon guillemot chicks, and many crested, least, and parakeet auklet chicks would have been too young to leave the nest (Drummond and Larned, 2007; Buchheit and Ford, 2008) and, therefore, perished (Table 2). Most glaucous-winged gull chicks were incapable of flight at that time (Drummond and Larned, 2007) and given most nests were inside the caldera, probably died (Table 2). Finally, except for fledgling bald eagles and peregrine falcons, young of most land birds were either too small for long flights when the eruption occurred (e.g., black oystercatchers) or unlikely to disperse (e.g., non-migratory passerines). Based on preeruption population estimates (Table 2), average reproductive performance at Kasatochi (Drummond and Larned, 2007) or nearby sites (e.g., Ewins, 1993; Hejl et al., 2002), and projections of eruption-induced chick mortality (Table 2), we estimate that approximately 20,000 to 40,000 chicks died during the eruption.

INDIRECT EFFECTS

Indirect effects of the Kasatochi eruption on wildlife consisted primarily of the loss of breeding and foraging habitat. The near-complete loss of almost all types of breeding habitat following the eruption had a substantial impact on post-eruption nesting attempts and success of species that formerly bred on the island (Table 2). Much of the wildlife at Kasatochi is strongly marine in character and used the island primarily as a nesting location. Almost all the former breeding sites were destroyed when the eruption covered the island in up to 30 m of ash (Scott et al., 2010 [this issue]). Steller's sea lions were the only species for which substantial re-exposure of breeding habitat occurred by 2009 and, as such, the only species to breed successfully at Kasatochi one year after the eruption.

Loss of foraging habitat following the eruption also impacted a number of species at Kasatochi (Table 2), although to a lesser extent than loss of breeding habitat. Most marine birds at Kasatochi are fully dependent on the offshore marine environment away from the island for food (Drew et al., 2003, 2010 [this issue]; Dragoo, 2007), so their foraging grounds were probably minimally affected by the eruption. The island's interior, beaches, and nearshore kelp community out to about the 20 m isobaths, however, were buried under extensive debris (Jewett et al., 2010 [this issue]; Scott et al., 2010 [this issue]). Therefore, species that foraged in terrestrial vegetation or intertidal and nearshore-subtidal areas were impacted (Table 2), with the degree of impact depending on the flexibility of their foraging strategies. For instance, black oystercatchers forage primarily in the intertidal zone (Andres and Falxa, 1995) and, thus, would have suffered a complete loss of foraging habitat. Glaucous-winged gulls, in contrast, historically fed on a mix of intertidal invertebrates and auklets at Kasatochi (Drummond and Larned, 2007) and were able to shift and feed exclusively on auklets and eggs for part of the 2009 breeding season.

POST-ERUPTION RESPONSE OF WILDLIFE

As indicated, many breeding species survived the 2008 eruption and returned to the island in comparable numbers, either immediately following the eruption (gulls and sea lions) or for the 2009 breeding season (most other species; Table 2). Individuals generally exhibited strong site fidelity, returning to former breeding locations and distributing themselves in nearshore waters in similar patterns as before the eruption. With the exception of sea lions, most species were unable to access their previous breeding sites and, despite various attempts to reproduce, were not successful. Eventually, most birds abandoned breeding attempts and left the island; by August 2009, only sea lions and a few bird species remained (Table 1).

Specific responses of different species varied depending on life-history traits and availability of habitat. We categorized four different response levels (see Table 2). (1) Successful breeders. Steller's sea lions were the only species to return after the eruption and find their breeding habitat comparable to pre-eruption conditions. During the winter, the tephra debris fan that had originally covered the sea lion rookery to a depth of 30 m and extended hundreds of meters offshore had eroded away by wave action. With their breeding habitat re-exposed, their foraging habitat not completely destroyed, and low direct adult mortality from the eruption, sea lions bred successfully in 2009 with numbers of pups higher than in recent years (National Marine Fisheries Service, unpublished data). (2) Unsuccessful breeders. These species made some attempt to breed, with various levels of effort. Ancient murrelets and storm-petrels returned to former colony sites throughout the duration of what would have been their normal breeding season and were recorded advertising for potential mates, but did not appear to lay eggs or have chicks. Crested, least, and parakeet auklets exhibited ritualized pair behavior and copulated successfully but, with almost no nest sites available, they simply dropped eggs in the water and on the barren surface of their previous colonies, similar to observations at St. Lawrence Island when crevices were buried under deep snow (Sealy, 1975). Glaucous-winged gulls built a small number of nests and laid and incubated eggs, but all eventually failed. (3) Did not attempt to breed. These species, including raptors and several seabird species, were seen only offshore or were non-territorial when on land, showing no indication of any breeding attempts. Given the abundance of readily available auklet prey in 2009, the failure of bald eagles and peregrine falcons to attempt to breed at Kasatochi after the eruption is particularly surprising and may be because of lack of suitable nest sites. (4) Did not return. These species, including passerines and shorebirds, either did not return to the island or presumably died in the eruption.

THE FUTURE FOR WILDLIFE ON KASATOCHI

The future for wildlife at Kasatochi depends on when and how much breeding habitat becomes available and the return of former breeders. Although highly marine in nature for much of the year, seabirds and marine mammals at Kasatochi need the terrestrial environment for breeding sites and will be unable to re-establish on the island without it. Steller's sea lions have already re-established successfully with the exposure of their breeding habitat, but seabird species require further erosion of the thick tephra layer covering the island's surface to re-expose potential nest sites. Since the eruption, Kasatochi has been undergoing a continual secondary disturbance of erosion that eventually will expose former habitat, as the ocean removes unconsolidated debris material and exposes rocky coastline while precipitation and wind erode the island's surface (Scott et al., 2010 [this issue]). The speed at which this erosion continues will determine the rate at which seabird populations can re-establish. With timely reexposure of breeding habitat, recovery could occur quickly because Aleutian wildlife is adapted to rapid exploitation of newly available habitat in their geologically active environment. At Kiska Island, for example, crested and least auklets colonized a new lava flow and numbered in the millions just 10 years after the eruption (Day et al., 1979; Major et al., 2006). Seabird populations at Bogoslof Island responded similarly to changes in nesting habitat following eruptive events (Byrd et al., 1980). Given that seabirds are generally long-lived and faithful to breeding sites, it is likely that former breeders will continue to return to Kasatochi in the near future, ready to use habitat as soon as it becomes available. Over time, if erosion is slow and nest sites do not reappear, the birds which survived the eruption will either move to other colonies, establish a new colony elsewhere, or perish.

The recovery of species that were killed in the eruption and that rely on the terrestrial environment for foraging and breeding will likely be much slower to re-establish populations (Petersen, 2009). Recolonization of passerines and shorebirds will depend on the recovery of terrestrial plant and intertidal communities and new birds arriving from nearby islands. On tiny Bogoslof Island, early-successional-stage vegetation took nearly 50 years to become abundant and widely dispersed (Byrd et al., 1980) and it may take longer on the larger island of Kasatochi (Petersen, 2009; Talbot et al., 2010 [this issue]).

The recolonization of wildlife at Kasatochi will influence, in turn, the future pace and pattern of recovery and ecological succession of the greater terrestrial ecosystem on the island (Crissafulli et al., 2005). Much of the surviving biota, or biological legacy, is comprised of marine birds, which are effective vectors for transport of marine-derived nutrients (Stempniewicz, 1990; Maron et al., 2006) and plant material (Magnusson and Magnusson, 2000) to the terrestrial system. Therefore, seabirds can strongly affect the other land-based communities around their colonies (Petersen, 2009; Sigurdsson and Magnusson, 2009) and, thus, the recovery of breeding seabird colonies at Kasatochi could accelerate and shape the recovery of other island biota.

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