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Research Papers

Reproductive Consequences of Nest Site Use in Fork-tailed Storm-Petrels in the Aleutian Islands, Alaska: Potential Lasting Effects of an Introduced Predator

Conséquences de l'utilisation des sites de nidification sur la reproduction de l'Océanite à queue fourchue dans les îles Aléoutiennes, Alaska : effets potentiels à long terme d'un prédateur introduit

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ABSTRACT. We examined the reproductive consequences of differential nest site use in Fork-tailed Storm-Petrels (*Oceanodroma furcata*) in the Aleutian Islands, Alaska, where birds on islands where foxes were introduced nest in rocky substrate rather than in typical soil habitat. We investigated how physical and microclimatic nest site characteristics influenced storm-petrel breeding success 20 years after fox removal. We then examined whether those nest site characteristics that affected success were related to the amount of rock that composed the nest. In both years of our study, nest temperature had the strongest influence on chick survival and overall reproductive success, appearing in all the top models and alone explaining 14–35% of the variation in chick survival. The relationship between reproductive success and nest temperature was positive in both years, with higher survival in warmer nests. In turn, the best predictor of nest temperature was the amount of rock that composed the site. Rockier nests had colder average temperatures, which were driven by lower daily minimum temperatures, compared to nests with more soil. Thus, the rockiness of the nest site appeared to affect chick survival and overall reproductive success through its influence on nest temperature. This study suggests that the use of rocky nest sites, presumed to be a result of historic predation from introduced foxes, could decrease breeding success in this recovering population, and thus be a long-lasting effect of introduced predators.

RÉSUMÉ. Notre étude visait à examiner les conséquences de l'utilisation de sites de nidification différents par l'Océanite à queue fourchue (*Oceanodroma furcata*) dans les îles Aléoutiennes (Alaska), lieu où le renard a été introduit et où les oiseaux qui y vivent nichent dans des substrats rocheux plutôt que dans le substrat terreux habituel. Nous avons donc étudié dans quelle mesure les caractéristiques physiques et microclimatiques des sites de nidification ont influencé le succès de reproduction des Océanites, vingt ans après l'extermination des renards. Ensuite, nous avons cherché à vérifier si les caractéristiques des sites ayant des répercussions sur le succès de reproduction étaient reliées à la quantité de substrat rocheux qui composait le nid. Durant les deux années de l'étude, la température du nid représentait le facteur le plus important ayant une incidence sur la survie des oisillons et le succès global de reproduction. Il s'agissait d'un facteur récurrent des meilleurs modèles qui, à lui seul, expliquait 14 à 35% de la variation du taux de survie des oisillons. La relation entre le succès de reproduction et la température des nids était positive durant les deux années de l'étude, le taux de survie étant plus élevé dans les nids les plus chauds. Par ailleurs, le meilleur paramètre de prévision de la température du nid était la quantité de substrat rocheux qui composait le site. Comparativement aux nids composés principalement de substrats terreux, les nids contenant une plus grande quantité de substrats rocheux avaient des températures moyennes inférieures à cause des températures minimales quotidiennes plus faibles. Par conséquent, la roccosité du site de

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nidification semble avoir une incidence sur la survie des oisillons et le succès global de reproduction puisque cette caractéristique a une influence sur la température du nid. Cette étude suggère que l'utilisation des sites de nidification composés de substrat rocheux - probablement le résultat de la prédation historique par le renard - pourrait diminuer le succès de reproduction chez cette population en voie de rétablissement et représenter un effet à long terme des prédateurs introduits.

Key Words: *Aleutian Islands; breeding success; chick survival; habitat; introduced predator; Oceanodroma furcata; nest site characteristics; nest temperature; reproductive success; storm-petrel*

INTRODUCTION

The introduction of exotic species is one of the greatest causes of ecological change and loss of biodiversity around the world (Vitousek et al. 1997). Island ecosystems are exceptionally susceptible to disturbance by alien species (e.g., Chapuis et al. 1994, Blackburn et al. 2004) because they generally have low diversity and simplified food webs, and they contain a large number of endemic species with no co-evolved adaptations to invaders (Vitousek 1988, Courchamp et al. 2003). Introduced mammalian predators pose a particular threat to island-nesting seabirds, which generally evolved on islands without mammalian predators and thus lack effective anti-predator defenses (Moors and Atkinson 1984).

While direct mortality is the primary threat of introduced predators to insular island fauna, there is growing evidence that alien predators can exert a cascade of indirect effects on island ecosystems. For example, by altering food web dynamics, introduced predators can also impact soil nutrients, below- and above-ground invertebrate communities, and island vegetation, which can cause lasting changes to community structures and ecosystem processes (e.g., Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006, Kurle et al. 2008, Towns et al. 2009). Such indirect effects can persist long after predators are removed (e.g., Croll et al. 2005) and may help explain why some island populations do not recover immediately following predator eradication programs (Courchamp et al. 2003).

Fork-tailed Storm-Petrels (*Oceanodroma furcata*) are colonial, burrow-nesting seabirds that typically nest in soil habitat on islands in the Aleutian Islands, Alaska that are free from mammalian predators (Murie 1959, Gibson and Byrd 2007). On a small number of Aleutian Islands, however, this species nests in rock habitat, and uses crevices in talus slides, lava deposits, and rock cliffs, despite the extensive availability of soil habitat (Gabrielson and Lincoln 1959, Drummond and Larned 2007, Gibson and Byrd 2007). The use of this atypical nesting habitat is assumed to be a result of the introduction of arctic foxes (*Vulpes lagopus*) to the islands during the nineteenth and twentieth centuries (Bailey 1993). Before foxes were introduced, burrow-nesting seabirds, including storm-petrels, nested in soil habitat on these islands (Murie 1959). Following fox introductions and decades of subsequent predation, birds were found instead in rocky nesting substrate (Drummond and Larned 2007, Gibson and Byrd 2007), which presumably provides better protection from mammalian predators than does soil habitat (Quinlan 1983). When foxes have been removed and the protection gained from rocky nests is no longer a benefit, storm-petrels continue to use rock habitat for decades (Drummond and Larned 2007, Gibson and Byrd 2007), likely because of strong philopatry, nest site fidelity, and conspecific attraction (Boersma and Silva 2001, Igual et al. 2007). Consequently, current patterns of rock and soil nest site use by storm-petrels across the Aleutian Islands correspond to the historic presence or absence of introduced foxes; major rock- and soil-nesting colonies do not co-exist on the same islands (Gibson and Byrd 2007; G. V. Byrd, *personal communication*).

Given that characteristics of the nest site often influence reproductive success in birds (e.g., Stokes and Boersma 1998, Rowe and Jones 2000), we hypothesized that differential habitat use due to past fox predation in the Aleutian Islands could have consequences for storm-petrels. We predicted that the continued use of rock habitat decades after fox removal could have negative effects on reproductive success. Our goal was to test this prediction by examining how characteristics of rocky nest sites affected storm-petrel reproductive success in the absence of predators. We examined how physical and microclimatic features of the nest site affected reproductive success on an island where introduced foxes had been removed two decades earlier and storm-petrels continued to use rock habitat. We then investigated whether those nest site features associated with reproductive success were related to the amount of rock that composed the nest. If the use of rocky nest sites in the Aleutian Islands is indeed due to historic fox predation, as the evidence suggests, then reproductive consequences of nesting in rock habitat after foxes have been removed may represent a lasting indirect effect of these introduced predators.

METHODS

Study area

This study was conducted primarily at Kasatochi Island (52º11' N, 175º30' W), located within the Alaska Maritime National Wildlife Refuge in the central Aleutian Islands, Alaska. Field work was conducted from 25 May to 23 August 2005 and from 21 May to 1 September 2006. The island is composed of grassy slopes interspersed with rock falls and talus areas, which provides potential soil and rock habitat for thousands of nesting seabirds (Scharf et al. 1996). Introduced arctic foxes were present between 1927 and 1985 (Bailey 1993). There were no mammalian predators on the island prior to the fox introductions and there have been none since the foxes were removed. Biological surveys of Kasatochi Insland in the 1930s, soon after foxes were introduced, documented burrow-nesting seabirds using soil burrows in the grassy slopes on the island (Murie 1959). At present, however, four years of intensive island-wide surveys have indicated that storm-petrels and other formerly burrow-nesting species on Kasatochi Island nest only in habitat that has some rocky substrate despite the presence of extensive soil habitat around the island. None of the historic soil burrows previously documented on the island remain (B. A. Drummond, *personal observation*).

The current breeding population of Fork-tailed Storm-Petrels on Kasatochi Island is estimated at about 2000 birds. The birds are concentrated in a patch of rock habitat on the western side of the island (Fig. 1a), where they nest in cracks in cliffs, crevices formed by rock piles, and spaces underneath boulders (Drummond 2007). Hundreds of Glaucous-winged Gulls (*Larus glaucescens*) and several pairs of Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*) breed on the site but do not appear able to access storm-petrel nests (B. A. Drummond, *personal observation*), nor do they prey heavily on adults at the colony (Drummond and Larned 2007).

We also collected limited temperature data in a small number of nests at Ulak Island (52º02' N, 175º54' W), 46 km west of Kasatochi, where storm-petrels nest entirely in soil habitat (Drummond 2007). Although comparisons of nest temperatures between the rockier nests of Kasatochi Island and the soil nests of Ulak Island are constrained by potential island effects, both islands share the same climate and, because of their proximity, are exposed to the same weather conditions (U.S. Fish and Wildlife Service [USFWS], *unpublished data*).

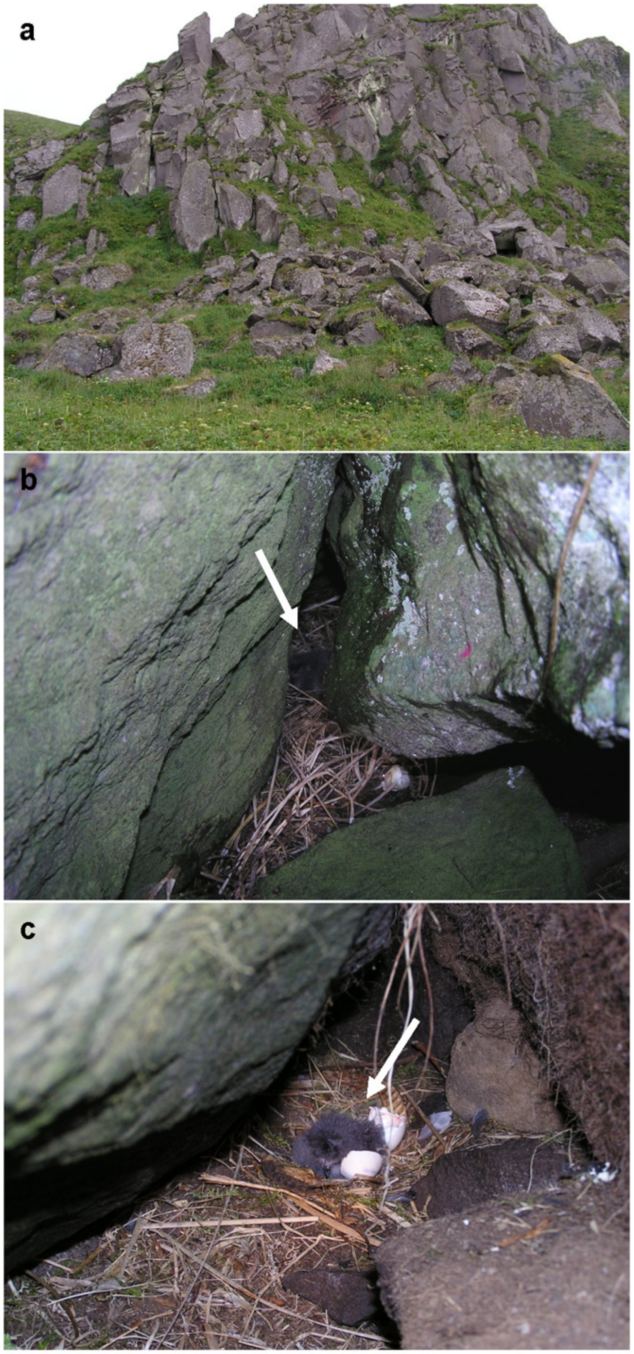
Study species

Fork-tailed Storm-Petrels breed in dense colonies on islands in the North Pacific during the spring and summer. Birds are highly colonial and have strong fidelity to the nest site and natal site (Boersma and Silva 2001). The breeding period is prolonged by episodes of egg neglect (Boersma et al. 1980, Simons 1981) and slow chick growth (Boersma et al. 1980), and thus, lasts up to four months. Females lay a single egg, and both sexes participate in incubation and chick rearing. Chicks are brooded for about five days (Boersma et al. 1980), after which time they can thermoregulate (Wheelwright and Boersma 1979). Adults return to the nest only briefly every one to four nights to deliver food (Simons 1981). Chicks fledge after about two months (Boersma et al. 1980).

Reproductive success

We determined reproductive success by monitoring nests throughout the breeding season. Nests were selected based on whether the nest cavity could be viewed from the exterior of the crevice by flashlight (n = 79 in 2005; n = 103 in 2006). Limiting nests to only those we could observe without destructive sampling (estimated 10% of population; Drummond 2007) will have biased our sample towards the more exposed nests (possibly with the less experienced

Fig. 1. (a) Rock nesting habitat used by Fork-tailed Storm-Petrels (*Oceanodroma furcata*) on Kasatochi Island, Alaska. Nest sites vary from (b) nests made entirely of rock (here, nest material covers solid rock substrate), to (c) nests made up of a mix of rock and soil (here, soil composes substrate, right side, and part of roof; quantified as 40% rock). Arrows indicate location of chicks.



breeders) in the population. We considered this a necessary limitation, however, given that storm-petrels are very sensitive to investigator disturbance (Morse and Buchheister 1979, Boersma et al. 1980, Marks and Leasure 1992). This bias would have applied to all of the nests at our site, and so should not confound relationships between reproductive success and the nest site across our sample of accessible nests.

To minimize disturbance to incubating adults, we checked nests once in late May to determine nest status and then not again until close to the predicted hatch in mid June. Once chicks hatched, we visited nests every two days until the nest failed or the chick fledged. Hatching success was determined by either egg failure (abandoned, ejected, or broken eggs) or hatch (chick observed). Chick survival was determined by either chick failure (chicks that died or disappeared from the nest at less than 50 days) or fledging (chicks that were missing from the nest at a minimum of 50 days old). Overall reproductive success was determined by overall nest failure (egg or chick failure) or success. In the cases when we left the island while the chick was still in the nest (n = 14 in 2005, n = 44 in 2006), we considered that chicks at those nests were successful if they were at least 40 days old and apparently healthy at our departure (n = 11 in 2005; n = 40 in 2006). This assumption was based on patterns of chick mortality in Fork-tailed Storm-Petrels, in which mortality occurs almost entirely in chicks younger than 20 days (Boersma et al. 1980). In our study, only a single chick in each year died after the age of 20 days and none died after the age of 40 days (Drummond and Leonard 2009). The few chicks that were less than 40 days old at our departure (n = 3 in 2005, n = 4 in 2006) were not assigned a reproductive fate and were omitted from analyses of chick survival and overall reproductive success.

Physical and microclimatic nest site characteristics

Because storm-petrels generally select burrows or crevices both for protection from predation (e.g., Quinlan 1983, Warham 1990) and for a stable, favorable nest environment (e.g., Grimmer 1980, Boersma 1986, Warham 1990), we expected that following the removal of all predators, any effects of rock habitat on storm-petrel reproductive success would be due to indirect influences of physical or microclimatic characteristics that affected the quality of the nest environment (e.g., stability, exposure, internal environment). Therefore, to examine how characteristics of rocky nest sites influenced storm-petrel breeding success, we measured a number of physical and microclimatic features at each nest. We chose the following 11 physical variables that described the size, orientation, and vegetation of each nest: entrance volume (ENTV: the product of entrance height, width, and length measurements), chamber depth (DEP), vertical nest angle (ANGV), horizontal nest angle (ANGH), slope (SLP), aspect (ASP), mean rock size (MRS: the size class of rocks that composed the nest, categorized as 0–50 cm, 50–100 cm, 100–200 cm, and >200 cm), nest material (NMAT: the amount of vegetation lining the nest cup, categorized as small [bare substrate to a few pieces of vegetation but not enough to fully cover bottom], medium [enough vegetation to fully line the nest cup], and large [vegetation that overflowed the nest cup]), height above sea level (HASL), percent vegetative cover (VEGC), and mean vegetative height (VEGH: mean height of vegetation at six randomly-determined points within a quadrat). We used a Silva compass with a clinometer to measure all angles, a Garmin map76S GPS (Olathe, Kansas, USA) to measure height above sea level, and a 0.5-m quadrat centered on the nest entrance to measure vegetative variables.

We measured microclimatic conditions inside nests by recording internal air temperature and relative humidity using an Extech Hygro-Thermometer (Extech Instruments, Waltham, Massachusetts, USA). For consistency and to prevent the body temperature of the chick from influencing the data, measurements were made at a standardized distance of 9 cm from the edge of each nest cup. We took measurements every two days between 1500 and 1900 h HAST (median 1612 h) and calculated mean and range values of temperature (TEMP and TEMPR) and relative humidity (RH and RHR) for each nest throughout the season. We varied the order of nest measurements randomly each day, did not take measurements when adults were present to minimize disturbance, and did not record humidity on stormy days (n = 4 in 2005; n = 2 in 2006).

In 2006, we also gathered more detailed measurements of daily temperature extremes and fluctuations in nests on Kasatochi Island (n = 82) and in a small sample of nests composed entirely of soil on neighboring Ulak Island (n = 15) using DS1922L iButton temperature loggers (Maxim

Integrated Products/Dallas Superconductor, Sunnyvale, California, USA). Loggers were programmed to record temperature at 1-hr intervals and were placed 9 cm from the side of the nest cup. We downloaded data using ExpressThermo software (Eclo, Portugal) and calculated the average daily mean, minimum, and maximum temperatures and daily temperature range (difference between daily maximum and minimum) for each nest. To account for potential differences in ambient conditions between the two islands, we measured air temperature at 15-minute intervals on each island using StowAway TidbiT temperature loggers (Onset, Bourne, Massachusetts, USA) positioned in the open on the surface at the center of each colony.

Parental characteristics

Given that differences in parental quality can affect reproductive success independently of the nest site (Ramos et al. 1997), we attempted to account for variation in parental quality. We measured three variables that may influence reproductive success in Fork-tailed Storm-Petrels: egg volume, feeding rate, and brooding duration (Boersma et al. 1980, Boersma 1986). To determine egg volume (EGGV), we measured width and length of eggs to the nearest 0.1 mm and calculated volume as $V = 0.51LW^2$, where L is length and W is width (Hoyt 1979). To reduce disturbance to incubating adults, eggs were measured later in the incubation period in mid June and, whenever possible, on days when an adult was not present. Potential bias against nests that failed earlier in incubation was low given that only a single egg (out of a total of 182 nests during both years) was lost before egg measurements were taken.

To estimate feeding rates, we quantified parental visitation rate (VIS) using toothpick knockdowns (Quinlan 1979). Toothpicks were placed across nest entrances in the evening and were checked the following morning; if they were knocked down during this time, it indicated that the nest had been visited that night by a parent carrying food. We calculated visitation rate as the percent of nights a nest was visited between the day brooding ended and the day the chick fledged or died. We consider this measure of feeding rate to be conservative because it does not record incidents of two parental visits in a single night (occurred 30% of nights in a single observed pair; Simons 1981) and because older chicks close to fledging age may knock down toothpicks when wandering near the nest entrance. We did not, however, expect this error to be biased across nests with varying amounts of rock. At nests we monitored, we could not quantify individual meal size or prey type, which could also reflect parental quality (e.g., Granadeiro et al. 2000, Wanless et al. 2005).

We measured brooding duration (BRD) in 2006 using a second set of iButton temperature loggers that recorded temperature at 5-min intervals between hatching and the end of brooding. We pressed loggers into the substrate at the edge of the nest cup so that a brooding adult would contact the logger. We assumed that temperature would increase when parents were brooding and would decrease when parents left the nest (Pefaur 1974). Given that adults return to and leave from the nest only at night (Simons 1981), we used temperature increases or decreases of at least 1°C that occurred at night and persisted through the following day to identify attendance by brooding adults. To determine that recorded temperature changes were due to adult attendance and not chick interference, we checked if adult birds were on the nest during scheduled bi-daily nest checks to corroborate temperature data. Brooding duration at each nest was defined as the total number of days adults brooded a chick.

Rockiness of the nest site

To explore whether nest site characteristics that influence breeding success were directly related to the rockiness of the nest site, we quantified the relative amount of rock that composed each nest (ROCK). Within rock habitat, individual nest sites ranged in composition, with some made entirely of rock while others had various amounts of soil in the walls, substrate, or ceiling (Fig. 1b and 1c). We used a flashlight to visually estimate, in 10% increments, the percentage of the nest site (including the entrance, tunnel, and chamber) that was composed of rock (as opposed to soil). To maintain consistency, the same person conducted estimates in both years, and we used nests from the first year as a standard against which to estimate rockiness of new nests in the second year.

Statistical analysis

We analyzed each year separately rather than include year as a variable in our models because the sample of nests used in our study was neither entirely independent nor identical between years. Not all nests were reused between years (26 nests were used in 2005 only, 50 nests in 2006 only, and 53 nests in both years), but reused sites were likely occupied by the same pair in both years (Boersma and Silva 2001, Drummond 2007). In addition, not all data exist for both years because brooding data and more detailed temperature data from iButtons were collected in 2006 only. Therefore, models with brooding duration as a potential factor, for example, could be evaluated only for 2006 data.

We used an information-theoretic approach to model selection to evaluate factors that influenced reproductive success of Fork-tailed Storm-Petrels. The physical characteristics (ENTV, DEP, ANGV, ANGH, SLP, ASP, MRS, NMAT, HASL, VEGC, VEGH), microclimatic characteristics (TEMP, TEMPR, RH, RHR), and parental characteristics (EGGV, VIS, BRD) measured at nest sites were used as explanatory variables in logistic regression models of hatching success, chick survival, and overall reproductive success in each year. The candidate model set for each measure of success included all additive combinations of explanatory variables and a null model. Visitation rate and brooding duration were excluded from models of hatching success because those variables could be measured only for eggs that hatched. Brooding duration was included only in models for 2006 because data did not exist for 2005.

Following Burnham and Anderson (2002), we calculated Akaike's information criterion for small sample sizes (AIC_c) for each candidate model, as well as the difference in AIC_c between each model and the model with the lowest AIC_c score (ΔAIC_c). For each success parameter in each year, the model with the lowest AIC_c value was considered to be the best fitting, most parsimonious model, and all models with $\Delta AIC_c < 2.0$ were considered to have strong support (Burnham and Anderson 2002). We also calculated the Akaike weights (w_i) to determine the probability of each model being the best, given the data and model set.

From the set of best supported models ($\Delta AIC_c < 2.0$), we examined the relative effects of individual explanatory variables on breeding success. We determined the relative importance of explanatory variables by calculating the importance value of each variable, defined as the sum of the Akaike weights across all competing models in which the variable occurred (Burnham and Anderson 2002). Importance values ranged from 0 to 1, with larger values indicating the variable had greater importance in predicting breeding success relative to the other variables. We also assessed the effect size, and thus the biological significance, of these explanatory variables by calculating their model-averaged parameter estimates. For uncertainty around parameter estimates, we calculated unconditional standard errors (SE that includes variance due to model selection uncertainty; Burnham and Anderson 2002) and 95% confidence intervals as 95% CI = 1.96 x SE.

Next, we investigated how factors that affected breeding success may be related to the rockiness of the nest site. Given that nest temperature had the strongest impact on storm-petrel reproductive success in the above models (*Results*), we used the same model selection approach to evaluate whether physical structure and composition of the nest site, including rockiness, influenced temperature. We used percent rock (ROCK) and the 11 physical nest site variables as explanatory variables in multiple linear regression models fit to mean nest temperature data. Model fitting and calculations of associated parameters were conducted as described above. To further describe how rock related to nest temperature in 2006 using more detailed temperature data from iButtons, we used Pearson's correlation to examine how percent rock varied with minimum or maximum nest temperature. We also compared temperature in nests on Kasatochi Island to those on Ulak Island using a repeated measures ANOVA with island as a between-subject factor. To account for differences in ambient conditions between islands, we used a paired t-test to compare mean daily ambient temperatures between islands over the 2006 season.

We used SYSTAT 13.0 (Systat Software 2009) for all model fitting and statistical analysis. For linear regression models, we used the "Best Subset" function to build and rank models; for logistic regression models, we built all possible models manually and calculated AIC_c scores by hand from reported AIC values. We normalized data using arcsine-transformations for percent rock, visitation rate, relative humidity, and percent vegetative cover variables, and log-transformations for temperature variation, entrance length, width, and length, chamber depth, height above sea level, and vegetation height variables (Zar 1984). Categorical variables were converted to dummy variables for model fitting. We reported means ± 1 SD, unless otherwise noted, and set significance at $P = 0.05$.

RESULTS

Reproductive success and nest site variables

Competing models ($\Delta AIC_c < 2.0$, Burnham and Anderson 2002) for hatching success (89% in 2005, 91% in 2006; Drummond and Leonard 2009) included a total of seven physical, microclimatic, and parental variables (Table 1). None of these parameters appeared to have a strong effect on hatching success, however, as none had a high importance value (< 0.60) and parameter estimates were equal to or smaller than standard errors in all cases (Table 2).

Top models for chick survival (58% in 2005, 89% in 2006; Drummond and Leonard 2009) and overall reproductive success (51% in 2005, 81% in 2006; Drummond and Leonard 2009) included various combinations of nest temperature, egg volume, visitation rate, and brooding duration (Table 1). Nest temperature was included in all competing models and exhibited high importance values (1.00) and parameter estimates (Table 2), which suggests temperature was an important predictor of chick survival and overall reproductive success. Indeed, nest temperature was the only explanatory variable in the best supported model of chick survival in 2005 and the second best supported model of chick survival in 2006; it alone explained 14–35% of the variation in chick survival (Table 1). The relationship between nest temperature and storm-petrel reproductive success was positive in both years, with higher chick survival (2005: $t_{63} = -5.79$, $P < 0.001$; 2006: $t_{89} = -2.45$, $P = 0.016$) and overall success (2005: $t_{72} = -6.22$, $P < 0.001$; 2006: $t_{97} = -3.66$, $P = 0.020$) in warmer nests (Fig. 2).

Although less important than nest temperature, brooding duration had a moderately strong (importance 0.70–0.73) effect on chick survival and overall reproductive success in 2006 (the only year for which brooding data existed; Table 2), with higher survival and reproductive success occurring in nests associated with longer brooding duration. Although egg volume and visitation rate appeared in some of the top models, their actual effects on chick survival and overall reproductive success were weak, as evident from low importance values and parameter estimates that were smaller than standard errors (Table 2). Models with brooding duration, egg volume, or feeding rate explained only slightly more variation in chick survival than those with nest temperature alone (Table 1).

Nest temperature and the rockiness of the nest site

Nests on Kasatochi Island ranged from 30% to 100% rock (mean = 70 ± 15%, $n = 129$). The rockiness of the nest site was included in all competing models of nest temperature in both years, and was the only parameter in the best supported model in 2005 and the second best supported model in 2006 (Table 3). This suggests that rock had a strong effect on nest temperature, which is supported by high importance values in both years (1.00; Table 4). Percent rock was inversely related to mean nest temperature in both years, with lower temperatures in rockier nests (Fig. 3). Other variables that appeared in competing models that explained nest temperature (Table 3) appeared to have only weak effects. Vertical crevice angle, slope, and percent vegetative cover were all positively related to nest temperature but importance values were small for all three parameters (0.14–0.45), and standard errors for crevice angle and vegetative cover were larger than parameter estimates (Table 4).

In 2006, when more detailed daily temperature data were available, we found that colder temperatures in rockier nests were driven by daily temperature lows, as rockier nests experienced colder minimum temperatures ($r = -0.366$, $n = 82$, $P < 0.001$) but not colder maximum temperatures ($r = 0.017$, $n = 82$, $P = 0.167$). Rocky nests on Kasatochi Island were significantly colder (island effect: $F_{1,94} = 64.29$, $P < 0.001$) and more variable in temperature (island effect: $F_{1,94} = 19.71$, $P < 0.001$) than entirely soil nests on Ulak Island (Fig. 4). Mean daily ambient air temperature did not differ significantly between islands (paired $t_{70} = 0.42$, $P = 0.679$).

Table 1. Summary of model selection results for logistic regression models predicting hatching success, chick survival, and overall reproductive success in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests at Kasatochi Island, Alaska. Models are listed in order of best fit for each success parameter in each year based on Akaikeâ€™s information criterion for small sample sizes (AIC_c). Except for the null model, only models with $\Delta AIC_c < 2.0$ are shown. Log(L) is the log-likelihood value, k is the number of parameters in the model, ΔAIC_c is the difference in AIC_c value between each model and the top model, w_i is the Akaike weight, and R^2 is the proportion of the total variation in success explained by the model. Brooding duration (BRD) data are available only for 2006.

Success	Year	Model	log(L)	k	AIC_c	ΔAIC_c	w_i	R^2
Hatching success								
	2005	DEP+SLP+VEGH+TEMPR+RH+EGGV	-7.33	7	31.96	0.00	0.30	0.345
		DEP+RH	-12.02	3	32.31	0.35	0.25	0.270
		VEGH+VEGC+RH	-11.01	4	32.47	0.51	0.23	0.232
		SLP+VEGH+TEMPR	-8.97	4	32.63	0.67	0.21	0.093
		Null	-35.34	1	72.74	40.78	0.00	0.000
	2006	DEP+VEGC+EGGV	-13.60	4	34.61	0.00	0.29	0.217
		EGGV	-14.96	2	35.92	1.31	0.15	0.062
		VEGH+VEGC	-12.91	3	36.07	1.46	0.13	0.072
		Null	-30.53	1	63.10	28.49	0.00	0.000
Chick survival								
	2005	TEMP	-28.81	2	57.80	0.00	0.42	0.348
		TEMP+EGGV	-25.94	3	59.13	1.33	0.22	0.368
		TEMP+VIS	-24.49	3	59.78	1.98	0.16	0.328
		Null	-48.87	1	99.80	42.00	0.00	0.000
	2006	TEMP+BRD	-4.57	3	17.42	0.00	0.39	0.190
		TEMP	-5.49	2	19.13	1.71	0.17	0.138
		TEMP+VIS+BRD	-4.58	4	19.22	1.80	0.16	0.145
		Null	-31.51	1	65.07	47.65	0.00	0.000
Overall reproductive success								
	2005	TEMP+VIS	-12.26	3	34.96	0.00	0.45	0.328
		TEMP+EGGV	-14.62	3	35.18	0.22	0.41	0.224
		Null	-57.38	1	116.81	81.85	0.00	0.000
	2006	TEMP+BRD	-5.39	3	20.19	0.00	0.39	0.140
		TEMP+VIS+BRD	-5.05	4	20.45	0.26	0.34	0.145
		TEMP+VIS	-8.00	3	22.12	1.93	0.15	0.144
		Null	-48.41	1	99.05	78.86	0.00	0.000

†BRD: brooding duration; DEP: chamber depth; EGGV: egg volume; RH: relative humidty; SLP: slope; TEMP: temperature; TEMPR: temperature range; VEGC: vegetation cover; VEGH: vegetation height; VIS: visitation rate

Table 2. Importance values, model-averaged parameter estimates, and associated unconditional standard errors (SE) and 95% confidence intervals (CI) for parameters predicting hatching success, chick survival, and overall reproductive success in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests at Kasatochi Island, Alaska. Parameters are listed in order of importance for each success variable in each year based on importance values; only those appearing in competing models ($\Delta AIC_c < 2.0$) are shown. Brooding duration data are available only for 2006.

Success	Year	Parameter	Importance	Estimate	SE	95% CI
Hatching success						
	2005	DEP	0.55	0.509	1.321	2.589
		TEMPR	0.52	-0.200	0.288	0.565
		SLP	0.51	-0.014	0.014	0.028
		RH	0.48	1.024	1.458	2.858
		VEGH	0.45	-1.084	1.161	2.276
		EGGV	0.30	-0.001	0.050	0.100
		VEGC	0.23	-0.004	0.010	0.020
		Intercept		8.602	10.122	19.839
	2006	EGGV	0.58	0.001	0.026	0.050
		VEGC	0.57	-0.047	0.062	0.122
		DEP	0.52	-0.431	1.743	3.416
		VEGH	0.34	-0.399	0.819	1.605
		Intercept		15.312	7.864	15.413
Chick survival						
	2005	TEMP	1.00	5.513	0.918	1.799
		EGGV	0.26	0.002	0.003	0.004
		VIS	0.16	0.017	0.027	0.053
		Intercept		12.833	8.423	16.510
	2006	TEMP	1.00	4.304	1.159	2.272
		BRD	0.70	0.156	0.032	0.063
		VIS	0.30	0.026	0.058	0.114
		Intercept		16.573	9.412	18.448
Overall reproductive success						
	2005	TEMP	1.00	3.395	0.577	1.131
		VIS	0.56	0.015	0.023	0.045
		EGGV	0.46	0.001	0.030	0.059
		Intercept		7.630	8.547	16.751
	2006	TEMP	1.00	2.400	0.472	0.925
		BRD	0.73	0.156	0.121	0.237
		VIS	0.49	0.005	0.045	0.088
		Intercept		9.522	7.202	14.116

†BRD: brooding duration; DEP: chamber depth; EGGV: egg volume; RH: relative humidty; SLP: slope; TEMP: temperature; TEMPR: temperature range; VEGC: vegetation cover; VEGH: vegetation height; VIS: visitation rate

Fig. 2. Mean (± 95% CI) nest temperature (°C) in relation to chick survival and overall reproductive success in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests on Kasatochi Island, Alaska in 2005 and 2006. Asterisks indicate significant differences ($P < 0.05$) between success (white bars) and failure (grey bars).

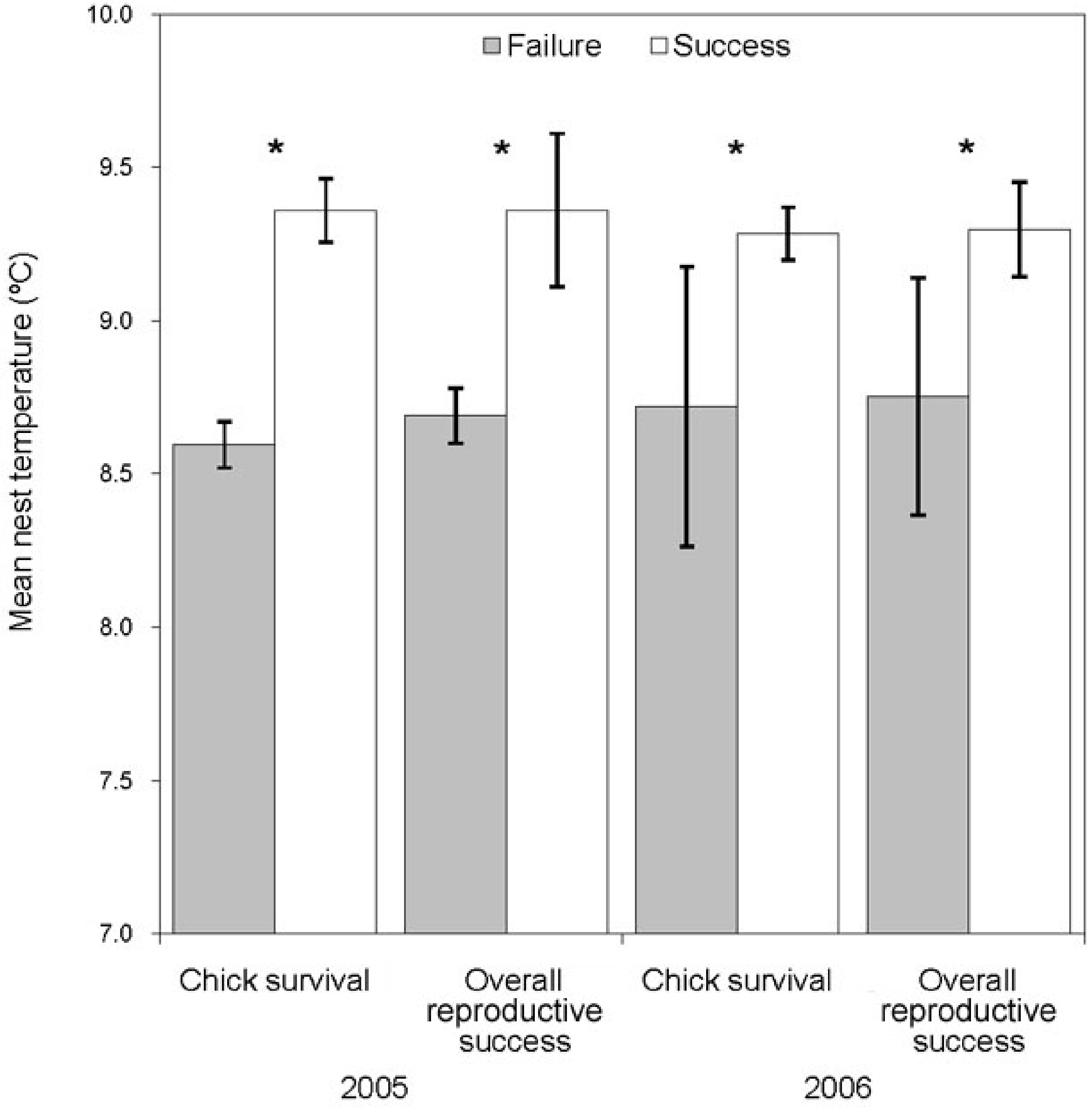


Table 3. Summary of model selection results for models of explaining mean temperature in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests at Kasatochi Island, Alaska. Models are listed in order of best fit in each year based on Akaike's information criterion for small sample sizes (AIC_c). Except for the null model, only models with $\Delta AIC_c < 2.0$ are shown. SSE is the sum of squared error, k is the number of parameters in the model, ΔAIC_c is the difference in AIC_c value between each model and the top model, w_i is the Akaike weight, and R^2 is the proportion of the total variation in success explained by the model.

Year	Model†	SSE	k	AIC_c	ΔAIC_c	w_i	R^2
2005	ROCK	14.69	2	55.20	0.00	0.25	0.535
	ROCK+VEGC	14.45	3	55.46	0.26	0.22	0.551
	ROCK+ANGV+VEGC	13.48	4	56.68	1.48	0.12	0.581
	ROCK+SLP	14.65	3	56.97	1.77	0.10	0.544
	ROCK+SLP+VEGC	14.43	4	57.20	2.00	0.09	0.552
	Null	32.52	1	160.21	105.01	0.00	0.000
2006	ROCK+SLP	27.88	3	112.28	0.00	0.31	0.228
	ROCK	28.85	2	113.19	0.91	0.64	0.166
	ROCK+SLP+VEGC	27.86	4	113.64	1.36	0.16	0.229
	ROCK+ANGV+SLP	27.84	4	114.08	1.80	0.12	0.222
	Null	45.67	1	192.00	79.72	0.00	0.000

†ANGV: vertical nest angle; ROCK: relative amount of rock that composed each nest; SLP: slope; VEGC: vegetation cover

DISCUSSION

The results of our study show that nest temperature was one of the main factors that affected reproductive success in Fork-tailed Storm-Petrel nests. Nest temperature, in turn, varied with the amount of rock that composed the nest, with colder temperatures occurring in rockier nests. Below, we discuss these relationships and their implications for introduced predator removal from islands.

Reproductive success and nest temperature

Nest temperature had the strongest influence on chick survival, and hence overall reproductive success, in both years, with lower survival occurring in colder nests. Most mortality in our study occurred in chicks less than 15 days old (Drummond and Leonard 2009), which suggests that higher mortality in colder nests may be due to increased thermoregulatory demands. Young seabird chicks are likely more vulnerable to colder temperatures than older chicks because they have less insulation, a higher surface to volume ratio, and less food

Table 4. Importance values, model-averaged parameter estimates, and associated unconditional standard errors (SE) and 95% confidence intervals (CI) for parameters explaining mean temperature in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests at Kasatochi Island, Alaska. Parameters are listed in order of importance for each year based on importance values; only those appearing in competing models ($\Delta AIC_c < 2.0$) are shown.

Year	Parameter†	Importance	Estimate	SE	95% CI
2005	ROCK	1.00	-0.042	0.004	0.008
	VEGC	0.45	0.001	0.002	0.004
	SLP	0.32	0.005	0.003	0.006
	ANGV	0.14	0.001	0.003	0.006
	Intercept		3.552	3.930	7.703
2006	ROCK	1.00	-0.022	0.005	0.010
	SLP	0.43	0.008	0.003	0.006
	ANGV	0.29	0.001	0.002	0.004
	VEGC	0.16	0.001	0.002	0.004
	Intercept		4.072	4.653	8.943

†ANGV: vertical nest angle; ROCK: relative amount of rock that composed each nest; SLP: slope; VEGC: vegetation cover

storage capacity than older chicks (Hudson et al. 1974, Boersma 1986, Vongraven et al. 1987). Given that thermoregulation is presumably more difficult in a colder environment (Obst and Nagy 1993), young chicks in colder nests would be expected to suffer increased mortality. This is supported by brooding data in 2006, when chicks that were brooded longer had higher survival rates than chicks that were brooded for less time. In addition, differences in chick survival between years (58% in 2005, 89% in 2006; Drummond and Leonard 2009) correlate with interannual differences in both ambient and nest temperature, with higher chick survival occurring in the warmer year (Drummond 2007, Drummond and Leonard 2009).

The results of our study are consistent with studies on a range of bird species that have shown that the thermal characteristics of the nest site can influence chick survival (Jehl and Mahoney 1987, Dawson et al. 2005), and that even small changes in microclimatic conditions can have substantial impacts on breeding success (D’Alba et al. 2009). In seabirds that breed at high latitudes, survival depends in part on the chick’s ability to maintain body heat in a cold nest environment when adults are absent (Vongraven et al. 1987, Gebczynski 1995). For single-egg seabird species, chicks lack siblings with which to huddle to preserve heat (Boersma 1986). Some species, such as Wilson’s Storm-Petrels (*Oceanites oceanicus*) in Antarctica, appear to preferentially select warmer nest sites (Olivier and Wotherspoon 2006). Once sites are selected, however, most seabirds have limited ability to compensate for a colder nest environment. Attempts to increase nest insulation with additional

Fig. 3. Inverse relationship between percent rock and mean nest temperature (°C) in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests on Kasatochi Island, Alaska in 2005 and 2006. Lines are fit to untransformed data; statistics represent relationships between temperature and arcsine-transformed values of percent rock.

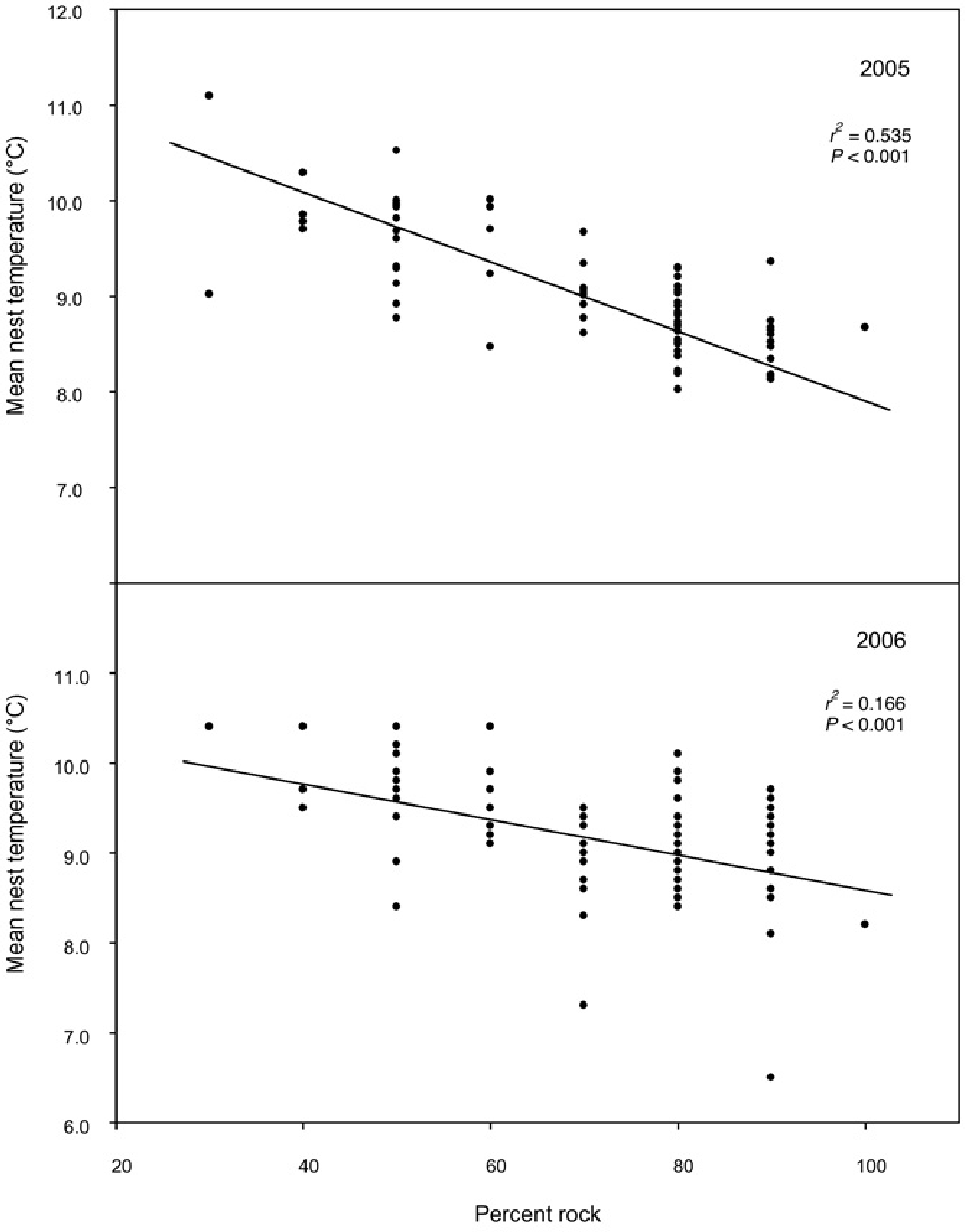
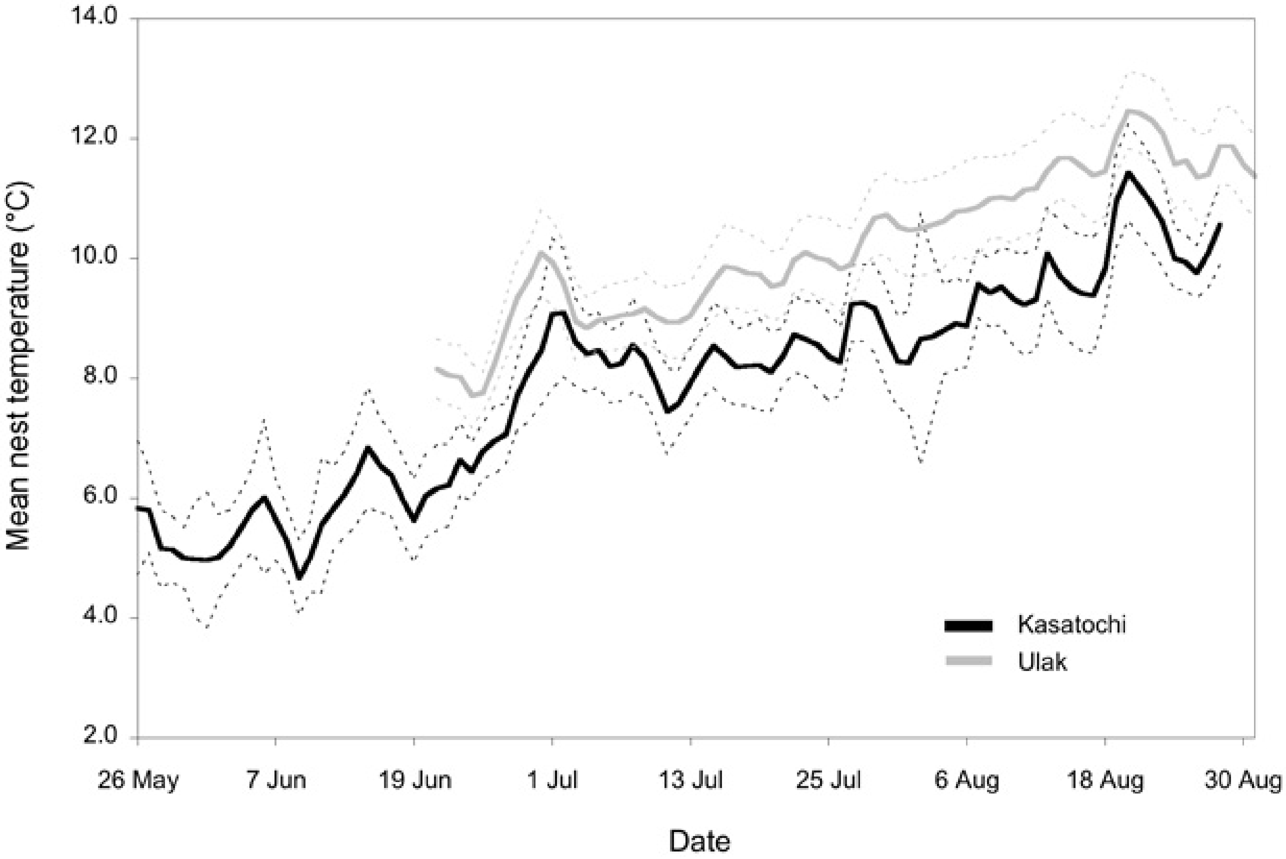


Fig. 4. Mean daily nest temperature (°C) in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) nests on Kasatochi (*n* = 82) and Ulak (*n* = 15) Islands, Alaska in 2006. Dashed lines represent 95% confidence intervals.



nest material, for example, may actually increase chick mortality because nest material can both retain moisture and increase the risk of fungal beetle parasitism (Wheelwright and Boersma 1979), and individual adult seabirds may not be able to alter their brooding patterns in different nest environments (Catry et al. 2009). Therefore, the inherent thermal conditions of the nest site can be critical to reproductive success.

Nest temperature had a greater effect on chick survival in 2005 than in 2006, which suggests that the relationship between breeding success and the thermal characteristics of a nest may vary based on interactions with other environmental factors. Weather conditions and food availability may both indirectly influence the effect of nest temperature on chick survival given that nest temperatures are correlated to outside temperatures (Drummond 2007) and thermoregulatory ability in seabird chicks is often linked to food supply (Petit et al. 1982, Boersma 1986). In our study, chick survival was higher in 2006 (Drummond and Leonard 2009), the year when atypically warm, dry local weather conditions (Drummond 2007; USFWS, *unpublished data*) resulted in significantly warmer nest temperatures, especially in June when chicks were young (mean June nest temperature = 6.7°C in 2005 and 7.9°C in 2006; Drummond 2007; B.A. Drummond, *unpublished data*). In addition, foraging conditions at Kasatochi Island may have been better in 2006 than in 2005 because adults fed chicks more frequently in the second year (48% of nights in 2005, 58% in 2006; Drummond and

Leonard 2009). If nests were warmer and chicks were better fed in 2006, chicks may have been better able to meet thermoregulatory demands and may have been less susceptible to temperature-induced mortality than chicks in 2005.

Nest temperature and the rockiness of the nest site

Temperatures inside Fork-tailed Storm-Petrel nests in our study were affected by the amount of rock that composed the nest site. Across a continuum from entirely rocky to mostly soil nests, in both years rockier nests were colder than nests with less rock. Similarly, entirely soil nests on neighboring Ulak Island had warmer and less variable temperatures than rock nests on Kasatochi Island, although this comparison should be treated with some caution because of potential island effects. Given that percent rock influenced the daily minimum but not the daily maximum nest temperature, the rockiness of a site may affect heat loss but not heat gain. Rockier nests may retain less heat than soil nests because rock has higher thermal conductivity than soil (Farouki 1986, Arya 2001). The potential for the physical structure of the nest site to affect the nest's thermal properties, including heat retention and temperature extremes, has been documented in other burrow- and crevice-nesting seabird species (e.g., Frere et al. 1992, Stokes and Boersma 1998), such as Cassin's Auklets (*Ptychoramphus aleuticus*) on the Farallon Islands, where soil burrows had more stable temperatures than rocky crevices (Manuwal 1974).

Consequences of rocky nest sites

Our results, although correlative, suggest that rockier nests are colder and have lower chick survival rates compared to nests in soil. A comparison of reproductive success at Kasatochi Island to that at three soil-nesting storm-petrel colonies in the Aleutian Islands supports the hypothesis that storm-petrel breeding success may be higher in soil habitat. From 2004 to 2007, breeding success in rock habitat at Kasatochi Island was lower than the average breeding success at the three soil sites in all years except in 2006 (Andersen 2007, Drummond and Larned 2007, Helm et al. 2007), the year of warmer nest temperatures on Kasatochi Island (Drummond 2007). The conclusion that lower chick survival in rockier nests is a function of colder temperatures in those nests should be viewed with some caution, however, because we could not compare reproductive success in rock and soil habitat on the same island. In addition, the apparent negative effect of rocky nests on breeding success in our study may have been exaggerated because the accessible nests we used may have been occupied by less experienced breeders with poorer provisioning skills. Despite these limitations, evidence from rocky nests at Kasatochi Island, along with differences in both temperature and breeding success between rock and soil nests on different islands, supports the idea that rockier nest sites may affect reproductive success in Fork-tailed Storm-Petrels.

It is interesting to speculate why storm-petrels would not recolonize soil habitat following fox removal if breeding success decreases in rock habitat. One possibility is that rapid changes in selective pressures, such as predator removal, could cause a mismatch between previously evolved cues used for nest selection and actual nest quality, and lead individuals to choose suboptimal nest sites (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004). Storm-petrels have high nest site fidelity and are strongly attracted to conspecifics. These traits make them particularly vulnerable to such maladaptive habitat use (Cooch et al. 1992, Spear et al. 1998, Igual et al. 2007) because the birds are more likely to return to the existing colony in rock habitat year after year rather than recolonize soil habitat on their own. Furthermore, historic soil burrows on Kasatochi Island no longer exist (B. A. Drummond, *personal observation*), so the birds may expend less energy using ready-made rock crevices rather than excavating new burrows in the soil. Finally, the soil habitat on the island may have been negatively affected by the fox introductions because mammalian predators can alter soil nutrient levels and below-ground microbial communities on islands where they have been introduced (Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006). Some combination of these factors may contribute to the continued use of rock habitat by storm-petrels in the Aleutian Islands following fox removal.

If storm-petrel use of rock habitat in the Aleutian Islands is due to historic fox predation, as the evidence suggests, then reduced chick survival and overall breeding success in rocky nests after foxes are removed may represent a lasting indirect effect of these introduced predators. This is consistent with mounting evidence of the indirect effects introduced predators can exert on island communities long after their eradication (e.g., Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006, Kurle et al. 2008, Towns et al. 2009). Therefore, worldwide conservation efforts to control and eradicate alien predators as a means of restoring natural avifauna (Courchamp et al. 2003) should consider these types of lasting impacts when developing restoration plans.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss2/art4/responses/

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