Egg neglect under risk of predation in Cassin's Auklet (*Ptychoramphus aleuticus*)

R.A. Ronconi and J.M. Hipfner

Abstract: We tested predictions concerning the significance of egg neglect for the burrow-nesting seabird Cassin's auklet (*Ptychoramphus aleuticus* (Pallas, 1811)) at a colony where endemic Keen's mice (*Peromyscus keeni* Merriam, 1897) depredate unattended eggs. A video-camera probe was used to monitor neglect and predation in 32 burrows, and mass loss of incubating adults was measured in 12 separate burrows. Incubating birds lost 8.1% of their body mass over obligate 24 h incubation shifts, suggesting that incubation is costly. In response, most pairs (79%) neglected their egg at least once. As predicted, rates of neglect decreased as incubation progressed, and the costs of neglect increased. Rates of neglect increased during periods of strong winds, which create poor foraging conditions at sea. Contrary to predictions, rates of neglect did not increase when burrows were colder and self-maintenance costs were higher. Neglect was risky in that rates of egg loss by predation increased with frequency of neglect. Increased neglect early in incubation and during periods of poor foraging conditions, despite high rates of predation on neglected eggs, is consistent with the existence of a fitness trade-off between costs and benefits of neglect.

Résumé : Nous testons des prédictions au sujet de l'importance de la négligence des œufs chez le starique de Cassin (*Ptychoramphus aleuticus* (Pallas, 1811)), un oiseau marin qui niche dans des terriers, dans une colonie dans laquelle des souris à pieds blancs de Keen (*Peromyscus keeni* Merriam, 1897) pillent les œufs laissés sans soins. Une surveillance à la camera vidéo a permis de suivre la négligence et la prédation dans 32 terriers; nous avons aussi mesuré la perte de masse des adultes en train d'incuber dans 12 terriers différents. Les adultes qui couvent pendant une période imposée de 24 h perdent 8,1 % de leur masse corporelle, ce qui indique que la couvaison coûte cher. En réaction, la plupart des couples (79 %) ont négligé leur œuf à au moins une reprise. Comme prédit, les taux de négligence diminuent au cours de l'incubation et le coût de l'incubation augmente; ils s'accroissent aussi durant les périodes de vents forts qui créent de mauvaises conditions de recherche de nourriture en mer. Contrairement aux prédictions, les taux de négligence n'augmentent pas quand les terriers sont plus froids et les coûts de maintien individuel plus élevés. La négligence entraîne des risques; les taux de pertes d'œufs par prédation augmentent en fonction de la fréquence de la négligence. Une négligence plus importante au début de l'incubation et durant les mauvaises périodes de recherche de nourriture, malgré les forts taux de prédation des œufs négligés, s'explique par un compromis associé à la fitness entre les coûts et les bénéfices de la négligence.

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Introduction

For avian parents, the costs of incubation can be high owing to the energetic expenditures of heating eggs (Vleck 1981), the depletion of mass reserves (Spaans et al. 1999; Criscuolo et al. 2002), and the risk of being depredated on the nest (Magrath 1988). In response, incubating birds occasionally leave their eggs unattended in the nest to feed themselves or escape from predators. However, this behavior can be costly in that it causes embryonic development to slow (Conway and Martin 2000; Hepp et al. 2006), and thus prolongs the incubation period (Martin 2002). Moreover, unattended offspring also are under a heightened risk of predation (Weathers and Sullivan 1989; Martin and Ghalambor 1999). Thus, we can expect egg neglect to reflect the fitness balance between adult self-maintenance needs and the risk of offspring mortality.

Many pelagic seabirds lay single-egg clutches in enclosed nest sites on remote islands where adults and offspring are safe from terrestrial predators. Their incubation periods are long and their eggs are variably resistant to chilling (Matthews 1954; Boersma 1982; Gaston and Powell 1989), adaptations that allow adults to neglect their eggs for periods of hours to days (Boersma and Wheelwright 1979; Murray et al. 1980; Chaurand and Weimerskirch 1994). Though widely recognized, the adaptive significance of egg neglect is poorly understood in seabirds. Neglect may enable parents to adjust the length of incubation so that chicks fledge when food is most abundant (Prévost and Bourliere 1955), to prolong foraging trips (Murray et al. 1980), to nest farther from primary food sources (Warham 1990), and perhaps most importantly, to enable incubating parents to replenish depleted reserves (Boersma and Wheelwright 1979; Chaurand and Weimerskirch 1994). In most situations, however,

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the safety of their nest sites ensures that there is little risk that eggs which are neglected will be taken by predators.

We studied egg neglect in the Cassin's auklet (*Ptychoramphus aleuticus* (Pallas, 1811)), a nocturnal, zooplanktivorous seabird that lays a single-egg clutch in an earthen burrow, at a very large colony where an endemic species of mouse (Keen's mouse, *Peromyscus keeni* Merriam, 1897) preys on unattended eggs. The habit of consuming seabird eggs is widespread within the large population of large-bodied mice, rather than being restricted to specialist individuals (Drever et al. 2000). As a result, these endemic mice undoubtedly take many auklet eggs every season (Drever et al. 2000), but more in unfavourable years in which the birds neglect more frequently (Blight et al. 1999). While Cassin's auklets often relay after egg loss, we can expect relaid eggs to be less successful than first eggs because of a strong seasonal decline in food availability around Triangle Island (Hipfner 2008). Thus, it is possible that during their long period of coexistence, the Keen's mice have acted as selective agents to reduce the rates of neglect relative to sites without mice.

We hypothesized that under these atypical but natural conditions, incubating auklets face a trade-off between the costs (loss of eggs to mice) and benefits (the opportunity to replenish reserves) of egg neglect. Based on this hypothesis, we predicted that rates of neglect would (*i*) increase during periods of strong winds, when foraging conditions at sea are poor (Finney et al. 1999), (*ii*) increase when burrows were colder and the energetic demands on incubators higher (Williams 1996), and (*iii*) decline as incubation progressed and the cumulative investment in offspring, which become decreasingly resistant to chilling, increases (Astheimer 1991). To assess the costs of incubation, we also quantified adult mass loss over the course of an obligate 24 h incubation shift. Finally, to assess the risks of neglect, we modeled the relationship between rates of neglect and rates of predation on unattended eggs.

Materials and methods

The study took place on Triangle Island, British Columbia, Canada (50°52′N, 129°05′W), during the very unsuccessful 2005 breeding season (Sydeman et al. 2006). Male and female Cassin's auklets alternate incubation duties at 24 h intervals for the 38 days it takes eggs to hatch (Manuwal 1974). Because they return to nests only at night, neglect involves a period of at least 16 h during which eggs are left vulnerable to mice. Experiments were conducted under Migratory Birds (Environment Canada) and Animal Care (Simon Fraser University) permits.

We used a portable infrared video probe (Sandpiper Technologies, Manteca, California) to monitor 45 burrows, identified prior to laying, where the probe could slide easily through to the end of the chamber. Eggs were laid in 32 of these burrows. Burrows were checked daily, within 3 h of sunrise, between 30 March and 21 May, when the probe failed. Incubation status was scored as "egg incubated" (adult present) or "egg neglected" (absent). Depredated eggs were easily recognized by tooth marks and shell remains (Blight et al. 1999). In four instances eggs went unaccountably missing; we scored these as depredated because we occasionally found shell remains outside of burrows. Daily mean and maximum wind speed records were recorded at an Environment Canada weather station located at nearby Sartine Island, and daily maximum and minimum temperatures were obtained using temperature probes placed into two empty burrows within the study plot.

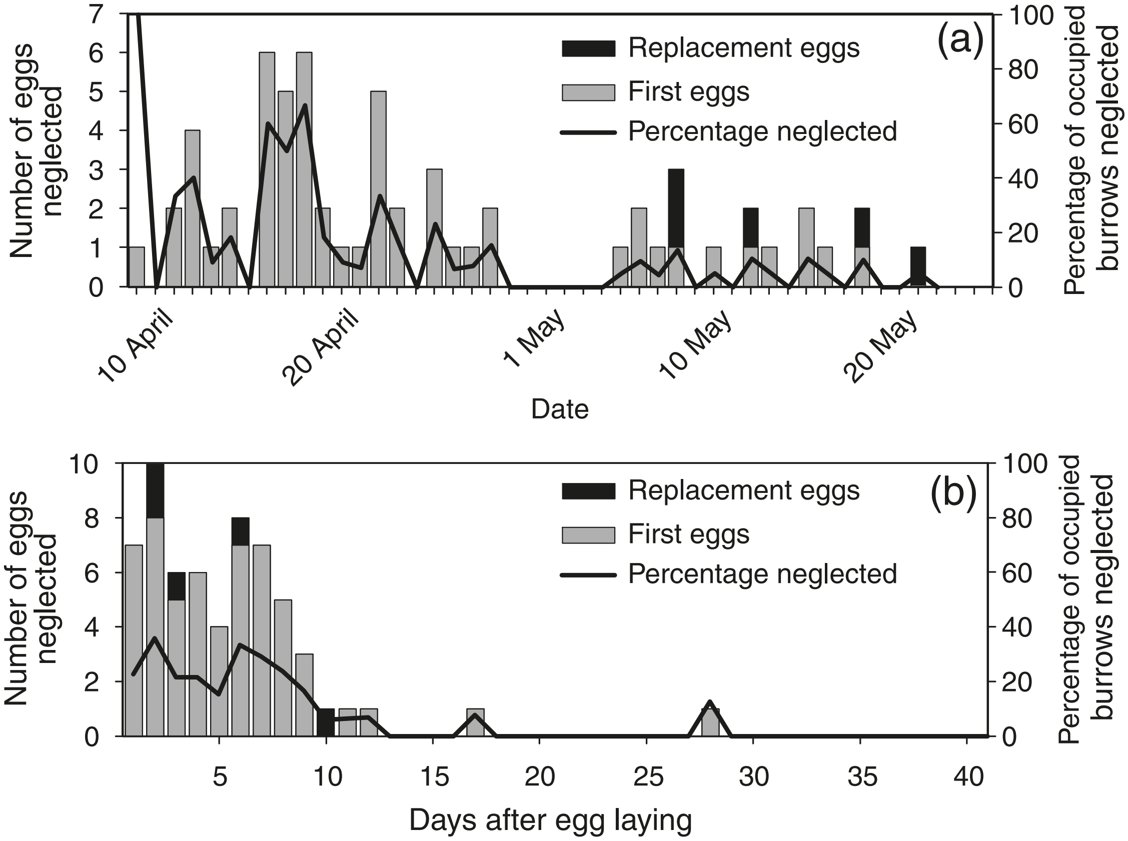
We weighed incubating birds at dawn (0600–0700) and dusk (1940–2040) on two consecutive days (27 and 28 April) in 12 burrows not included in the neglect study. Because auklets usually return to the colony between 2200 and 0000, birds had been fasting for at least 4 h when first weighed and by that time probably had largely or entirely emptied their stomachs. We weighed and banded both members of six pairs, one member of five pairs (the egg was neglected on the 2nd day), and a single bird on 2 days at one burrow. Sex was determined by comparing bill depths between pair members in the same burrow (Pyle 2001).

We modeled rates of neglect with individual egg-days (a total of 656 from 32 nests) as the sampling unit. We used logistic regression (0 = egg incubated, 1 = egg neglected) in relation to the number of days since the egg was laid, laying date, calendar date, egg type (first or replacement), and daily weather conditions (mean and maximum wind speeds, minimum burrow temperatures). Because the auklets relieve incubating partners once daily, at night, we examined neglect in relation to weather variables during three time periods: (1) the predawn period (0000–0600), when foraging birds either do or do not return and incubating birds must decide whether to stay or go; (2) the previous 24 h, which determines conditions during the bulk of the foraging trip of the mate; and (3) the previous 24–48 h, which determines conditions during the last foraging trip of the current incubator. Burrow temperatures increased through the season, so we constructed models for April only, May only, and April and May combined. Logistic regression analysis was performed with backward stepwise variable selection with entry and exit set at $P = 0.05$ and 0.1, respectively, using SPSS version 15.0 (SPSS Inc., Chicago, Illinois). Final models contained all significant variables and, thus, controlled for confounding effects of interacting variables. Hosmer and Lemeshow (1989) tests showed that logistic model fit was adequate for all three time periods (April: $P = 0.67$; May: $P = 0.56$; April–May: $P = 0.21$; a larger P value indicates a better fit to the data).

With 32 burrows included, each egg-day is not a completely independent unit. However, "burrow" could not be used in models because it was a categorical variable with 32 categories. Instead, we tested for burrow effects using a χ^2 test comparing observed to expected numbers of neglect incidents, i.e., with the total number of neglect incidents divided equally among all burrows. Observed versus expected numbers of neglect incidents differed little for first eggs in 32 burrows ($\chi^2_{[31]} = 37.08$, $P > 0.1$) or replacement eggs in 15 burrows ($\chi^2_{[14]} = 11.00$, $P > 0.75$), indicating that individual burrows did not contribute disproportionately to the rates of neglect.

Finally, we used logistic regression (0 = not predated, 1 = predated) to model predation rates on neglected eggs for 656 egg-days at 32 burrows in relation to laying date, cumulative days of neglect, egg type (first or replacement), number of study burrows with eggs, and the proportion of eggs on the plot that were neglected. Again, model fit was

Fig. 1. Incidents of egg neglect from 32 burrows of Cassin's auklets (*Ptychoramphus aleuticus*) monitored daily on Triangle Island in 2005. Frequency of neglect with respect to calendar date (*a*) and laying date (*b*).



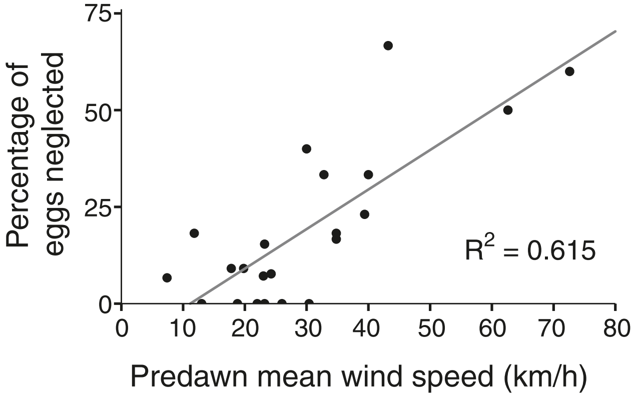
adequate (Hosmer and Lemeshow test: $P = 0.39$). Values are means ± SD.

Results

Eggs were laid in 32 of the 45 (71%) monitored burrows. We observed 62 instances of neglect involving 25 of 32 pairs (78%), mostly early in the breeding season (Fig. 1). First eggs were neglected 1.75 ± 1.52 times until they were depredated or the study ended. Of 15 replacement eggs, only 5 (33%) were neglected, all only once.

As predicted, rates of egg neglect increased with wind speed (Fig. 2), and especially with wind speed in April during the predawn period (Table 1). However, wind speed did not predict the lower rates of neglect in May (Table 1), despite mean daily wind speeds being similar in May (32.7 ± 16.9 km/h) as in April (34.3 ± 17.5 km/h). Conversely, contrary to predictions, neglect did not increase with decreasing burrow temperatures (Table 1). In fact, after controlling for other factors, neglect increased with burrow temperatures during the previous 24–48 h, during the current incubator's previous shift. And again as predicted, rates of neglect decreased as incubation progressed, with little effect of calendar date (Table 1, Fig. 1). We made no predictions regarding differences in rates of neglect on first and replacement eggs (one could argue both ways), replacement eggs were neglected less often than first eggs in the May and April–May models after controlling for other factors (Table 1).

Fig. 2. Percentage of active burrows of Cassin's auklets (*Ptychoramphus aleuticus*) neglected as a function of mean wind speeds of the previous day in April 2005. Regression line fit to the plotted data.



As expected, bill depths were bimodally distributed (10.3 ± 0.38 and 9.1 ± 0.22 mm) at the six burrows where both pair members were measured (paired *t* test: $t_{[5]} = 8.48$, $P < 0.001$). For the five burrows where only one bird was measured, sexes were assigned by comparing bill depths to these 12 individuals. Larger billed putative males and smaller billed putative females differed by <5% in initial mass ($t_{[5]} = 1.37$, $P = 0.23$; overall mass = 185.9 ± 10.8 g). Adults weighed 8.4 ± 3.15 g lighter after 14 h of incubation (paired *t* test: $t_{[17]} = 11.38$, $P < 0.001$). Mass loss did not differ between the sexes ($t_{[16]} = 0.83$, $P = 0.42$), averaging

Table 1. Factors affecting egg neglect by Cassin's auklets (*Ptychoramphus aleuticus*) on individual days at individual burrows, modeled with multiple logistic regression.

Model and variable	β coefficient	SE	Wald's statistic	df	*P*
April–May					
Incubation days	–0.139	0.032	18.776	1	<0.001
Calendar date	–0.068	0.027	6.379	1	0.012
First* versus replacement eggs	–1.414	0.560	6.384	1	0.012
Previous 24 h maximum wind speed	0.012	0.006	3.212	1	0.073
Previous 24–48 h minimum burrow temperature	0.307	0.145	4.473	1	0.034
Predawn mean wind speed	0.034	0.012	8.016	1	0.005
Constant	2.564	2.438	1.106	1	0.293
April only					
Incubation days	–0.250	0.071	12.192	1	<0.001
Laying date	–0.181	0.067	7.253	1	0.007
Previous 24–48 h minimum burrow temperature	0.477	0.197	5.844	1	0.016
Predawn mean wind speed	0.057	0.013	20.337	1	<0.001
Constant	14.267	6.369	5.019	1	0.025
May only					
Incubation days	–0.091	0.048	3.565	1	0.059
Laying date	0.078	0.042	3.349	1	0.067
First* versus replacement eggs	–1.374	0.577	5.677	1	0.017
Constant	–11.853	5.555	4.554	1	0.033

Note: Only significant variables ($P < 0.1$) are included in the table. Variables tested included calendar date, lay date, incubation days (i.e., days since egg laid), first versus replacement egg, and all weather variables.

*Indicates comparison group for categorical variables.

Table 2. Logistic regression results of factors affecting Cassin's auklet (*Ptychoramphus aleuticus*) egg predation by Keen's mice (*Peromyscus keeni*) (1 = predated, 0 = not predated) on individual days ($N = 656$).

Variable	β coefficient	SE	Wald's statistic	df	*P*
Incubation days	–0.129	0.044	8.618	1	0.003
Cumulative days of neglect	0.954	0.183	27.213	1	<0.001
First* versus replacement eggs	1.265	0.639	3.920	1	0.048
Number of burrows occupied	0.170	0.072	5.531	1	0.019
Percentage of burrows neglected	0.045	0.015	9.385	1	0.002
Laying date	0.005	0.036	0.021	1	0.885
Constant	–6.239	1.456	18.359	1	<0.001

*Indicates comparison group for categorical variables.

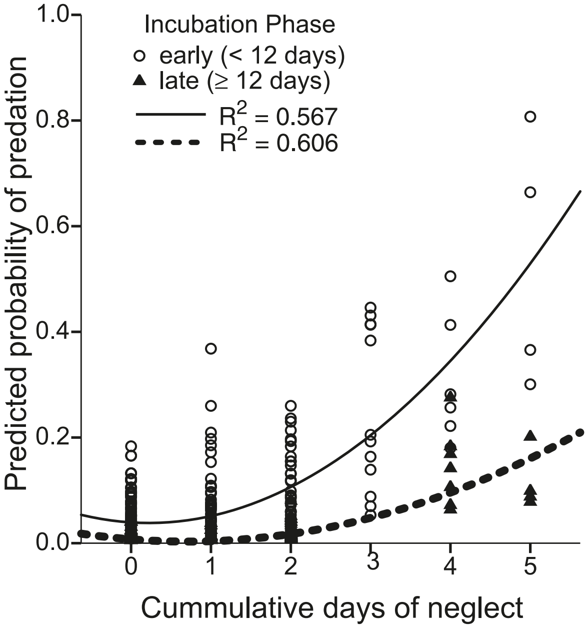
0.63 ± 0.23 g/h. The one adult that incubated for 2 days lost mass at a relatively constant rate of 0.68 g/h for the first 14 h, 0.79 g/h between 14 and 24 h, and 0.74 g/h between 24 and 37 h. Total mass loss for 1-day and 2-day incubation shifts were estimated to be 8.1% ± 2.9% and 16.1% ± 5.9%, respectively, of the initial body mass.

Neglect was risky in that 19 of 32 (59%) first eggs were depredated by Keen's mice, as were 9 of 15 (60%) replacement eggs. Some eggs were depredated even when no neglect was observed; because mice cannot take eggs from incubating adults (a Keen's mouse weighs approximately 45 g (Drever et al. 2000), which is <25% of the mass of a Cassin's auklet), these eggs probably were depredated in the morning prior to burrow checks. In May, when neglect was rare, all replacement eggs that were neglected were depredated. All variables except laying date were significant predictors of the predation rate on unattended eggs (Table 2). Thus, predation decreased as incubation progressed, and increased with the cumulative frequency of neglect at individual nests (Fig. 3). In addition, replacement eggs were more likely than first eggs to be depredated, after controlling for other factors. Predation rates also were higher when more burrows contained eggs and when more eggs were being neglected, suggesting that mice were more active under these conditions.

Discussion

A trade-off between current and future breedings is a central concept in life-history theory (Stearns 1992), and we conclude that a simple trade-off of this type exists for incubating Cassin's auklets. At Triangle Island, which supports a very large population of endemic Keen's mice that eat unattended eggs, the trade-off involves weighing self-maintenance needs against the risk of offspring mortality, and centers around the decision on whether or not to leave the egg unattended in the burrow. Because they prey heavily on neglected seabird eggs (Drever et al. 2000), and because Cassin's auklet breeding success at Triangle Island declines with later laying as the food supply decreases

Fig. 3. Predicted probability of predation by Keen's mice (*Peromyscus keeni*) on eggs of Cassin's auklets (*Ptychoramphus aleuticus*) modeled with logistic regression using eggs on individual days ($N = 656$) as the dependent variable. Early versus late incubation phases correspond with periods of slow and rapid embryonic growth in Cassin's auklets (Astheimer 1991).



(Hipfner 2008), we expect that mice might act as agents of selection for incubation constancy.

Incubation appears to be energetically costly for Cassin's auklets, as it is for other species of seabirds with single-egg clutches (Minguez 1998). In the course of a normal incubation shift of 24 h duration, Cassin's auklets lost about 8% of their initial mass, and the single bird that remained for a second shift continued to lose mass at a similar rate. For many birds, mass can play a critical role in regulating incubation behaviour (Chaurand and Weimerskirch 1994; Criscuolo et al. 2002; Bolduc and Guillemette 2003) and excessive mass loss can trigger clutch desertion (Numata et al. 2000). For nocturnal species such as Cassin's auklets, the decision to remain with the egg, rather than leaving it unattended, may be especially significant, because the decision entails a commitment of a full 24 h.

At Triangle Island, Cassin's auklets laid very late in 2005 (3-week delay in median date) and experienced the lowest breeding success in 13 years (8%), probably because of anomalous oceanographic conditions in the spring (Sydeman et al. 2006). However, burrow occupancy rates on an adjacent monitoring plot were similar in 2005 (77%) as in 2003 (82%) and 2004 (84%; J.M. Hipfner, unpublished data). This indicates that normal numbers of auklets laid eggs in 2005. Nonetheless, while our results match those of a previous study (Astheimer 1991) in showing that egg neglect was rare after the first 11 days after laying, the much higher rates of neglect in our study (78% vs. 26%–29% of eggs were neglected at least once) probably reflected that extreme oceanographic conditions tipped the balance of the trade-off in favour of the adults over the offspring.

Nonetheless, our results provide valuable information on the general ecological correlates of neglect in seabirds and its consequences. As predicted, auklets were more likely to neglect their eggs as wind speeds increased, which causes foraging conditions at sea to deteriorate (Birkhead 1976; Finney et al. 1999). The effect was particularly marked for the period during which off-duty birds had to decide whether to return to relieve their incubating partner at the nest or to continue feeding at sea for another 24 h period. Presumably, the decision to remain at sea was made because the off-duty bird had not accumulated sufficient reserves to begin its own 24 h incubation shift. In response, the incubating bird was more likely to leave the egg unattended. Similar weather effects have been observed in other marine birds (Murray et al. 1980; Warham 1990; Astheimer 1991). Yet despite effects of wind in April, similar wind strengths in May did not cause Cassins' auklets to neglect their eggs. In May, the needs of embryos may take precedent over parental requirements, thus environmental factors played less of a role in the parental decision to neglect eggs late in incubation.

We found that rates of neglect decreased as incubation and embryonic development progressed, as we had predicted. This suggests that adult Cassin's auklets become increasingly reluctant to neglect their eggs as their cumulative investment increases and the embryo becomes less resistant to chilling (Gaston and Powell 1989; Astheimer 1991). As the embryo nears hatching, we can expect the fitness trade-off to increasingly favor offspring survival. However, other factors probably also contribute; feeding conditions probably improve through the early part of the season and it might take breeding pairs some time to develop a coordinated incubation rhythm. In contrast, we found that adults were somewhat less likely, rather than more likely, to neglect when temperatures in burrows were colder. Adults may be more sensitive to the potential costs of leaving embryos exposed to colder temperatures, but less sensitive to the increased energetic demands associated with incubating under colder conditions.

Although neglect may confer fitness benefits by providing adults the opportunity to replenish depleted reserves, predation of neglected eggs by Keen's mice presents a serious risk at Triangle Island. Several factors influenced the predation risk. First, predation was more common during the early incubation period when rates of neglect were high. Second, replacement eggs suffered a higher risk of predation compared with first eggs, a surprising result given that replacements were neglected less frequently. Third, predation risk increased with increasing burrow occupancy in the plot and when more pairs of Cassin's auklets were neglecting. Thus, there was a synergistic aspect to mouse predation on eggs, rather than a predator-swamping effect as reported for sooty shearwaters (*Puffinus griseus* (Gmelin, 1789)) in a previous study (Jones 2003).

However, the strongest effect in our models was that predation risk increased with the cumulative number of days neglected. Thus, while the majority of breeding pairs in our study neglected their eggs at least once (78%), it was those pairs that neglected more often that were more likely to pay the ultimate price. The propensity for seabirds to neglect despite the risk of egg predation suggests that neglect generally has evolved in the absence of egg predators, which is certainly true for species exposed to introduced predators (Campos and Granadeiro 1999). Further comparison of neglect behaviour between colonies with and without egg predators may reveal how coevolution with predators should affect this behaviour. As in some passerines (Voss et al. 2006), our results for Cassin's auklets at Triangle indicate that neglect occurs to allow adults to replenish depleted reserves, despite the risk of egg predation by Keen's mice.

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