



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

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 $8.1\% \pm 2.9\%$ and $16.1\% \pm 5.9\%$, 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

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

(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

certainly true for species exposed to introduced predators (Campos and Granadeiro 1999). Further comparison of neglect behaviour between colonies with and without egg

- ment and parental self-maintenance in three species of intermittently incubating passerines. *J. Therm. Biol.* **31**: 453–460. doi:10.1016/j.jtherbio.2006.03.002.
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