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PREDATION ON RHINOCEROS AUKLET EGGS BY A NATIVE POPULATION OF *PEROMYSCUS*[1]

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Abstract. Predation by Keen's mice (*Peromyscus keeni*) was the single greatest cause of egg loss for Rhinoceros Auklets (*Cerorhinca monocerata*) at the seabird colony on Triangle Island, British Columbia in 1998. Despite studies suggesting that gape-limited rodents are unable to open large eggs, mouse depredation was likely responsible for the loss of more eggs than all other causes combined, with mice commonly opening and eating eggs of nearly twice their mass. In one study plot, mice depredated up to 34% of eggs. This high predation rate is likely related to temporary egg neglect by foraging parents. We suggest that egg depredation may increase in years of low marine productivity, when adults increase foraging time.

Key words: Cerorhinca monocerata, *egg neglect, egg predation, Keen's mouse,* Peromyscus, *Rhinoceros Auklet, Triangle Island.*

Depredation by deer mice (*Peromyscus* spp.) is a widely recognized source of egg mortality for passerines (Verbeek 1970, Guillory 1987, Rogers et al. 1997), and also has been documented for ground-nesting shorebirds (Maxson and Oring 1978). Marine birds nesting on remote islands largely avoid terrestrial predators. Indeed, predator avoidance may have been important in the evolution of island nesting (Furness and Monaghan 1987). To date, egg predation by *Peromyscus* has been documented for only two burrow-nesting seabird species (Murray 1980, Gaston 1992). In this paper we report depredation by native Keen's mice (*Peromyscus keeni*) on Rhinoceros Auklet (*Cerorhinca monocerata*) eggs.

Triangle Island is the site of western Canada's largest seabird colony. Over one million seabirds breed there, including an estimated 42,000 pairs of Rhinoceros Auklets (Rodway 1991). Two native species of rodents also occur there: Keen's mouse (formerly deer mouse *P. maniculatus triangularis*; Cowan and Guiguet 1975, Hogan et al. 1993) and an endemic subspecies of Townsend's vole (*Microtus townsendii cowani*; Carl et al. 1951). Island populations of rodents have different demographics and behavior, and larger body size, than mainland populations (Adler and Levins 1994), and those populations on Triangle Island contain some of the largest specimens known for the species' range (Carl et al. 1951, Cowan and Guiget 1975).

METHODS

In 1998 we monitored Rhinoceros Auklet burrows for depredated eggs throughout the incubation period at Triangle Island, British Columbia (51°52′N, 129°05′W). In the pre-laying period, a total of 217 burrows in two study plots—109 in Plot 1 and 108 in Plot 2—were prepared by excavating the entire burrow at arm's-length intervals. These access holes were then fitted with cedar shingles and covered with earth. Like most alcids, Rhinoceros Auklets lay a single egg annually. We checked the status of each burrow and egg once per week from 30 April to 25 May. By the latter date, the rate of occupation of new burrows had dropped to almost zero and any empty burrows were dropped from the study. We monitored the remaining burrows once per week until their eggs failed or until chicks hatched in June. Throughout the monitoring period, presence or absence of an incubating adult in the nest chamber was noted. Any unincubated, cold eggs were temporarily removed from the burrow and checked for signs of attempted depredation by rodents, such as chew marks or scratches.

Only eggs that had been chewed open and partially or completely eaten by mice were scored as depredated. Partially eaten eggs were replaced in the nest chamber, to be checked on the following week for signs of scavenging. We searched for missing eggs throughout the burrow. Missing eggs were those that had been present on the previous check. If not found, we then scoured the burrow floor for shell fragments. Missing eggs were recorded as depredated when chewed shell pieces were found inside the burrow, and as absent and likely rodent depredated when no shell was found. Eggs that had been found cold on two or more consecutive checks were considered to be abandoned. These abandoned eggs were readily distinguished from those that were temporarily neglected as the former quickly built up a film of moisture while intermittently incubated eggs remained dry. Corvid-

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depredated eggs also were readily distinguished from those eaten by mice. Although Rhinoceros Auklet burrows are generally too deep for avian egg predators to enter, in 1998, Northwestern Crows (*Corvus caurinus*) and Common Ravens (*C. corax*) learned to unearth our hidden access shingles and remove both incubated and unincubated eggs. Auklet eggs were recorded as being taken by corvids when shingles near the nest chamber were found torn up and a previously present egg was either missing or found eaten in the vicinity of the access hole.

In order to test whether observer presence increased rodent predation, 88 burrows in a third, control plot also were fitted with observation shingles. Each of these control burrows was monitored at 5-day intervals until an egg was found, and then left unchecked for 30 days. If an egg was still present on this later check, it was scored in the same manner as the eggs in the study plots, and the burrow was then monitored every 5 days until a chick was found. As these later 5-day checks necessarily involved observer presence, only those control eggs found depredated on the initial burrow check or on the check ending the 30-day control period were used for purposes of comparison with the study plots. We combined data for the two study plots and used z-tests (Zar 1984) to compare their rate of depredation with that in the control plot. Missing control eggs were recorded, but as we had very limited knowledge of incubation history for the control plot, data on missing eggs were excluded from all plots for the comparison of control vs. study plots.

In mid-May, to verify that mice could open an intact and viable egg, two burrows were monitored overnight for two nights each with a remote video camera attached to an infrared burrow probe (Peeper burrow probe, Christensen Designs, Manteca, California). The monitored burrows were selected from those in which a cold but intact and uncracked egg had just been found, and the probe was positioned so as not to impede any access of a returning parent. We ended video monitoring after footage of a predation event was obtained from the second burrow.

Mean rodent body mass was obtained in late May from mice trapped with Sherman live traps baited with peanut butter. Mouse body mass was recorded to the nearest g with a 100-g Avinet or Pesola balance. Auklet eggs also were weighed, and measured for width and length to the nearest 0.1 mm using vernier calipers.

In order to determine whether predation rate at Triangle Island fluctuated with locality, we used z-tests to check for inter-plot differences in predation rates. We also tested the hypothesis that the risk of egg predation was higher early in incubation, when the rate of egg neglect is reportedly higher (Wilson 1977). Data for the two study plots were combined and chi-square analysis was used to test for differences in number of egg predation events in the first half of incubation vs. incidents in the latter half of the incubation period. Mean incubation time for Rhinoceros Auklets is 45 days (Wilson and Manuwal 1986) and the mid-point was rounded down to 22 days. Laying date was calculated conservatively. Burrow checks were done every 7 days, so egg age of day 1 was backdated to 6 days before an egg was first found. Eggs that were classified as abandoned and were later eaten were excluded from these analyses. Values below are reported as mean ± SD.

RESULTS

A total of 124 eggs were laid in the 217 study burrows. Causes of egg loss other than mouse depredation were varied, but totaled to less than all possible loss to rodents in both plots (Table 1). Depredated eggs were always chewed open at one end, usually on the small end, but on one occasion the large end. The egg was then opened along the top surface (Fig. 1). When found initially, egg contents were sometimes completely removed but most often were only partially eaten. Most (78%) of the depredation on Rhinoceros Auklet eggs took place during the first half of the incubation period ($\chi^2_1 = 5.7$, $P < 0.02$).

Although predation rate initially appeared to vary by plot, with 25% of eggs consumed by rodents in Plot 1 and 13% in Plot 2 (Table 1), the differences were not significant ($z = 1.3$, $P > 0.18$). Depredated eggs replaced by us in their burrows were generally chewed into fragments and widely scattered, often without a trace, by the following weekly burrow check. It was for this reason that we recorded missing eggs as having been likely depredated. When missing eggs were included, there was still no inter-plot variation ($z = 0.5$, $P > 0.6$), and rodent predation may have occurred in as many as 34% and 30% of nests in Plots 1 and 2, respectively (Table 1). Egg loss from all causes totaled to over 50% in each study plot (Table 1).

A total of 28 eggs were found cold on at least one occasion throughout May and June, although not all depredated eggs were cold on the previous check. Although many of these cold eggs were later found depredated, 7 of the 28 (25%) later hatched, indicating that egg-eating rodents have the opportunity to take viable embryos as well as those that have been abandoned. Of 49 eggs laid in the control plot, 6 (12%) were found depredated by rodents immediately before or after the 30-day non-monitoring period. Despite the increased likelihood of predation events being missed due to the length of the control period, the observed rate of egg depredation in the control plot did not differ significantly from the overall depredation rate for the two study plots ($z = 0.8$, $P > 0.4$) . We concluded that observer presence in the study plots did not increase egg predation artificially, either through disturbance of incubating birds or by providing olfactory clues to mice about an egg's location.

On average, auklet eggs were nearly twice the mass of mice. Mouse body mass was 43.8 ± 5.1 g ($n = 56$), and egg mass was 79.0 ± 5.4 g ($n = 18$). Mean egg size was 69 × 47 mm ($n = 18$). Despite this size difference, mice were still able to open intact eggs. The mouse filmed in our study took approximately 17 min to chew through the eggshell and begin consuming its contents. While chewing on the egg, the mouse alternated between lodging it against the camera lens and holding it immobile against the burrow floor. The mouse also rolled the egg vigorously about the burrow as well as chewing on it.

DISCUSSION

At Santa Barbara Island, California, deer mice (*P. m. elusus*) preyed upon Xantus' Murrelet (*Synthliboram-*

TABLE 1. Causes of Rhinoceros Auklet (*Cerorhinca monocerata*) egg loss at Triangle Island. Values are *n* (%).

Study plot	Eggs in plot	Rodent predation (A)	Missing eggs (B)	Total likely rodent pred. (A + B)	Corvid predation	Egg abandoned[a]	Egg cracked in burrow	Other[b]	Gone at hatching	Total egg loss
1	61	15 (24.6)	6 (9.8)	21 (34.4)	3	2	2	2	2	32 (52.5)
2	63	8 (12.7)	11 (17.5)	19 (30.2)	4	4	3	0	2	32 (50.8)

[a] Egg found cold on two or more consecutive checks.
[b] One nest chamber collapse, one adult dead in burrow from Peregrine Falcon (*Falco peregrinus*) attack.

phus hypoleucus) eggs only when parents were absent from the nest during the early post-laying period (Murray 1980, Murray et al. 1983). Gaston (1992) also reported that *Peromyscus* predation on the eggs of the Ancient Murrelet (*Synthliboramphus antiquus*) occurred during periods of parental absence. Our observations suggest that the situation is similar for Rhinoceros Auklets. Rhinoceros Auklets may neglect their egg during the first 8 days of incubation, although it is not known whether these neglected eggs are incubated at night (Wilson 1977). They may also neglect the egg for intervals of 1 to 3 days later in incubation (Wilson 1977, Wilson and Manuwal 1986, L. K. Blight, unpubl. data). In Cassin's Auklets (*Ptychoramphus aleuticus*), the incidence of natural egg neglect also is highest early in the incubation period, and lowest later on during the period of incubation corresponding to the most rapid embryonic development (Astheimer 1991). Consistent with this, most depredation on Rhinoceros Auklet eggs on Triangle Island occurred in the first half of the incubation period and likely coincided with the period of greatest egg neglect. An alternative explanation for these results is that incidents of egg neglect may be equally spaced throughout the incubation period and mice may simply switch to new, emerging food sources near the end of May. Given that unattended eggs are a large, high-energy food source, however, we predict that mice should take eggs whenever they find them available.

Egg predation by herbivorous voles has been reported elsewhere (Sealy 1982, Bureš 1997), but appears to be rare. We found no evidence that herbivorous Townsend's voles were present as predators in auklet burrows. Voles were observed eating only vegetation, and chew mark patterns on depredated eggs did not vary from those known by us to be caused by mice (pers. observ.). Although Larivière (1999) points out the problems involved in identifying nest predator species through examination of eggshell remains, particularly in diverse, terrestrial ecosystems, we are confident that identification of nest predators on Triangle Island presented few such difficulties. Introduced rabbits (*Oryctolagus cuniculus*) are the only other terrestrial, non-avian vertebrates found on Triangle Island (Carl et al. 1951).

Various experiments have used Japanese Quail (*Coturnix coturnix*) eggs to study predation by small mammals (Roper 1992, Haskell 1995, DeGraaf and Maier 1996). The results of these studies have generally been interpreted to mean that small rodents are gape-limited and cannot open any egg larger than that of a moderately-sized passerine. Rhinoceros Auklet eggs are about double the size of 33 × 23 mm reported for quail eggs by DeGraaf and Maier (1996). In addition, the shells of auklet eggs are thicker (0.29–0.40 mm; Gaston and Dechesne 1996) than quail eggs (0.22–0.23 mm; DeGraaf and Maier 1996). Mice preying on Rhinoceros Auklet eggs on Triangle Island are handling an item that is considerably larger, and thicker shelled, than a quail egg and in fact on average approaches two times rodent mass. The filming of a mouse depredating an auklet egg clearly illustrates that some murid rodents are able to open an intact egg despite a pronounced size difference between predator and prey item (Fig. 2). Gaston (1992) suggests that most suc-

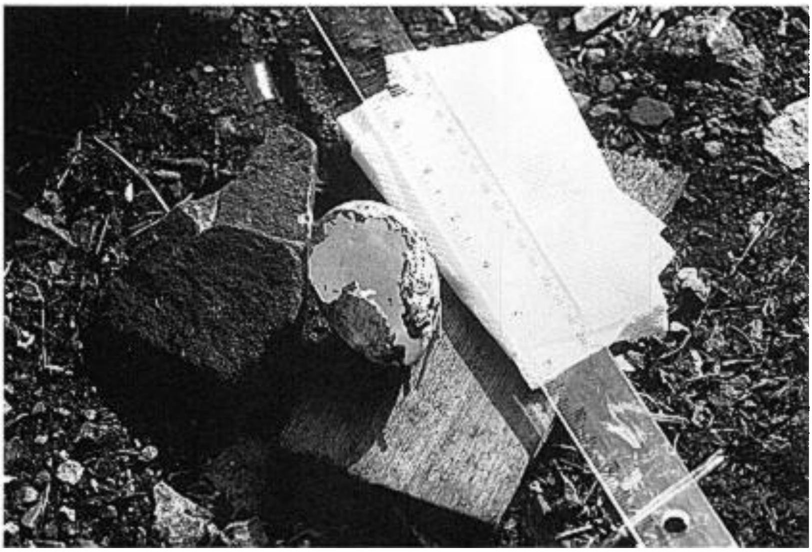

FIGURE 1. Mouse-depredated Rhinoceros Auklet (*Cerorhinca monocerata*) egg, Triangle Island, British Columbia, showing entry point at small end of egg.

FIGURE 2. Keen's mouse (*Peromyscus keeni*) opening intact Rhinoceros Auklet (*Cerorhinca monocerata*) egg, Triangle Island, British Columbia. Infrared video-camera image.

cessful mouse predation on Ancient Murrelet eggs was on those that were previously cracked. The mixed rock and earth substrate of auklet burrows may sometimes assist mice in opening eggs at Triangle Island, although the filmed egg did not appear to be cracked by rolling. Craig (1998) reports that least chipmunks (*Tamias minimus*) were only able to open quail eggs when the egg was lodged between the predator's body and the inside of the nest. Once this was achieved, the small end of the egg was readily bitten through. The consistency with which auklet eggs were found opened from the small end indicates that whether a depredated egg is initially cracked or intact may be unimportant. Scarcity of food supply through the winter months is likely the limiting factor controlling the mouse population at Triangle Island (Carl et al. 1951). Egg laying for Rhinoceros Auklets there begins in mid-April, and seabird eggs may provide mice with an alternate high-protein food source at a time when seeds are unavailable and other foods still scarce.

In conclusion, depredation by *Peromyscus* can contribute substantially to egg mortality for Rhinoceros Auklets nesting on Triangle Island. Total egg loss appears to be higher there than on islands where mice are absent: at a Washington State Rhinoceros Auklet colony with no rodent predators, an estimated 81.5% and 91.1% of eggs hatched over a two-year study (Wilson 1977). Our preliminary data show a probable link between egg neglect and predation. Given that egg neglect is an adaptation in marine birds to deal with patchy and distant food sources (Lack 1967), there is likely to be inter-annual variation of neglect with more frequent or longer periods occurring in years of poor food availability. As El Niño conditions appeared to affect prey composition and availability for Triangle Island seabirds in 1998 (Triangle Island Research Station, unpubl. data), the rate of egg predation by mice may have been higher during our study than in other years. Whether egg predation shows inter-annual fluctuations related to neglect patterns remains to be tested.

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THE PROXIMATE EFFECTS OF RAINFALL ON CLUTCH SIZE OF THE CALIFORNIA GNATCATCHER[1]

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Abstract. It has been hypothesized that clutch size in bird species occurring in arid habitats is influenced by annual rainfall. We propose an alternative hypothesis that avian clutch size in resident species should be more strongly associated with rainfall in the short-term (during egg-formation) than during the long-term (cumulative across the season). We tested this hypothesis with museum egg-sets for California Gnatcatcher (*Polioptila californica*) nests taken in southern California combined with rainfall data from the geographically closest weather station to nest collection site. Clutch size was independent of laying date. Seasonal rainfall was not a good predictor of clutch size; rainfall during egg formation was a better predictor. Using isotonic regression, we detected a strong positive trend in the association between clutch size and cumulative rainfall, with cumulative rainfall across 1 month prior to the estimated month of clutch completion having the strongest positive association. These data support the hypothesis that smaller clutches result from more immediate conditions, not from the wet-year/dry-year dichotomy.

Key words: California Gnatcatcher, clutch size, isotonic regression, nutritional constraints, Polioptila californica, *rainfall.*

In arid environments, the availability of energy and nutrients essential for egg formation in birds, namely fats, proteins, calcium, and water (Perrins 1996), often varies in direct proportion to rainfall. As a result, variation in the timing of egg-laying and clutch size in many species often is strongly associated with precipitation (Newton 1998). In some arid regions, however, precipitation is strongly seasonal, concentrated in one portion of the year and alternating with a dry period, frequently with no rain at all. Furthermore, the onset, duration, and quantity of precipitation that occur during the wet season are usually highly variable from year to year, frequently with little temporal autocorrelation across years (Rotenberry and Wiens 1991). Thus, favorable conditions also may be ephemeral. It follows that birds living in such environments are most likely under strong selection for flexibility to lay the number of eggs that closely matches current and predicted future conditions. Although the physiological mechanisms by which this prediction and matching might be achieved are not known, it must involve the integration of internal and external conditions over some previous period of time. The question arises, then, over what period of time does this integration and response occur?

Traditionally, the statistical assessment of clutch size variation in birds inhabiting such seasonal environments is based on a correlation between clutch size and total precipitation accumulated across the rainy season (Newton 1998); larger clutches are expected in wetter years. This analysis implicitly assumes that the clutch size "decision" is based on conditions summed over the entire period, which may be up to 6 months long. However, it is reasonable to assume that if desert species have been selected to respond appropriately to possibly ephemeral conditions, then the relevant period for assessing that response may be shorter than the full wet season. In this case, clutch size should be better predicted by rainfall in a much shorter term, perhaps just that during the period of egg formation itself, just prior to laying.

To test these alternatives, we examined data from museum egg-sets for the California Gnatcatcher (*Po-*

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