INTERANNUAL VARIATION IN EGG NEGLECT AND INCUBATION ROUTINE OF RHINOCEROS AUKLETS *CERORHINCA MONOCERATA* DURING THE 1998-1999 EL NIÑO / LA NIÑA EVENTS

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SUMMARY

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We used artificial eggs containing miniature temperature loggers to quantify nest attendance patterns by breeding Rhinoceros Auklets *Cerorhinca monocerata* over two seasons. The first year coincided with a strong El Niño event and low breeding success, while the second was one of La Niña conditions and high colony-wide productivity. Logger data revealed highly variable patterns of parental nest attendance between the two years. In 1998, we recorded 0–17 periods of neglect per breeding pair (n = 7), as well as nest abandonment part way through the incubation period. In 1999, the number of periods of egg neglect ranged from 0–3 (n = 13), and no monitored nests were abandoned. As in other seabird species, more pairs (62%) exhibited neglect during the first third of incubation than during the subsequent two-thirds. The longest period an egg was left unattended was nearly 3 d (69 h); the shortest was 9 h. We conclude that incubating Rhinoceros Auklets were able to modulate nest attendance behaviour in response to changing oceanographic conditions and prey availability, likely mediated via their own body condition. We recommend use of similar egg models for future studies on avian nest attendance.

Key words: nest attendance, incubation temperature, incubation period length, life-history, foraging behaviour, artificial eggs, nest monitoring

INTRODUCTION

Unlike terrestrial birds, many species of seabirds forage far from their breeding sites. Alternating nest attendance by the two parents allows for long distance foraging trips during lengthy incubation periods. Even so, limited food availability or poor weather can sometimes delay birds in their return to the nest. Thus, egg temperatures may drop to ambient levels for periods of a day or more (Wheelwright & Boersma 1979, Gaston & Powell 1989, Warham 1990), even in localities where the ambient summer temperature is as low as 0°C (Roberts 1940, Pefaur 1974).

Repeated occurrences of this behaviour ("egg neglect") do not necessarily compromise embryo viability (Boersma & Wheelwright 1979, Gaston & Powell 1989) and embryonic resistance to chilling in seabirds has been suggested as an adaptation for foraging on distant and patchy food resources. Irregular nest attendance during incubation has also been proposed as an explanation for the wide intraspecific variation in incubation periods of some marine birds (Boersma & Wheelwright 1979, Roby & Ricklefs 1984, Sealy 1984, Astheimer 1991), for interspecific variation in passerines (Martin 2002), and for variation among egg-laying vertebrates in general (Deeming & Ferguson 1991). Though labile incubation behaviour is frequently noted, and potential fitness costs are inherent in such variability (e.g. Martin 2002), the phenomenon of egg neglect remains inadequately studied.

Egg neglect is widely reported in burrow-nesting members of the Alcidae (Summers & Drent 1979, Murray *et al.* 1979, 1983, Sealy 1984, Gaston & Powell 1989, Blight *et al.* 1999). We used artificial eggs containing miniature temperature loggers to quantify nest attendance patterns of one member of the family, the Rhinoceros Auklet *Cerorhinca monocerata*, throughout the incubation period in two seasons at a colony in the northeast Pacific. The first season (1998) coincided with a strong El Niño event and some of the highest regional sea surface temperatures (SSTs) recorded for the century, resulting in poor forage fish availability and low breeding success at the colony. In the second year (1999), oceanographic conditions shifted and cold, productive La Niña conditions prevailed, with seabird breeding parameters indicating above-average availability of high-quality fish prey (i.e. Pacific Sand Lance *Ammodytes hexapterus*) in the region (Department of Fisheries and Oceans 2000, Bertram *et al.* 2001, 2002, Hedd *et al.* 2006). Lack (1967) and others have suggested that egg neglect in marine birds is directly determined by food availability. On that premise, and with demonstrated links between oceanographic conditions and availability of seabird prey at our study site (Bertram *et al.* 2001, 2002, Gjerdrum *et al.* 2003, Hedd *et al.* 2006), we inquired whether patterns of nest attendance at the colony differed between the two years of our study. In addition, we wanted to know whether the incidence of egg neglect decreased as incubation progressed, as reported for other alcids (Murray *et al.* 1983, Gaston & Powell 1989, Astheimer 1991).

STUDY AREA AND METHODS

Fieldwork took place at the seabird colony on Triangle Island, British Columbia (50°52'N, 129°05'W), from April to July of 1998 and 1999. In 1998, we built artificial eggs by placing miniature temperature loggers (Hobo Tidbits, Onset Computer Corp., Pocasset, MA) inside hollow plastic hobby eggs. The two halves of each egg were filled with an agar solution to approximate the thermal conductivity of a real egg and to hold the temperature logger in place. The eggs were glued shut and painted white once the agar solution solidified; the eggs' seams were filled and smoothed with glue and paint and were thus not evident to the touch. These artificial eggs were equivalent to the minimum size reported for Rhinoceros Auklets (length range 63.2 – 73.6 mm; width range 42.8 – 48.9 mm; n = 45; Gaston & Dechesne 1996). In 1999 we used more durable artificial eggs that were slightly larger, measuring 68.6 × 48.4 mm on average. Data loggers were encased in an agar medium inside a plastic hobby egg, as in 1998, but each egg was augmented with a thin coating of Dry-hard modelling clay and plaster of Paris. Eggs were then painted with a white enamel to guard against possible disintegration in the auklets' damp nesting burrows. As the size of both models fell within the natural range for eggs of this species, we assumed they were equally acceptable to incubating parents. Data loggers were set to read temperatures to the nearest 0.01°C at intervals of 10 min in 1998, and 30 min in 1999. We compared the relative temperature sensitivity of the two egg models by placing two of each type in a drying oven set at approximate incubation temperature (35.0°C) for 48 h. For analysis purposes, and based on observed acceptance patterns, we assumed that the differences in egg models between years did not affect the difference in parental egg neglect behaviour between years.

In 1998, we checked auklet burrows once per week for newly-laid eggs, beginning in late April. Artificial eggs were warmed to body temperature prior to placement, and then carefully substituted for the auklets' own eggs. Of 18 artificial eggs used the first year, we substituted 14 for a bird's own egg within 3 days of it being found (i.e. within ≤10 days of lay date). The remaining four artificial eggs were initially field-tested and were not available to be placed until mid-May, about a week after the eggs they replaced were found. In 1999, study burrows were monitored for a newly-laid egg at least twice a week, and we placed artificial eggs within seven days of the actual lay date. In 1998, we left artificial eggs in place until the peak period of hatching in the colony. As we had more accurate knowledge of laying dates in 1999, we modified our protocol and removed our data loggers slightly earlier in the season, when the parents' real egg would have been a minimum of 42 d old. That interval approximated the average incubation period (45 d, range 39–52 d; Wilson 1977) in Rhinoceros Auklets. In all, incubation behaviour was monitored with the temperature loggers for at least 40 d per burrow in 1998. In 1999, all burrows were monitored for at least 36 d, with all but two being monitored for 40 d or more. As in other marine birds, laying dates of Rhinoceros Auklet vary with breeding experience. Therefore, we attempted in both years to eliminate confounding effects of parental experience by placing artificial eggs with birds whose laying dates spanned the laying period, i.e. study burrows were representative of Rhinoceros Auklet egg-laying dates for the colony. Rhinoceros Auklets lay only a single egg, so we could not determine hatching success in the monitored burrows.

We defined a period of egg neglect as one where artificial eggs dropped to ambient burrow temperature for >3.5 h, followed by a parent resuming incubation (i.e. abandoned eggs were placed in a different category). This cut-off value was based on apparent daytime behaviour by incubating birds. Occasionally, egg temperature dropped steadily for short periods (≤3.5 h), either to ambient levels or fluctuating around a lower mean than the normal incubation temperature. Such brief incubation recesses occurred during daylight hours, when breeding birds did not leave their burrows, and also at night when birds come and go from the colony. We therefore assumed that brief nocturnal temperature drops could indicate either an individual's incubation recess within the burrow or an asynchronous incubation exchange between parents. Because we were unable to ascertain the precise nature of the shorter nocturnal temperature fluctuations, we did not consider them to be incidents of neglect *per se* and we excluded them from our analyses. Our cut-off value of 3.5 h was a non-arbitrary indicator of different behaviours, as the shortest period we interpreted as true neglect was 9 h.

Artificial eggs incubated for only 1–2 days at the onset of egg placement, i.e. by a single parent, were considered to be rejected by nesting birds, and their data were not incorporated in results.

Statistical analyses

We conducted a comparison (unequal variance *t*-test) between annual means of the number of per-burrow egg neglect events. Because we were also interested in whether individual birds might be variably affected by interannual differences in environmental conditions, we analysed the same data using Levene's test for equality of variances. In addition, we used a two-tailed *t*-test to compare annual means of mean per-burrow duration of neglect events. In 1998, two of our monitored burrows were deserted approximately halfway through incubation. We included the data from both burrows to increase our sample size for that year. To determine whether most egg neglect took place early in incubation, as has been shown in other alcids, we contrasted periods of neglect for the first third versus the remainder of the incubation period. Here we used Fisher's exact test, as we had low numbers of egg-neglect periods later in incubation. Because we placed artificial eggs later relative to lay date in 1998, our 1999 data better represented nest attendance behaviour over the entire incubation period, and thus we used only 1999 data for the latter analysis. To compare the rates of acceptance each year, we used a 2-sided test of equal proportions.

To compare temperature sensitivity between our two models of artificial eggs, we determined the mean time required by each egg type to stabilize at the drying oven's set temperature (calibrated against the factory-tested data loggers' output) and the mean maximum temperature attained by each model. Mean values are reported with their standard errors (SE).

RESULTS

In the drying oven, plastic and Dry-hard clay models (n = 2 of each type) attained similar mean maximum temperatures (34.25°C and 34.96°C in plastic models; 34.34°C and 34.73°C in Dry-hard models; **t** = 0.17, *df* = 1, **P** = 0.89), and on average, they attained maximum temperature in similar amounts of time (plastic 67 and 72 min, Dry-hard 67 and 69 min; *t* = 0.56, *df* = 1, *P* = 0.68).

In 1998, 7 (39%) of 18 artificial eggs were accepted by incubating birds as substitutes for their own egg, while in 1999 we obtained data with 13 (65%) of 20 model eggs (*z* = –1.67, *P* = 0.10). Whether an artificial egg had been accepted or rejected was readily evident from logged temperature data, with nesting pairs that accepted an egg continuing with incubation from the time of substitution, and individuals that rejected an artificial egg abandoning the egg immediately.

For accepted eggs, nest attendance patterns were well-represented by temperature logger data (Fig. 1). When artificial eggs were left unattended by the incubating adult, internal temperatures dropped rapidly (<1 h) to the ambient burrow temperatures (range 5.7°C – 12.2°C) consistent with parental absence. Though we found no difference in the mean number of neglect incidents per monitored burrow (6.14 ± 2.6 and 1.38 ± 0.31 for 1998 and 1999, respectively; *t* = 1.78; *df* = 6, *P* = 0.13), the logger data revealed greater among-burrow variability in the number of neglect events in 1998 (*W* = 8.46, *df* = 1, *P* = 0.009). That year, nest abandonment occurred approximately halfway through the incubation period in 28.5% (2 of 7) of the monitored burrows, and total incidents of neglect per burrow ranged from 0 to 17. In 1999, all accepted artificial eggs were incubated for the entire incubation period, and the number of neglect periods per burrow ranged from 0 to 3. Similar percentages of burrows (29% in 1998, 31% in 1999) experienced no egg neglect at all during the monitored period.

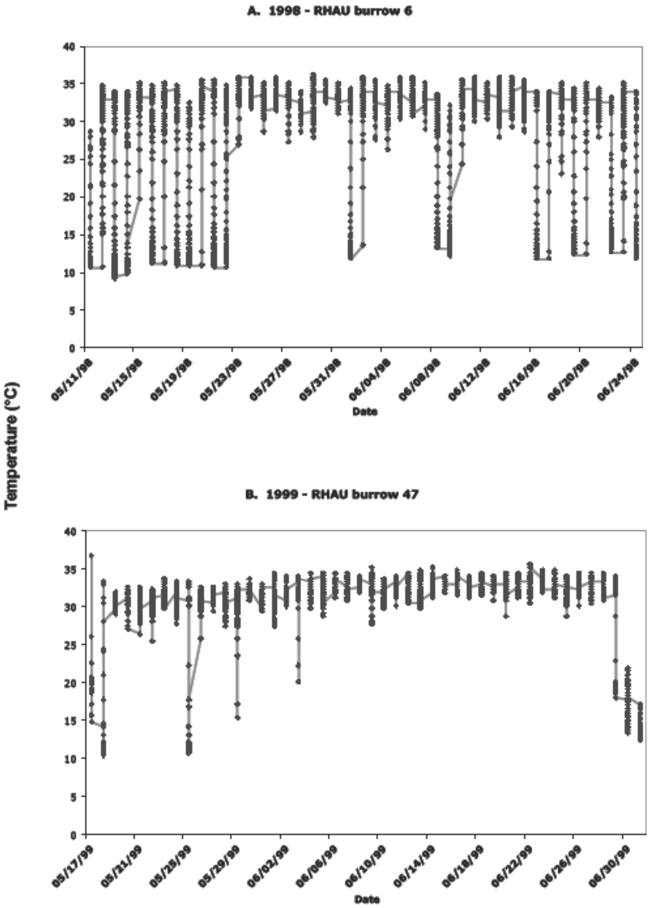

Fig. 1. Examples of temperature profiles for two incubated artificial Rhinoceros Auklet (RHAU) eggs in (A) 1998, and (B) 1999. Neglect periods show as decreased temperatures, with an overall mean length of 24.1 h. Final drops in temperature are due to egg removal from nests at the end of the monitoring period.

Despite interannual variability in nest attendance patterns, the mean length of neglect periods was invariant (*t* = –0.10, *df* = 13, *P* = 0.92), lasting about 1 d on average (overall mean of mean per-burrow egg neglect periods: 23.7 ± 3.58 h and 24.5 ± 4.93 h in 1998 and 1999, respectively). The maximum time that an egg was left unattended in 1998 was 49 h, while in 1999 both parents were absent from one burrow for 69 h. The minimum duration of egg neglect over the two years of the study was 9 h.

In 1999, we placed most artificial eggs within one week of individual laying dates. The 1999 data, better representative of the whole incubation period than 1998, indicated that a higher proportion of burrows experienced neglect during the first third of the incubation period (monitored days 0–10; *P* = 0.04, *df* = 1). Specifically, eggs were neglected in 62% of monitored burrows during the first third of incubation versus 15% of monitored burrows in the subsequent two-thirds of the monitored period.

DISCUSSION

Temperature data showed more variable incubation behaviour among auklets in 1998 than in 1999, though we found no difference in the average number of per-burrow bouts of neglect between years. However, low statistical power suggests the possibility of a type II error in our test of egg neglect frequency (retrospective power analysis; β = 0.65). Also, as most egg neglect appears to take place earlier in incubation, we would expect any bias in our data to underestimate neglect frequency in 1998 relative to 1999. If anything, the frequency of egg neglect was higher in 1998 than is reported here.

It is possible that interannual variability in recorded incubation patterns was an artefact of changing egg models between years, despite the absence of a statistically significant difference in acceptance rates. Here again, low statistical power may have masked a difference in egg model acceptance rates, as the data suggested a possible effect. Nonetheless, we suggest that for accepted eggs, temperature loggers recorded real variability in incubation behaviour. In both years, birds that did not reject an artificial egg upon placement continued attendance for all or most of the incubation period; once a pair made the decision to accept an egg model, they appeared to treat it as their own. Moreover, we would predict decreased acceptance in 1998 based on the hypothesis of low food availability, as disturbance can more readily induce nest desertion in food-stressed birds (O'Dwyer *et al.* 2006).

More variable nest attendance and the trend toward a higher frequency of neglect events in 1998 was coincident with unusual environmental conditions, and is consistent with the suggestion that differences in parental performance are accentuated under such circumstances. This phenomenon is well documented for a range of species and systems (e.g. Murphy *et al.* 1992). The year 1998 was characterised by an El Niño event that produced some of the highest sea surface temperatures recorded on the southern British

Columbia coast in the 20th century (Hedd *et al.* 2006). In our study region, Rhinoceros Auklet prey primarily on juvenile fish in summer (Hobson *et al.* 1994, Hedd *et al.* 2006), and we suggest that incubation patterns observed in 1998 were due to breeding birds having difficulty in locating forage fish during their time away from the nest. The suggested relationship between recorded incubation behaviour and reduced forage fish availability is corroborated by multi-species, colony-wide data on chick growth and diet in 1998, reflecting low availability of high-quality fish (Department of Fisheries and Oceans 2000, Bertram *et al.* 2001, 2002, Gjerdrum *et al.* 2003, Hedd *et al.* 2006). In 1999, a La Niña year of above-average breeding performance in Rhinoceros Auklets and other seabird species on Triangle Island (Department of Fisheries and Oceans 2000, Bertram *et al.* 2001, Hedd *et al.* 2002, Gjerdrum *et al.* 2003, Hedd *et al.* 2006), artificial eggs recorded egg neglect in a similar percentage of monitored burrows, but with reduced variability. Our observations of variability in incubation behaviour are also consistent with colony-wide rates of hatching success, which differed between the two years of our study (46.7 % of 75 eggs in 1998 and 70.5 % of 61 eggs in 1999; $z = -2.90$, $P = 0.004$: Triangle Island Research Station, unpubl. data). At Triangle Island, hatching success of this species is highly dependent on nest attendance. Though Rhinoceros Auklet embryos tolerate considerable periods of chilling (see below), egg neglect facilitates egg predation by native mice *Peromyscus keeni* (Blight *et al.* 1999).

The maximum duration of continuous neglect by Rhinoceros Auklets at Triangle Island was nearly three consecutive days—much shorter than the maximum of seven continuous days recorded for a viable egg of the highly pelagic Fork-tailed Storm-Petrel *Oceanodroma furcata* (Boersma *et al.* 1980), but similar to that recorded in other alcids (e.g. Murray *et al.* 1979). However, the mean duration of recesses was about 24 h. As Rhinoceros Auklets return to the colony only at night, an incubating parent departing from the nest before its mate returns most likely results in an egg being unattended for an entire day, until sometime during the following evening.

We found that the majority of egg neglect occurred in the first third of incubation. Nest attentiveness increases as the incubation period progresses in a number of avian taxa, even when measured from the time of clutch completion (Webb 1987, Stoleson & Beissinger 1999, Poussart *et al.* 2000). The pattern is observed in various seabirds, including alcids (Gaston & Powell 1989, Astheimer 1991, Ronconi & Hipfner 2009). Decreasing neglect has been attributed to poor initial coordination of incubation exchanges by inexperienced breeders (Wilson 1977), stringent developmental requirements in older embryos (Webb 1987, Astheimer 1991), facilitation of synchronous hatching in multi-egg clutches (Sealy 1984), or an initial period of neglect that allows females to gain resources for the second egg of a clutch (Murray *et al.* 1983). As Rhinoceros Auklets lay single-egg clutches, the latter two explanations do not apply. We suggest the greater neglect early in incubation is a response to the body condition of breeding Rhinoceros Auklets early in incubation, but that hypothesis remains to be tested by future studies. Body condition reportedly plays a role in pelagic birds such as the Blue Petrel *Halobaena caerulea*, in which the decision to desert an egg temporarily is triggered at a mass threshold below which the parent's own survival is compromised (Chaurand & Weimerskirch 1994).

Rhinoceros Auklet eggs have been observed hatching after periods of natural neglect lasting 4 or 5 consecutive days (Summers & Drent 1979), and tolerance of up to 4 days of continuous neglect has been reported for embryos of other Alcidae (Murray *et al.* 1979, Gaston & Powell 1989). We therefore consider it likely that embryos would have survived the prolonged absences recorded by our data loggers. Embryonic tolerance of periodic chilling is adaptive for seabird species that feed on ephemeral resources at a distance from the colony. Selection generally favours the evolution of shorter incubation periods in birds (Ricklefs & Starck 1998, Martin 2002), but in many marine birds, incubation is protracted compared to other birds of similar body size (Ricklefs 1984). Although that contrast is apparent even in the absence of egg neglect (Ricklefs 1984), periodic chilling of the embryo increases the incubation period commensurate with the combined duration of cooling periods (Boersma & Wheelwright 1979, Blight 2000). The historical absence of terrestrial predators on islands, and relaxed selection for short incubation periods, has likely allowed the evolution of embryonic resistance to periodic chilling, or its retention as an ancestral reptilian trait (cf. Ricklefs & Starck 1998, Deeming & Ferguson 1991).

We found temperature loggers placed in artificial eggs to be an effective technique for monitoring parental nest attendance and recommend the approach for nest monitoring elsewhere. We note that our methods differed from the majority of studies using artificial eggs, in which models have been anchored in place among other eggs in a clutch to maintain wire connections to external data loggers (e.g. Hoover *et al.* 2004). Other nest monitoring studies have used a temperature probe in the nest cup itself, an approach that cannot accurately measure incubation temperature and is limited to monitoring presence or absence of an incubating bird (e.g. Gaston & Powell 1989). Though we did not report incubation temperature using our self-contained egg model, if calibrated it would function well in a study of incubation temperature. Overall, our model better simulated a real egg, an important consideration particularly when monitoring incubation in species with small clutches.

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