NATURAL INCUBATION, EGG NEGLECT, AND HATCHABILITY IN THE ANCIENT MURRELET

ANTHONY J. GASTON AND DAVID W. POWELL[1]
Canadian Wildlife Service, 100 Gamelin Boulevard, Hull, Québec K1A 0H3, Canada

ABSTRACT.—We monitored natural incubation in the Ancient Murrelet (*Synthliboramphus antiquus*) with temperature probes fixed in the nest cup. At undisturbed nests, eggs hatched after 30.1 ± 0.6 days of incubation. Egg neglect was common during the early stages of incubation, but did not occur in the second half of incubation unless the incubating bird was disturbed. We removed eggs from burrows after 10 and 20 days of incubation and kept them for 48 h at the prevailing burrow temperature. Where desertion did not occur, hatchability was unaffected. In Thick-billed Murres (*Uria lomvia*), eggs removed similarly during the second half of incubation did not hatch. The ability of Ancient Murrelet embryos to withstand chilling during late incubation is matched only by some Procellariiformes. *Received 21 October 1988, accepted 19 March 1989.*

INTERRUPTIONS to incubation occur routinely in many species of birds. They range from excursions of a few minutes in many Passeriformes (Drent 1975, Haftorn 1988) up to periods of several days in some Procellariiformes (Boersma 1982). Interruptions of a day or more are referred to as *egg neglect* and have a considerable effect on the length of the incubation period (Murray et al. 1980, Boersma and Wheelwright 1979).

Most Alcidae lay single-egg clutches and normally incubate continuously from laying (Harris and Birkhead 1985, Sealy 1984). Ancient Murrelets (*Synthliboramphus antiquus*) lay two eggs and frequently do not begin to incubate until 1 or 2 days after the second is laid (Sealy 1976). Sealy (1976) observed frequent egg neglect by Ancient Murrelets after the start of incubation, but he was unable to ascertain how much this neglect was caused or aggravated by the disturbance involved in making observations. Moreover, it was unclear how the observed neglect might have affected hatchability, because most burrows were deserted before hatching.

In the closely related Xantus' Murrelet (*Synthliboramphus hypoleucus*), egg neglect is frequent after the start of incubation even in the absence of physical disturbance to incubating birds (Murray et al. 1980, 1983). In this species, the total number of days for which eggs were incubated decreased with increasing neglect, presumably because ambient temperatures (average ca. 20°C) were sufficient for some development to continue without incubation. Neglect had little effect on subsequent hatching success. Murrelets of the genus *Synthliboramphus* incubate in shifts of ca. 3 days (Sealy 1976, Murray et al. 1983, Gaston pers. obs.), longer than those recorded for any other alcid (Sealy 1976, Harris and Birkhead 1985).

Temperatures in areas where Ancient Murrelets breed (average during the incubation period < 10°C) are much lower than those recorded for Xantus' Murrelets. It is therefore less likely that development will continue in the absence of incubation (Webb 1987). In addition, if neglect is not a normal feature of Ancient Murrelet biology, but an effect of observer disturbance, we might expect a greater risk of embryos failing to hatch as a result of chilling.

We examined incubation in breeding Ancient Murrelets to determine the occurrence of egg neglect after clutch completion in the absence of disturbance to incubating birds, its effect on incubation periods, and the effect of neglect at different stages of incubation on subsequent hatchability. We compared our results for Ancient Murrelets with those obtained by Murray et al. (1983) for Xantus' Murrelet, which breeds in a much warmer climate.

Because little information is available on the hatchability of alcid eggs that have been neglected at different stages of incubation, we collected similar data for Thick-billed Murres (*Uria lomvia*). Egg neglect is very infrequent in this

[1] Present address: 352 North Dollarton Highway, North Vancouver, British Columbia V7G 1N1, Canada.

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species, which lays a single egg that is incubated continuously from laying (Gaston and Nettleship 1981).

METHODS

Observations on Ancient Murrelets were made at Reef Island, British Columbia (52°52′N, 131°31′W), in 1984–1988. Ancient Murrelets breeding at this colony, like those studied by Sealy (1976), lay their eggs in burrows constructed so that the incubating bird normally cannot be seen from the entrance (Gaston et al. 1988). Samples of occupied burrows were checked once daily in 1984 and 1985 to determine the presence of eggs, chicks, and incubating birds. Eggs were marked to identify laying order. In 1984, the presence of an incubating bird was ascertained by touch or directly in the few cases where it was visible. Procedures in 1985 were similar, but plastic tags were placed in burrow entrances to reduce disturbance, and burrows were inspected only when these were displaced. In 1986 procedures were similar to 1985, but inspections began only after clutches were complete, so that we obtained no information on incubation periods. By working back from observed dates of hatching, however, we were able to obtain records of neglect in the second half of incubation. In 1987 inspections were made every 4 days, and only anecdotal observations were obtained.

In 1988 we inserted a temperature probe (Yellow Springs Instruments 400 series) in each burrow, after the first egg was laid. We secured the tip in the nest cup with wire hoops fixed into the floor of the burrow. No bird was ever present in a burrow when the probe was inserted. Subsequently, we checked daily for the presence of an incubating bird by connecting a telethermometer (Yellow Springs Instruments 400 series) to the probe and reading the temperature. When originally fixed, the tip of the probe was either beside and within 1 cm of the egg, or directly underneath it. Because we could not inspect burrows once incubation had begun, we could not be certain of the exact position of the probe relative to the eggs during incubation. Hence, we could not use our observations as a measure of incubation temperature.

In most cases there was a difference of at least 4°C between initial burrow temperatures (5–7°C) and those recorded once incubation had begun (9–25°C). Probes were 2-m long, which enabled us to remain at least 1 m from the burrow entrance and 1.5 m from the nest chamber while we read nest temperatures. This non-intrusive technique for study of the constancy of incubation in seabirds using concealed nest sites was used previously by Pefaur (1974).

After 28 days of incubation had been recorded at the study burrows, the eggs were inspected visually every 2 days for pipping; once pipped, they were checked daily for hatching. In 1984 and 1985, eggs that were not pipped on one day had rarely hatched the next day. In a few cases, eggs that were not pipped one day were found hatched two days later: we assumed that these eggs had hatched in the second of the two days before inspection.

Incubation period is that time between the laying of the last (second) egg and the hatching of that egg (Drent 1975). The method used in 1988 did not allow us to determine the exact incubation period, because we did not know exactly when the second egg was laid, but it allowed us to measure the number of days of incubation. The advantage was that we caused no disturbance to the burrow while birds were incubating, until close to hatching. Because burrows were inspected only once daily in all years, all measurements were made in whole days. During the incubation period, however, breeding birds arrived at and departed from the colony during a period of <6 h (Jones 1985). Hence, one day of neglect represented at least 18 h without incubation; two days represented at least 42 h.

To investigate the effect of egg neglect, eggs were experimentally removed for 48 h after ca. 10 days of incubation at six burrows, and after ca. 20 days of incubation at four burrows. The eggs were placed in unoccupied burrows close to the nest site, so that they experienced conditions similar to those of "neglected" eggs. To prevent desertion, only one egg was removed initially. The second was removed when the first was returned to the burrow, so that the second egg had been incubated for 12 or 22 days when removed. In two cases, the burrow was "neglected" for 1 day after the first egg had been removed. When this occurred, we returned the second egg after only 1 day's removal, so that both eggs were unincubated for the same number of days.

We observed Thick-billed Murres at Coats Island, Northwest Territories (62°57′N, 82°00′W), in 1988. Eggs were removed for 48 h after 5, 15, and 25 days of incubation. Initially six eggs were used in each test. An additional six eggs were removed for 96 h after 15 days of incubation. Each batch included some eggs laid early in the laying period and some laid close to the peak, about a week later. All were replaced with model eggs made from plaster of paris and painted to resemble typical Thick-billed Murre eggs, but no attempt was made to match the models to the eggs removed. All models were accepted and incubated immediately.

The eggs that were removed were kept beneath a blind close to the top of the breeding colony, where the shade temperature was close to that on the colony. Concealment was necessary to avoid predation by gulls. We recorded maximum and minimum shade temperatures daily. After they were returned to their original site, eggs were checked every two days for signs of hatching. Because some eggs were subsequently removed by predators, an additional four eggs

TABLE 1. Numbers of Ancient Murrelet clutches for which incubation periods and the number of days of actual incubation were recorded in 1984 and 1985, and the number of days of incubation observed for experimental and control clutches in 1988.

	Incubation period (days)									Days incubated					
Year	29	30	31	32	33	34	35	36	37	28	29	30	31	32	33
1984		1	2	1			2			1	2	2	1		
1985	1	1	3	2	1	2	1	2	1	1	1	6	5		1
1988 (control)											4	15	7		
1988 (10-day removal)											1	3			
1988 (20-day removal)														3[a]	
Totals[b]	1	2	5	3	1	2	3	2	1	2	7	23	13		1

[a] Compared with 10-day removals, Mann-Whitney $U = 0$, $P = 0.028$. Compared with controls, Mann-Whitney $U = 0$, $P < 0.0001$.
[b] Excludes experimental burrows.

were removed for 48 h after 15 days of incubation. These were either replacement or late-laid eggs.

RESULTS

Incubation periods recorded for Ancient Murrelets in 1984 averaged 32.3 ± 2.2 days (n = 6, range 30–35), and in 1985 the average was 32.9 ± 2.5 days (n = 14, range 29–37). The corresponding figures for the mean number of days incubated were 29.5 ± 1.0 days (n = 6, range 28–31) in 1984 and 30.3 ± 1.1 days (n = 14, range 28–33) in 1985 (Table 1). The interval between the laying of the second egg and the start of incubation averaged 0.5 days in 1984 and 1.6 days in 1985, hence neglect after the start of incubation averaged 2.3 days per nest in 1984 and 1.0 days in 1985. Many nests were neglected for much longer, but, as in Sealy's (1976) study, most of these were deserted before the eggs hatched. Combining data for 1984 and 1985, the number of days of neglect explained 64% of the variation in incubation periods ($r = 0.799$, $n = 20$).

The duration of periods of neglect tended to become shorter as incubation progressed, although the effect was rather weak ($r = 0.306$, $n = 40$, $P \simeq 0.05$). Eggs hatched successfully after being unincubated for one or more days at up to 29 days of incubation, by which time they were pipping (Fig. 1). In 1984 and 1985, neglect after >7 days of incubation occurred at 9 of the 12 nests affected. In 1986, out of 22 clutches that hatched, 2 clutches were neglected for 1–2 days at 10 days before hatching, and 1 was neglected for 3 days at 5 days before hatching. In 1987 one clutch was neglected for 2 days at 16 days before hatching and one for 1 day at 5 days before hatching. Both hatched successfully.

In 1988 we placed temperature probes in 46 control burrows. Of these, 34 clutches survived to the check after 28 days of incubation; 6 were deserted after <7 days of incubation (3 were never incubated at all); eggs in 5 clutches were destroyed by mice; and 1 set of eggs disappeared after the burrow collapsed. We obtained complete data on incubation for 26 clutches. The remainder were either found after the clutch was complete, or temperature records did not differentiate clearly between periods of incubation and neglect, presumably because the activities of the birds dislodged the temperature probe from the nest cup.

Neglect after the beginning of incubation occurred at 19 of the 26 control burrows in 1988 (73%), compared with 12 of 20 (60%) in 1984 and 1985 ($\chi^2 = 1.01$, df = 2, $P > 0.10$). At 9 burrows (35%), the only period of neglect occurred after just one day of incubation. Of the 19 clutches neglected at least once in 1988, only 1 was neglected after >7 days of incubation, significantly less than in the combined 1984 and 1985 sample ($\chi^2 = 16.4$, df = 2, $P < 0.01$). However, 2 clutches were neglected for 1 day following the physical examination on the 28th day of incubation, and 1 of these was destroyed by mice. One other clutch was deserted completely at the same point. The mean amount of neglect in 1988, up to the day 28 examination, was 1.6 days per clutch. The number of days of neglect that occurred after the beginning of incubation explained 82% ($r = 0.91$, $n = 26$, $P < 0.001$) of the variation in the length of time to hatching at the control burrows, or 69% ($r = 0.83$) if the single 7-day period of neglect is omitted (Fig. 2). The regression coefficient (0.88 ± 0.08) does not differ significantly from the value of unity expected if one day of neglect

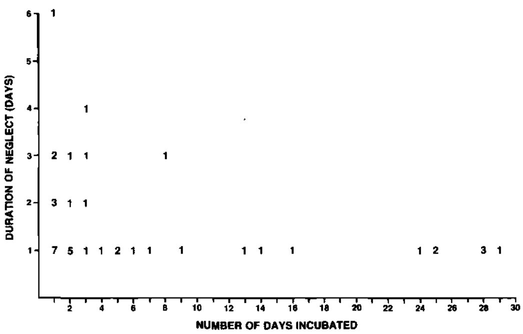

Fig. 1. The amount of neglect after the number of days from the start of incubation to hatching for Ancient Murrelet eggs at Reef Island in 1988. Figures represent number of clutches.

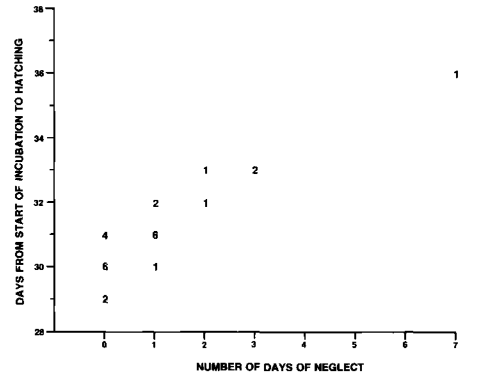

Fig. 2. The number of days of neglect and the duration of incubation prior to the period of neglect. Figures represent number of clutches.

causes a one-day increase in the length of the incubation period. Likewise, the y intercept (predicted duration of incubation in the absence of any neglect) is 30.2 days, very close to the mean number of days of incubation recorded for the control sample in 1988 (30.1 ± 0.6, $n = 26$).

Three of the burrows from which eggs were removed temporarily were deserted after our disturbance. All but one of the eggs in the other experimental burrows hatched, including all six in those where eggs were removed at 20–22 days. The one egg that failed to hatch was infertile. Clutches removed at 10–12 days were incubated for similar numbers of days to the undisturbed control clutches. Those removed at 20–22 days were incubated significantly longer than either the 10–12 day, or the control samples (Table 1).

Average temperatures recorded once daily between 1200–1700 during 23 April (median clutch completion) to 8 May, in burrows without an incubating bird, ranged from 6.2° to 6.9°C ($n = 11$), with extremes of 5–7°C. Between 9 May and 24 May (median hatching), means ranged from 7.5° to 8.6°C ($n = 6$), with extremes of 7–9°C. Average daily temperatures at the Coats Island Thick-billed Murre colony (means of daily maxima and minima) during the egg removals ranged from 6° to 11°C; minima ranged from 4° to 6°C. Temperatures were similar to those recorded during incubation at Reef Island.

Among the Thick-billed Murre eggs removed for 48 h after 5 days of incubation, and incubated for a total of at least 30 days, 3 out of 4 hatched. None of the eggs removed after 15 or 25 days of incubation showed any sign of hatching, although 6 of the former, and 3 of the latter were incubated for at least 34 days. The normal incubation period in this species is 32–33 days, but pipping has usually begun by 30 days after laying (Gaston and Nettleship 1981). Two of the 15-day sample, broken open and examined after 34 days of incubation, contained small, dead embryos, which suggests that they had been killed by the removals. The remainder of the 15-day eggs were incubated for at least 37 days without signs of pipping. At Digges Island, Northwest Territories, two Thick-billed Murre eggs neglected during the first 10 days of incubation for between 24 and 48 h at an air temperature which reached a minimum of 6°C subsequently hatched (Gaston pers. obs.). Hence, while some Thick-billed Murre embryos can withstand neglect for as much as 48 h during the first 10 days of incubation, those older than 15 days do not usually survive such treatment.

DISCUSSION

We have shown that Ancient Murrelets regularly neglect their eggs during incubation for periods of up to several days, even in the absence of any physical disturbance to the burrow. It appears, however, that neglect in this species is less frequent than in the population of Xantus' Murrelet studied by Murray et al. (1983). The mean number of days for which burrows were neglected in 1988 was similar to 1984 and 1985, but neglect after the first 7 days of incubation was less frequent in 1988 than in other years. The pattern of neglect in 1988 was presumably representative of natural neglect in that year, and may be typical of the species. We cannot rule out the possibility that observed differences were related to year-specific effects rather than to differences in the degree of disturbance, because Murray et al. (1980) found interyear variation in the amount of neglect among Xantus' Murrelets. However, neglect during the second half of incubation was observed more often in four years when examinations also involved physical disturbance than for the 1988 control burrows. Furthermore, the only neglect during the second half of incubation at the 1988 control burrows occurred immediately following the physical check at 28 days. We believe that, in this population, neglect during the latter half of incubation is usually the result of disturbance.

The results of the removals at 20–22 days, and the incidental observations of eggs hatching after being neglected during the last third of the incubation period, suggest that most Ancient Murrelet eggs can experience periods of >24 h at a temperature of <10°C throughout the incubation period and still remain viable. However, the number of days of incubation required to hatch eggs neglected late in the incubation period was greater than the number of days otherwise required. Neglect at a late stage of incubation carries a penalty for the breeders. It prolongs the total number of days spent at the colony, with the attendant possibility of predation. A Crested Auklet (*Aethia cristatella*) egg, neglected for 2 days during the latter half of the incubation period, had an incubation period 7 days longer than usual (Sealy 1984).

Most avian embryos cannot tolerate exposure to temperatures <10°C for >24 h during the latter part of the incubation period (Webb 1987, Haftorn 1988). Among Charadriiformes, most embryos of the Western Gull (*Larus occidentalis*) are killed by exposure to temperatures between 5–10°C for 10 h in the second half of the incubation period (Bennett et al. 1981). This also applies to Thick-billed Murre embryos >15 days old. The ability of late Ancient Murrelet embryos to remain viable when neglected at temperatures <10°C is matched only by members of the Procellariiformes (Pefaur 1974, Boersma and Wheelwright 1979, Boersma 1982, Roby and Ricklefs 1984). The possibility remains that this ability may be found in other Alcidae, but has not been observed. The results for Thick-billed Murres suggest that the *Synthliboramphus* murrelets are probably exceptional in this respect.

Both Sealy (1976) and Murray et al. (1983) assumed that the long incubation shifts and frequency of egg neglect seen in *Synthliboramphus* species are related to constraints imposed by their particular foraging behavior. An alternative hypothesis is that prolonged incubation shifts relate to avoidance of predators, which take a heavy toll on adults of both species on their colonies (Murray et al. 1983, Vermeer et al. 1984). In either case, neglect may occur when the off-duty bird has difficulty in accumulating sufficient energy reserves to cope with the lengthy incubation shift.

The virtually complete cessation of neglect in the Ancient Murrelet in the second half of incubation may relate to the effect that such neglect has in prolonging incubation. Any increase in the length of the incubation period exposes the breeders to an increased risk of predation. In Xantus' Murrelet, neglect shortens the number of days of actual incubation and imposes no penalty in terms of risk to the breeders. In Xantus' Murrelet, there is no decline in the frequency of neglect with embryo age (Murray et al. 1980). The difference in behavior between the two species is apparently mediated by differences in the temperatures that prevail during the incubation periods. Breeding Ancient Murrelets lose mass over the incubation period (Gaston in prep.), whereas Xantus' Murrelets gain mass (Murray et al. 1983). This difference may relate to the need for Ancient Murrelets to maintain greater constancy of incubation.

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