EMBRYO METABOLISM AND EGG NEGLECT IN CASSIN'S AUKLETS[1]

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Abstract. Incubation attendance by Cassin's Auklets (*Ptychoramphus aleuticus*) was determined by daily nest monitoring. The incidence of natural egg neglect was highest during the first third of the incubation period (incubation length of 38 days when parents were continuously present) and lowest between 12 and 25 days after laying. The latter corresponds to the period of most rapid embryonic growth rate. The pattern of auklet embryo metabolism is similar to that of other precocial species with prolonged incubation periods, with two differences: unpipped auklet embryos show their most rapid rise in metabolic rate relatively earlier in the incubation period. Auklet embryos have an unusually long plateau (10 days) in metabolic rate before beginning pipping. A rapid increase in metabolism is coincident with the five- to seven-day hatching process. Embryos surviving chilling had lower metabolic rates (after rewarming) than continuously incubated eggs of the same chronological age. The reduction of metabolic rate and resulting retarded development may account for the prolonged duration of incubation observed for both naturally and experimentally neglected auklet eggs.

Key words: Incubation; embryo metabolism; egg neglect; Cassin's Auklet; Alcidae.

INTRODUCTION

Many avian parents temporarily abandon incubation duties, resulting in exposure of the developing embryo to ambient thermal conditions. Depending upon species, egg size, stage of embryonic development, incubation and ambient temperatures, and duration of neglect, such interruptions may affect the overall length of incubation, threaten normal embryonic development, or may be lethal (Romanoff 1972, Webb 1987). For embryos to survive periods of egg neglect, they must tolerate chilling to low ambient temperatures and be able to resume normal development when rewarmed.

Embryonic tolerance of periodic neglect can be highly adaptive for species that forage on patchy, unpredictable resources at great distances from the breeding colony. Some Procellariiform embryos are notable in their ability to survive extended periods of exposure to low temperatures during adult absences (Boersma and Wheelwright 1979, Wheelwright and Boersma 1979, Williams and Ricklefs; reviews in Boersma 1982 and Webb 1987). Such absences result from asynchronous exchange of parents at the nest.

For example, in species with long incubation bouts, the sitting parent may leave the nest before its mate returns from feeding (Boersma 1982). The most dramatic examples of egg neglect have been documented in smaller members of Procellariiformes. For example, eggs of Fork-tailed Storm Petrel (*Oceanodroma furcata*) hatched after seven continuous days of neglect and up to 23 days of intermittent neglect (Boersma and Wheelwright 1979).

Some members of the Alcidae neglect their eggs up to three consecutive days with little or no effect on hatchability (Murray et al. 1983, Sealy 1984, Gaston and Powell 1989). Although most alcid species forage closer to nesting islands than Procellariiform species, both groups are constrained by the unpredictable abundance and location of marine resources. As might be expected, similarities in reproductive and developmental characteristics occur in these groups. Alcids and Procellariiforms produce a single large egg with a proportionately high energy content and have a longer-than-predicted incubation period (based on fresh egg mass, Rahn and Ar 1974). Boersma (1982) has suggested that these characteristics, and slower embryonic growth rates may preadapt embryos of some species for tolerance of egg neglect.

Cassin's Auklets (*Ptychoramphus aleuticus*) have the longest incubation period (38 days) relative to egg mass (28 g) of all members of the

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Alcidae (Rahn and Ar 1974). Although this is only 77% of the incubation time of Procellariiformes having eggs of similar mass (20–35 g, Rahn et al. 1984), these auklet eggs are known to have reduced functional pore area and lower rates of vapor conductance than predicted by egg size (Roudybush et al. 1980). These adaptations are typical in species with long incubation periods (Ar and Rahn 1978, Ricklefs and Rahn 1979).

Cassin's Auklets occasionally neglect their single egg (Carter and Fry, 1986; Astheimer, pers. obs.), and this study was undertaken to determine the frequency, duration, and timing of egg neglect. In addition, I measured embryo metabolic rates at normal incubation temperature throughout incubation to identify periods of rapid growth and, thus, possible periods of greater sensitivity to chilling. Finally, selected known-age eggs were subjected to 24, 72, or 144 hr of experimental neglect to determine their ability to survive chilling.

METHODS

The studies described below were conducted during 1981 and 1982 on Southeast Farallon Island, California, which supports a large breeding population of Cassin's Auklets. Most pairs that I studied nested in artificial wooden nest boxes, which auklet readily occupy (Ainley et al. 1981). Use of these boxes, although subject to greater daily temperature fluctuation than natural subterranean burrows, do not affect incubation duration (Manuwal 1972). The nest-boxes permit frequent checking or handling of incubating birds and eggs without the ill effects of erosion or burrow collapse which often occur when monitoring natural nests.

MONITORING EGG NEGLECT

The incubation exchange of auklet parents usually occurs nightly, when the off-duty auklet returns to the burrow shortly after dark. Often, both parents remain in the burrow until dawn, when the previously incubating bird leaves to feed at sea. Thus, a once-daily nest check made between 08:00 and 11:00 hr was was adequate to determine incubation status of an egg for the daylight period (12–15 hr depending on date). The incubating adult usually remained quiet on the egg during the nest check. Birds were individually marked with U.S. Fish and Wildlife Service bands and gender was determined by either

cloacal appearance after laying or bill characteristics (Nelson 1981, Astheimer 1986). This was done on the first and second days of incubation since parents typically alternate incubation duties nightly. Female auklets lay their eggs during the night, but for convenience I have called the day after laying day 1 of incubation.

Because nests were not checked at night, I could not assume that an egg found cold during the day had been neglected any part of the nights preceding or following a neglect incident. For example, an egg found cold on two consecutive days may have either been neglected continuously or been incubated during the intervening night.

In 1981, adult presence on the day of laying was noted for all first eggs laid in 139 nest boxes and 88 natural burrows. Although many first eggs were subsequently removed as part of another study in 1981 (Astheimer 1986), adult attendance was monitored daily for one month following laying of either a first (72 boxes) or a replacement egg (15 boxes). In 1982, first eggs laid in the 139 nest boxes were monitored daily for three months to determine dates of laying and hatching and adult presence. Unattended eggs were only considered as incidents of neglect when it was clear from the fate of that egg over the breeding season that the egg was not broken or abandoned for other reasons.

EMBRYO METABOLIC MEASUREMENTS

Oxygen consumption (V_{O_2}) was measured using Warburg constant volume respirometers (Umbreit et al. 1957). The usual sample receptacles for this apparatus were replaced with 200 ml glass flasks of known exact volumes. Each flask had three glass arms extending toward the center of the flask, thus forming a shelf to support the egg and allowing air to flow freely around it. Carbon dioxide produced by the embryo was absorbed by 10 ml of fresh 10% KOH, the level of which was 2.5 cm below the egg shelf. The flasks were each fitted with a calibrated copper-constantan thermocouple which extended through a rubber stopper so the tip could be adjusted to lie on the surface of the egg. Flasks were immersed in a water bath maintained at constant temperature (35°C). During each set of measurements, one of the four respirometers did not contain an egg and served as a thermobarometer for pressure corrections during a run. Flask constants for each respirometery unit were calculat-

ed and each unit was calibrated by injecting known volumes of air (Umbreit et al. 1957).

Known-age eggs, which had not experienced neglect before measurement (based on daily checks), were removed from their nests and replaced with one of eight Cassin's Auklet eggs sacrificed to be used as "dummy" eggs. In all cases, the incubating parent readily accepted the pre-warmed dummy egg. Sample eggs were weighed, egg width and length were measured, and volume was determined by displacement of fine sand (egg volume was needed to calculate the volume of air in each flask). In several instances, egg volumes were estimated as per Hoyt (1979; using equation 1 with mean $K_v = 0.507$). At the beginning of each set of metabolic measurements, the respirometers were allowed to warm in the water bath. Warm sample eggs were placed in the flasks and then allowed to equilibrate for at least one hour before $\dot{V}O_2$ measurements were begun. Egg surface temperatures during all metabolic determinations ranged from 34.5 to 36°C, similar to those measured for naturally-incubated eggs (see below). At least four manometric determinations of $\dot{V}O_2$ were taken for each egg and up to 15 were made for eggs older than 35 days. The duration of each sample period was dependent on embryo age and ranged from 30 min for younger embryos to 2–3 min for pipped eggs. All metabolic measurements were made between 09:00 and 15:00 hr, thus allowing sample eggs to be returned and accepted by the incubating parent well before the evening shift in incubation duties. The rate of oxygen consumption was calculated according to Umbreit et al. (1957) and corrected to standard conditions (STPD).

An estimate of natural incubation temperature was made in 1980 using auklet eggs that had been emptied of contents and refilled with Elvax (J. Stewart Enterprises), a paraffin-plastic mixture with thermal characteristics similar to the contents of a natural egg. A calibrated thermistor was embedded in each wax-filled egg to record incubation temperature. These egg-probes were placed in two nests, replacing the natural eggs which were estimated to be between 1–10 days old. Temperature was recorded at these nests using a Rustrak chart recorder.

METABOLISM OF EXPERIMENTALLY-NEGLECTED EGGS

In 1981, a total of 22 known-age embryos were subjected to one- ($n = 16$), three- ($n = 4$), or six-

($n = 2$) day periods of continuous experimental egg neglect by placing them in unused burrows, the entrances of which were blocked to prevent entry by auklets attempting to use these sites. The number of eggs experimentally neglected for more than one day was small due to the very low survival of the first group of eggs tested. During the egg neglect period, the natural parents of each experimental egg were provided with a warm dummy egg to discourage nest abandonment. Metabolism of these neglected eggs was either measured after eggs were rewarmed in an incubator (34°C) for 1 hr or several days following return to their parents. This protocol difference was due to unexpected power outages. All neglected eggs were eventually returned to the parents. Those which had very low postneglect metabolic rates were subsequently sampled at least once more during the next week to determine whether the embryo survived the neglect event. Metabolic measurements were also made on eight eggs after periods of natural neglect.

Variation around mean values are presented as the standard error of the mean.

RESULTS

NATURAL INCIDENCE OF EGG NEGLECT

A total of 155 first eggs were laid in the 227 monitored nest sites in 1981. Of these, 18% (28) were cold to the touch on the morning after laying. In 1982, 14% (17) of first eggs ($n = 121$) were cold on day 1 of incubation. Eggs incubated on day 1 were attended by the male parent in 93% of the instances where adult gender was known (149 of 160 cases). Thus, initial neglect on day 1 likely results from low incubation motivation by the male or lack of synchrony between the pair on the night of laying. Interestingly, the incidence of initial neglect for replacement eggs is low (7.1%; 5 eggs in 70 nests in 1981).

In 1981, 26% (25) of the monitored first and replacement eggs known to have hatched experienced at least one day of neglect (total = 95; broken or otherwise disrupted eggs were not included). Nearly half of these incidents (23 of 45) occurred during the first five days of incubation (Fig. 1a). In 1982 29% (32 of 111; 87 of which hatched) of first eggs were similarly neglected, with most incidents occurring within the first 10 days of incubation (Fig. 1a). In the latter year there was a very high incidence of egg neglect on 7 and 8 April (Fig. 1b). Since these dates do not coincide with peak laying, it seems likely that
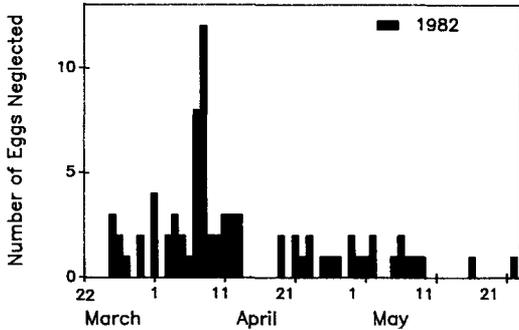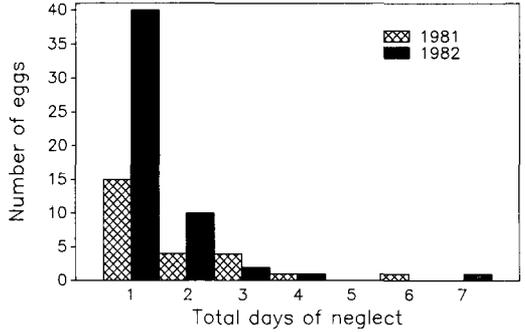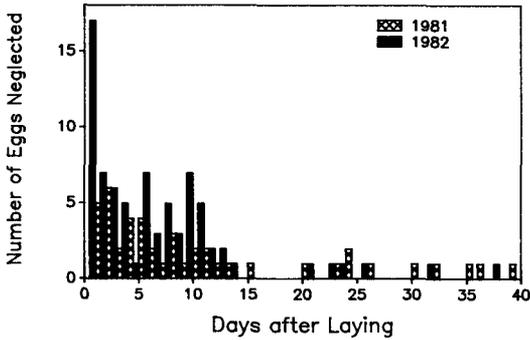
FIGURE 1.   a. Frequency of egg neglect in 1981 and 1982 with respect to laying; b. Frequency of egg neglect in 1982 with respect to calendar date.

FIGURE 2.   Frequency of neglected eggs in relation to the sum of neglect during the entire incubation period.

some environmental factor prevented or inhibited birds from returning to their nests (e.g., location of food supply). However, available information does not indicate unusual local or regional weather or ocean conditions associated with these dates (Pt. Reyes Bird Observatory Farallon Journal and Scripps Institute Of Oceanography Data for Ocean and Weather Observations, UCLA).

Chronological embryo age is not always a good indicator of developmental state for species prone to egg neglect, since embryonic development may be slowed or arrested during egg cooling (Dawson 1984). Because many eggs were neglected on more than one occasion, it is difficult to determine accurately the chronological periods during which embryos may be more sensitive to cooling. For example, one egg was neglected seven different days (1, 2, 4, 6, 8, 10 and 11 after laying) but eventually hatched and the chick fledged. The stage of development and correlated metabolic rate of that embryo on day 12 would likely be less than that of an embryo neglected only on day 2 or only on day 11. Although the former example strongly suggests that one parent was

not incubating during the first week, this is not certain since the identity of the incubating parent was not ascertained daily.

Egg neglect usually occurred as a single incident (33.3% of 45 in 1981 and 52% of 77 in 1982) during incubation (Fig. 2). Multiple days of neglect were more likely to occur on consecutive (5 of 12 in 1981; 5 of 17 in 1982) or apparently unrelated days (4 of 12 in 1981; 10 of 17 in 1982) than on alternate days (3 of 12 in 1981; 2 of 17 in 1982). This suggests that neglect does not rest solely with low incubation motivation by one parent.

The duration of the incubation period, on average, increased proportionately with the duration of neglect, from 38.0 ± 0.13 days ($n = 58$) in continuously incubated eggs to 39.0 ± 0.24 days ($n = 22$) in eggs neglected 1 day and 40.1 ± 0.57 days ($n = 12$) in those neglected two or more days. One egg, neglected a total of seven nonconsecutive days during the first 12 days after laying, hatched 45 days after being laid.

EGG TEMPERATURE DURING NATURAL INCUBATION

Egg temperature of the Elvax-filled auklet eggs averaged 32.7°C, ranging from 20.0 to 36.1°C over 160 hr of measurement (Fig. 3). This includes several nocturnal periods when egg temperature was allowed to drop well below 30°C, including one 11-hr period when egg temperature remained between 20–24°C. Note that the latter egg was not abandoned during this period, as burrow temperatures are typically 10–15°C and nocturnal air temperatures often fall below 10°C in April (Manuwal 1972; Astheimer, unpubl. data). Under these conditions a neglected Elvax-
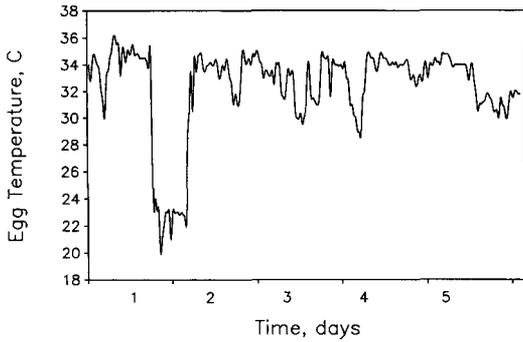
FIGURE 3. Temperature profiles of one incubated Elvax-filled auklet eggs containing a thermistor. The eggs used had been laid 1–10 days before being sacrificed.
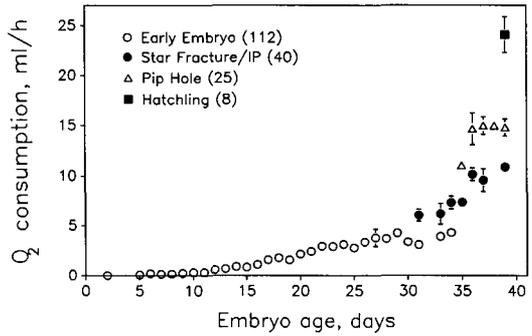

FIGURE 4. Oxygen consumption of Cassin's Auklet embryos over the incubation period. Error bars represent standard error of the mean. Symbols differentiate developmental stages: open circles: pre-internal pipping; filled circles: star-fracture apparent on shell surface; open triangles: pip hole present; filled square: hatched chick just emerged from the shell. All eggs were naturally incubated except during measurement and did not experience egg neglect (see text). Numbers in parentheses refer to sample sizes.

filled auklet egg reaches thermal equilibrium within 40 min (Astheimer, unpubl.). Periods of "tight" incubation occurred most frequently between 05:00 and 14:00 hr, and had egg temperatures of 34.5 ± 0.7°C during a total of 48 hr over 6.6 days of measurement.

The centrally-located thermistor in the Elvax egg provides an estimate of egg temperature that will lie between the higher temperature of the egg surface in contact with the auklet's lateral brood patch and the lower temperature of the burrow surface. (Cassin's Auklets have a brood patch on each flank; the single egg is placed under the wing against one of them [Manuwal 1972]). Therefore, the temperature of the embryo, which lies near the upper egg surface and closely apposed to the brood patch during tight incubation, is likely to be somewhat higher than values reported here (Drent 1975). Thus, I am confident that temperatures between 34.5–36.0°C used for embryo metabolism experiments reflect natural conditions experienced by auklet embryos, at least during periods of tight incubation.

NATURAL EMBRYO METABOLISM

A total of 227 measurements of embryo metabolic rate were made on 73 eggs during the course of incubation, none of which were neglected (Fig. 4). Metabolic rates were very low during the first two weeks and gradually rose between days 14 and 26 (Fig. 4). Between days 25 and 34, a plateau is apparent in those eggs not showing signs of internal pipping (e.g., star fractures on egg surface). Between days 34 and hatching, a rapid rise in $\dot{V}o_2$ occurs coincident with the lengthy process of pipping and initiation of pulmonary respira-

tion. Star fractures were usually apparent on the shells of 33 to 37 day old embryos and their first appearance was considered indicative of internal pipping (i.e., pipping into the air cell which marks the initiation of pulmonary respiration). External pipping was distinguished by the presence of a pip hole, emergence of the egg tooth or audible peeping by the chick. The transition from internal pipping through hatching took as long as six days in some eggs.

METABOLISM OF EXPERIMENTALLY NEGLECTED EMBRYOS

Only six eggs were experimentally neglected for longer than one day (2 eggs for 6 days, 4 eggs for 3 days; Table 1). Embryo metabolism measured within 24 hr of neglect was much lower than prior to neglect, with the exception of one egg neglected two days after laying. This embryo showed a slight increase in metabolic rate after being warmed (Table 1), but was abandoned later in incubation.

When metabolic measurements were made before returning neglected eggs to their original nests (but after rewarming them in an incubator), embryos had depressed metabolism and later most of these died (6 of 7; Table 1). However, experimentally neglected eggs that had been returned to nests before the post-neglect $\dot{V}o_2$ measurements were made had much higher survival (8 of 9; Table 1). This difference in survivorship may be explained by age differences between the

TABLE 1. Pre- and post-neglect metabolic rates compared with expected rates at chronological and developmental age of neglected auklet ambyros.

Age neglected	Pre-neglect		Post-neglect		Expected Vo₂ ml/hr	% Difference	Expected Vo₂[b]	% Difference	Days neglected	Hatch
	Age	Vo₂ ml/hr	Age	Vo₂ ml/hr						
2	1	0.03	6	0.15	0.2	25	0.08	−88	1	n
2	—	—	25	2.50	2.8	11	3.1	20	1	y
6	—	—	36	2.77	10.3	73	7.4	62	1(+)	—
7	7	0.25	10	0.07	0.3	77	0.16	55	3[2]	n
9	9	0.31	12	0.12	0.6	80	0.24	50	3[2]	n
1, 8, 10	—	—	37	4.71	12.9	63	7.3	36	3	y
10	10	0.49	13	0.14	0.7	80	0.32	57	3[2]	n
10	10	0.27	16	0.69	1.1	37	0.85	18	1	y
10	10	0.25	16	0.99	1.1	10	0.85	−14	1	y
11	11	0.28	17	1.08	1.6	33	1.1	3	1	y
11	11	0.46	17	0.11	1.6	93	1.1	90	1	n
12	12	0.72	18	0.19	1.8	89	0.6	67	6[2]	n
13	13	0.82	16	0.44	1.1	60	0.7	37	3[2]	n
13	13	0.56	19	1.51	1.6	6	1.8	16	1	y
13	13	0.72	20	1.92	2.2	13	1.6	−20	1	y
13	13	0.55	20	1.32	2.2	40	1.6	18	1	y
1, 13	13	0.69	20	1.87	2.2	15	1.8	−4	2[1]	y
16	16	0.97	22	0.07	2.9	98	2.4	97	1	n
16	16	0.89	22	2.28	2.9	21	2.3	1	2[1]	y
20	20	0.74	21	0.30	2.4	88	2.3	87	1	n
21, 26	21	2.56	22	2.08	2.9	28	2.3	10	2[1]	y
24	—	—	29	4.60	4.3	107	3.7	−26	1	y
25	25	1.43	26	0.44	3.4	87	2.8	84	1	n
24, 26	23	3.25	31	3.33	5.1	35	4.3	22	2	y
25	25	2.98	26	0.31	3.4	91	2.8	89	1	n
26	26	2.77	27	0.42	3.7	89	3.4	88	1	n
28	28	3.51	29	0.26	4.3	94	3.7	93	1	n
31	31	3.10	32	0.38	4.6	92	3.1	88	1	n
35	—	—	36	7.59	10.2	25	7.4	−2	1	y
37	36	7.13	38	10.99	10.2	−8	9.6	−14	1	y
39	37	11.80	—	—	—	—	—	—	1	y

[a] Expected metabolic rate based on data in Figure 4 and chronological embryo age.
[b] Expected metabolic rate based on data in Figure 4 and developmental embryo age (chronological age − days of neglect).
[1] Includes one day experimental and one day of natural neglect.
[2] Continuous neglect over time period.

groups; the latter group was between 10 to 16 days old, while the former ranged from 20 to 31 days at the beginning of neglect (Table 1).

DISCUSSION

NATURAL EGG NEGLECT

Temporary abandonment of eggs during incubation has been reported for a number of alcid species, but in many instances the neglect episode was thought to be due to nest disturbance (Winn 1950; Simons 1981; Sealy 1976, 1984; Murray et al. 1983; Gaston and Powell 1989). However, non-disturbance egg neglect is common and seems to be of adaptive importance for at least two alcid species: Ancient Murrelet *Synthliboramphus antiquus* and Xantu's Murrelet *Endomychura hypoleucus* (Sealy 1976; Gaston and Powell 1989; Murray et al. 1980, respectively).

These murrelets are unusual among the Alcidae in producing a clutch of two highly precocial chicks that fledge from the nest site 2–5 days after hatching. Murrelet parents have longer incubation shifts than most alcids (up to four days) and show sporadic incubation attendance. Egg neglect occurs with greater frequency and for longer duration in the subtropical to temperate nesting Xantu's Murrelet than in the Ancient Murrelet. Unattended nest temperatures are high enough in Xantu's Murrelet nests to support embryo metabolic activity of unincubated eggs. Consequently, although the total incubation period is extended for neglected eggs, the duration of parental attendance necessary for hatching is actually reduced in this species (Murray et al. 1980). In contrast, the temperate to sub-arctic nesting Ancient Murrelet neglect their eggs less frequent-

ly than Xantu's Murrelet and neglect incidents are largely restricted to the first third of the incubation period (Gaston and Powell 1989).

The frequency of neglect of Cassin's Auklet eggs is similar to the pattern observed in Ancient Murrelets; that is, largely restricted to the first third of the incubation period (see Gaston and Powell 1989). However, sporadic episodes of neglect occur throughout incubation (Fig. 1), which are tolerated by at least some auklet embryos (Table 1). In contrast to auklets, however, both aforementioned murrelet embryos often survive neglect periods of several consecutive days (Murray et al. 1980, Gaston and Powell 1989). In addition, the murrelets usually do not begin incubating until the second egg is laid; this results in first-laid eggs being at ambient temperatures until laying of the second egg (up to seven days in Ancient Murrelets, Sealy 1976).

In Cassin's Auklets, Carter and Fry (1986) found a similar pattern of neglect frequency during incubation. Because nest boxes were not monitored daily and not at all between days 2 and 14 after laying in their study it is difficult to compare nest attendance data. These researchers also correlated the increased frequency of neglect in 1984 with unusually windy conditions that year, suggesting adaptive significance for embryo tolerance of neglect in this species.

INCUBATION TEMPERATURE

The data obtained from telemetered eggs (Fig. 3) indicate that egg temperatures fluctuate, even when an adult auklet is present. This may be partially explained by the nocturnal activity of adults; there is often considerable vocal and physical activity in and around the burrow at night, especially early in the incubation period. Incubation responsibilities may be ignored during these periods of social interaction, perhaps explaining the lower and less stable egg temperatures at this time (Fig. 3). In other species the frequency of such fluctuation in egg temperature decreases as incubation proceeds (e.g., Rockhopper Penguin *Eudyptes chrysocome*; Burger and Williams, 1979). Williams and Ricklefs (1984) found mean egg temperatures of 35–36°C for continuously monitored eggs of three Procellariiform species, with fluctuations limited to within 4°C of the mean. However, Manuwal (1972) found abundant nocturnal auklet activity above ground during the entire incubation period, suggesting that a nocturnal drop in egg temperature

may be common throughout incubation. If this results in the average incubation temperatures over the same 38-day incubation period being lower than 34.5–36°C, my estimate of total incubation expenditures will be higher on average than those occurring under natural conditions.

EMBRYO METABOLISM

The pattern of oxygen consumption during auklet embryonic development is comparable to that described for other precocial species (Vleck & Vleck 1987). For several Procellariiform species studied, metabolic rate remains at very low levels during the first 40–50% of incubation, increases most rapidly during the latter 50–75% of the incubation period, afterwhich metabolic rate stabilizes. This metabolic plateau persists until internal pipping when metabolism again increases dramatically (Ackerman et al. 1980, Whittow 1983, Vleck & Kenagy 1980, Vleck & Vleck, 1987).

Cassin's Auklet embryos show two differences from this pattern. First, the period of rapidly increasing metabolic rate occurs earlier, during the first 30–55% (days 12–22) of the incubation period in Cassin's Auklets (Fig. 5). Secondly, the metabolic plateau for Cassin's Auklet embryos is unusually long (10 days) for an egg of its size (28 g). These two characteristics result in the incubation period being prolonged over the last, rather than the first half.

Assuming that increased metabolic rates accurately reflect increased embryonic growth rates during the pre-IP period (see Ackerman et al. 1980, Bucher and Bartholomew 1984), the auklet embryo metabolic profile indicates that the most rapid period of growth occurs between days 12–23 of incubation. In auklets, low embryonic growth rates occur before day 12 and after day 25, correlating well with the natural incidence of egg neglect (Fig. 1a). It is interesting to note that the frequency of egg neglect decreases markedly after day 12 of incubation, coincident with the beginning of this growth period.

In partitioning the costs of embryonic development into growth and maintenance components, several researchers have correlated the metabolic plateau observed in precocial species with a period of decreasing growth rates and increasing or stable maintenance costs (Vleck & Vleck 1987, Hoyt 1987). The very long metabolic plateau seen in auklet embryos is reminiscent of that observed in ratites during which there

is a sustained reduction in growth rate before pipping (Vleck et al. 1979).

The estimated total volume of O_2 consumed by auklet embryos during incubation was 2,590 ml (52.1 kJ, calculated from the area under a curve fit to the data in Fig. 4). This is likely to be an overestimate, because it is based on $\dot{V}o_2$ measurements made at 34–35°C. As previously mentioned, mean incubation temperatures may be lower. Nonetheless, this value is 91% of the total predicted by both energy content of fresh eggs (Vleck & Vleck 1987, Astheimer 1986) and egg mass (Hoyt 1987, Eq. 4), and represents only 28% of the total egg energy available to the embryo. Interestingly, the proportional use of energy during incubation (energy consumed/energy available) does not appear to be directly related to mode of development (Vleck and Vleck 1987); the value for auklet embryos is close to the mean estimated for altricial and precocial species combined (mean = 32.2 ± 1.9; range: 18–54%, calculated from Vleck and Vleck 1987).

On a mass-specific basis, Cassin's Auklet embryos consumed 92.5 ml O_2/g fresh egg mass. This is only 10% lower than the average of 102 ml/g found for 27 species independent of incubation length (Hoyt and Rahn 1980), although it is up to 45% lower than values reported for non-albatross procellariiformes which have been studied (Whittow 1983).

The total metabolic cost of embryonic development can be partitioned into the embryonic phase (before internal pipping) and the hatching phase (internal pipping through hatching). During the embryonic phase, auklet embryos consumed an estimated total of 1,545 ml O_2 (31.1 kJ, 59.7% total), while the hatching process required an estimated 1,045 ml O_2 (21 kJ, 40.3% total). These proportionate values are nearly the same as those reported for White Tern (Pettit et al. 1981), Wedge-tailed Shearwater (Ackerman et al. 1980), and two albatross species (Pettit et al. 1982).

Hoyt and Rahn (1980) suggest using $\dot{V}o_2$ just prior to internal pipping (PIP) in making interspecific comparisons. In Cassin's Auklet, PIP $\dot{V}o_2$ was 97.2 ml/day (equals the mean of values obtained from embryos 28 to 34 days old). This value is only 36% of that predicted based on the relation between PIP $\dot{V}o_2$ and egg mass. However, the PIP (and other metabolic parameters) of other species with long incubations periods are similarly overestimated (Hoyt 1987). Clear-
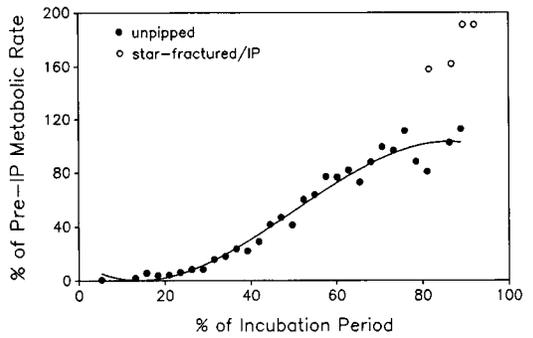

FIGURE 5. Oxygen consumption of unpipped eggs expressed as the percent of the PIP metabolic rate (4.05 ml/hr) over the incubation period, expressed as the percent of the total incubation period (38 days). Only 4 of 40 star fractured/internal pipped eggs are presented due to the scale of the graph.

ly, in spite of the increase in maintenance costs incurred by prolonging incubation, these species have lower-than-expected costs for embryonic development prior to pipping. Embryos of many of these species take a week or more between internal pipping and hatching, during which time metabolism can increase 3- to 4-fold with commensurate increases in growth (Fig. 4; Ackerman et al. 1980). Such temporal differences in the pattern of energy utilization may account for metabolic discrepancies noted between precocial species having "normal" incubation periods and those having unusually long periods (Hoyt 1987).

Embryos surviving experimental and natural neglect had metabolic rates averaging 22.3 ± 3.5% lower than those of continuously-incubated eggs of the same chronological age (Table 1). Among neglected eggs, no differences in proportional metabolic reduction could be identified in relation to embryo age at neglect. The retarding effect of chilling on growth rates of avian embryos (Romanoff 1972) appears to be physiologically reversible when neglect occurs in early development, with the only effect being a delay of one to two days in hatching (Spiers and Baummer 1990). Rates of oxygen consumption of neglected embryos measured during pipping and hatching were equivalent to those of continuously-incubated embryos at the same developmental stage.

Although comparable physiological information is unavailable, it is interesting that auklets and other alcid species show the greatest frequency of egg neglect during the first third of the incubation period. Naturally incubated Cassin's

Auklets survive such neglect with no apparent effect on hatching or fledging success, but seem to be less successful surviving neglect later in development. Poultry studies offer some insight into this developmental embryonic sensitivity to chilling. Exposure of three to eight day-old chicken eggs to 20°C for 48 hr resulted in a nearly linear increase in mortality as a function of age, from 44% to 97%, respectively (Ancel 1959). Chicken embryos older than eight days suffer over 95% mortality in response to chilling (Romanoff 1972). Interestingly, 14 to 25 day-old auklet embryos are at equivalent development stages as 7 to 14 day-old chicken embryos (Hirsch and Grau, unpubl. data). In chickens, this developmental period is associated with the initiation of physiological function in many organ and associated enzyme systems (e.g., digestion, excretion, Freeman and Vince 1974) which may require close thermal regulation. Whether auklet embryos are similarly more sensitive to chilling during periods when growth rates are highest, i.e., the middle third of incubation, remains to be tested.

ACKNOWLEDGEMENTS

LITERATURE CITED

ACKERMAN, R. A., G. CAUSEY-WHITTOW, C. V. PAGANELLI, AND T. N. PETTIT. 1980. Oxygen consumption, gas exchange, and growth of embryonic wedge-tailed shearwaters (*Puffinus pacificus chlororhynchus*). Physiol. Zool. 53:210–221.

ANCEL, P. 1959. Recherches sur les malformations determinees par le refroidissement temporaire de l'oeuf de poule et compatibles avec la vie des Pouissins. J. Embrol. Expt. Morphol. 7:330–334.

AINLEY, D. G., C. R. GRAU, T. E. ROUDYBUSH, S. H. MORRELL, AND J. M. UTTS. 1981. Petroleum ingestion reduces reproduction in Cassin's Auklets. Mar. Pollut. Bull. 12:314–317.

AR, A., AND H. RAHN. 1978. The interdependence of gas conductance, incubation length, and weight of the avian egg, p. 227–236. *In* J. Piiper [ed.],

Respiratory function in birds, adult and embryonic. Springer-Verlag, New York.

ASTHEIMER, L. 1986. Egg formation in Cassin's Auklet. Auk 103:682–693.

BOERSMA, P. D., AND N. T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the fork-tailed storm-petrel. Condor 81:157–165.

BOERSMA, P. D. 1982. Why some birds take so long to hatch. Am. Nat. 120:733–740.

BUCHER, T. L., AND G. A. BARTHOLOMEW. 1984. Analysis of variation in gas exchange, growth patterns, and energy utilization in a parrot and other avian embryos. *In* R. S. Seymour [ed.], Respiration and metabolism of embryonic vertebrates. Dr. W. Junk Publ., Boston.

BURGER, A. E., AND A. J. WILLIAMS. 1979. Egg temperatures of the Rockhopper Penguin and some other penguins. Auk 96:100–105.

CARTER, H. R., AND D. M. FRY. 1986. Egg neglect in Cassin's Auklets (*Ptychoramphus aleuticus*). Abst. Pacific Seabird Group. 1986.

DAWSON, W. R. 1984. Metabolic responses of embryonic seabirds to temperature, p. 139–158. *In* G. C. Whittow and H. Rahn [eds.], Seabird energetics. Plenum Press, New York.

DRENT, R. 1975. Incubation, p. 333–420. *In* D. S. Farner and J. R. King [eds.], Avian Biology, Vol. V. Academic Press, New York.

GASTON, A. J., AND D. W. POWELL. 1989. Natural incubation, egg neglect, and hatchability in the Ancient Murrelet. Auk 106:433–438.

FREEMAN, B. M., AND M. A. VINCE. 1974. Development of the avian embryo: a behavioural and physiological study. John Wiley & Sons, New York.

HOYT, D. 1979. Practical methods of estimating volume and fresh weight of birds eggs. Auk 96:73–77.

HOYT, D. 1987. A new model of avian embryonic metabolism. J. Exp. Zool. Suppl. 1:127–138.

HOYT, D., AND H. RAHN. 1980. Respiration of avian embryos—A comparative analysis. Respir. Physiol. 39:255–264.

MANUWAL, D. 1972. The population ecology of Cassin's Auklet on Southeast Farallon Island, California. Ph.D. thesis. University of California, Los Angeles.

MURRAY, K. G., K. WINNETT-MURRAY, AND G. L. HUNT. 1980. Egg neglect in Xantu's Murrelet. Proc. Colon. Waterbird Group 3:186–195.

MURRAY, K. G., K. WINNETT-MURRAY, Z. A. EPPLEY, G. L. HUNT, JR., AND D. B. SCHWARTZ. 1983. Breeding biology of the Xantu's Murrelet. Condor 85:12–21.

NELSON, D. A. 1981. Sexual differences in measurements of Cassin's Auklets. J. Field Ornithol. 52:233–234.

PETTIT, T. N. 1982. Embryonic oxygen consumption and growth of Laysan and Black-footed Albatross. Am. J. Physiol. 242:R121–R128.

PETTIT, T. N., G. S. GRANT, G. C. WHITTOW, H. RAHN, AND C. V. PAGANELLI. 1981. Respiratory gas exchange and growth of White Tern embryos. Condor 83:355–361.

RAHN, H., R. A. ACKERMAN, AND C. V. PAGANELLI.

1984. Eggs, yolk and embryonic growth rate, p. 89–112. *In* G. C. Whittow and H. Rahn [eds.], Seabird energetics. Plenum Press, New York.

RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. Condor 76:147–152.

RICKLEFS, R. E., AND H. RAHN. 1979. The incubation temperature of Leach's Storm-Petrel. Auk 96:625–627.

ROMANOFF, A. L. 1972. Pathogenesis of the avian embryo. Wiley-Interscience, New York.

ROUDYBUSH, T., L. HOFFMAN, AND H. RAHN. 1980. Conductance, pore geometry, and water loss of eggs of Cassin's Auklet. Condor 82:105–106.

SEALY, S. G. 1976. Biology of nesting Ancient Murrelets. Condor 78:294–306.

SEALY, S. G. 1984. Interruptions extend incubation by Ancient Murrelets, Crested Auklets, and Least Auklets. Murrelet 65:53–56.

SIMONS, T. R. 1981. Behavior and attendance patterns of the Fork-tailed Storm-petrel. Auk 98:145–158.

SPIERS, D. E., AND S. C. BAUMMER. 1990. Embryonic development of Japanese Quail (*Coturnis coturnix japonica*) as influenced by periodic cold exposure. Physiol. Zool. 63:516–535.

UMBREIT, W. W., R. H. BURRIS, AND J. F. STAUFFER. 1957. Manometric techniques. Burgess Publ. Co., Minneapolis, MN.

VLECK, C. M., D. F. HOYT, AND D. VLECK. 1979. Metabolism of avian embryos: patterns in altricial and precocial birds. Physiol. Zool. 52:363–377.

VLECK, C. M., AND G. J. KENAGY. 1980. Embryonic metabolism of the fork-tailed storm-petrel: physiological patterns during prolonged and interrupted incubation. Physiol. Zool. 53:32–42.

VLECK, C. M., AND D. VLECK. 1987. Metabolism and energetics of avian embryos. J. Exp. Zool. Suppl. 1:111–126.

WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874–898.

WHEELWRIGHT, N. T., AND P. D. BOERSMA. 1979. Egg chilling and the thermal environment of the Fork-tailed storm petrel (*Oceanodroma furcata*) nest. Physiol. Zool. 52:231–239.

WHITTOW, G. C. 1983. Physiological ecology of incubation in tropical seabirds. Studies in Avian Biology No. 8:47–72.

WILLIAMS, J. B., AND R. E. RICKLEFS. 1984. Egg temperature and embryo metabolism in some high latitude procellariiform birds. Physiol. Zool. 57:118–127.

WINN, H. E. 1950. The Black Guillemot of Kent Island, Bay of Fundy. Auk 67:477–485.