# NEST INATTENTIVENESS AND ITS INFLUENCE ON DEVELOPMENT OF THE YOUNG IN THE SUPERB LYREBIRD

ALAN LILL

The optimal temperature range for avian embryos and nestlings is usually narrow. Slight deviations from this range can retard growth, and, if prolonged, induce abnormal development and mortality (Lundy 1969). Incubation and brooding rhythms generally restrict significant temperature deviations even during periods of inattention (Huggins 1941), and parents can also adjust levels of heat transfer during contact with eggs and nestlings (Drent 1973). Most species breeding at low temperatures maintain fairly constant egg and early nestling temperatures through a high level of nest attentiveness, even when incubation and brooding are uniparental (White and Kinney 1974).

The Superb Lyrebird (*Menura superba*) inhabits mainly wet sclerophyll and temperate rainforest in southeastern Australia. Its domed nest is built at varying heights from ground level to 18 m. The single-egg clutch is laid in mid-winter and hatches in late winter or early spring. Daytime ambient temperatures are around 10°C or lower during the incubation and early nestling periods, and both incubation and brood-care are uniparental (Lill, unpubl. data).

Tregallas (1921), Ward (1940) and Reilly (1970) have suggested that lyrebird incubation does not begin immediately after egg-laying despite the prevailing low temperatures. Ward (1939), Reilly (1970) and Robinson (1977 and unpubl. data) also indicate that the egg *may* be deserted for a long period daily once incubation has commenced. Since the six to seven week incubation and nestling periods are very long for a passerine, the protracted nest recesses taken by the unassisted female parent may lead to marked cooling and retarded development of young. Here I explore this possibility through the first detailed examination of lyrebird incubation and brooding rhythms, and by monitoring embryonic and nestling temperatures during maternal absences.

## STUDY AREAS AND METHODS

The two areas used from 1973 to 1978 were: (a) Sherbrooke Forest Park, an approximately 821 ha wet sclerophyll (Mountain Ash, *Eucalyptus regnans*) forest reserve 37 km E of Melbourne (37°45′S, 144°56′E) with a 198–494 m altitudinal range; (b) Maroondah Catchment area near Healesville, 57 km NE of Melbourne, where research was conducted in a 0.62 km² stand of mature Mountain Ash forest with a 334–790 m altitudinal range on Mt. Riddell and in mixed-eucalyptus wet sclerophyll forest at Fernshaw. For the three sites mean annual rainfall ranges from 1,435 to 1,641 mm, mean daily maximal temperatures from 13.7–15.4°C and mean daily minimal temperatures from 6.9–7.6°C. Mean daily maximal and minimal temperature ranges for the months of June through September fall within the limits 6.8-11.7°C and 2.8-4.5°C respectively (Howard and O'Shaughnessy 1971, Langford and O'Shaughnessy 1977). Snow occasionally falls at Maroondah but rarely in Sherbrooke.

The incubation regime was determined from 138.3 h of observation, mainly while I was concealed, at and near to fourteen nests occupied by eleven different females. The daytime brooding regime (i.e., when and for how long nestlings were brooded) was determined from 67 h of concealed observation of six Sherbrooke and five Maroondah breeding attempts made by ten females. Observations covered all daylight hours and were spread over six breeding seasons.

Internal temperatures ($T_e$) of two eggs in ground level nests were monitored in situ over several days early in the incubation period using an implanted transmitter which emitted 12F pulses at a predetermined, temperature-dependent rate. The unit was implanted through a small opening cut in the shell and resealed with an instantaneous bonding agent. The signals from this transmitter and a larger one located near ground level close to the nest to measure air temperatures ($T_a$) were monitored on a transceiver fitted with a beat frequency oscillator operated by a concealed observer. Implantation times were 3 and 6–10 days post-laying. Results were clear-cut and the species has protected status, so a sample size greater than two was deemed unjustifiable.

Nestling core temperatures ($T_{nb}$) were taken by deep cloacal insertion of a thermocouple linked to an electronic thermometer. $T_a$ just outside the nest entrance was measured within 30 s of each $T_{nb}$ reading. Usually a series of readings was taken at intervals ranging from 1 to 120 min after a maternal post-brooding exodus on days 1–10 or commencing at an arbitrary time from day 11 onwards. I obtained cooling curves for seven nestlings, five of which were measured on two or more days. At least one curve was obtained for each of the ten daytime brooding phase days.

Nestlings were weighed regularly and also when $T_{nb}$ measurements were taken. Growth equations were fitted by Ricklef's (1967) method to the growth curves of five known-age nestlings which fledged. Asymptote estimations and K values were generated by a computer program and $t_{10-90}$ (time taken for growth from 10–90% of the asymptote) values generated in turn from the K values.

## RESULTS

### THE INCUBATION REGIME

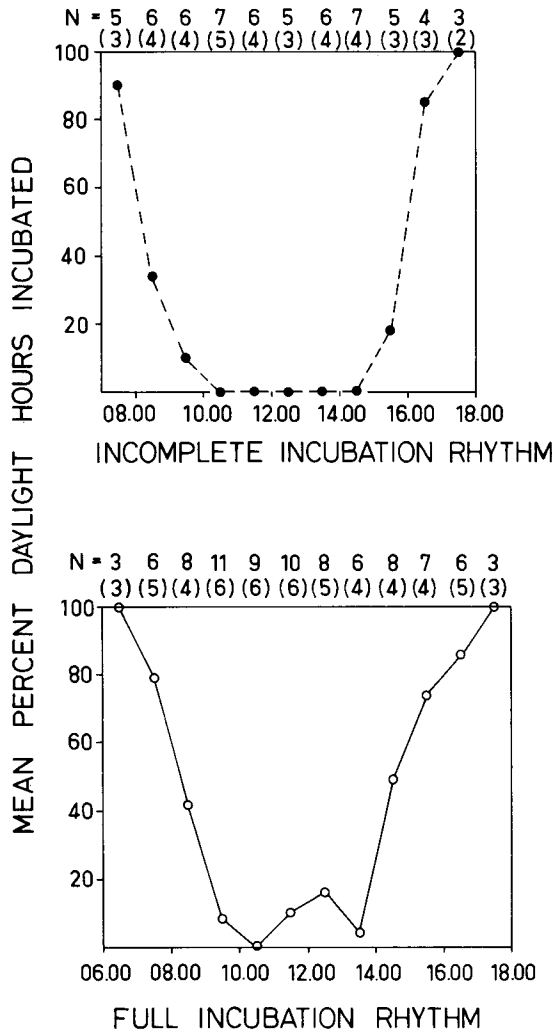Full daytime incubation rhythms developed gradually and with varying latencies

FIGURE 1. Daytime incubation rhythm of Superb Lyrebird females. Graphs show average percentage of each daylight hour that females spent incubating. N is the number of observations for a particular hour from which the means were calculated. Numbers in parentheses indicate the number of females observed for a particular hour. Means for the pre-08:00 and post-17:00 periods relate only to daylight segments of these periods. Ten Sherbrooke and four Maroondah nests studied.

(mean c. 18 days) at six nests observed early in the incubation period. During the incomplete incubation rhythm stage, females typically left the nest following nocturnal incubation within two hours after dawn and did not return until middle or late afternoon (Fig. 1). Three such recesses averaged 6.9 ± 0.75 h and several incompletely timed ones were of similar length (Table 1). Females typically returned to sit continuously through the night 47–112 min before dusk. Eggs were thus usually deserted for seven hours daily at mean daily maximum $T_a$'s ranging from 8–10°C.
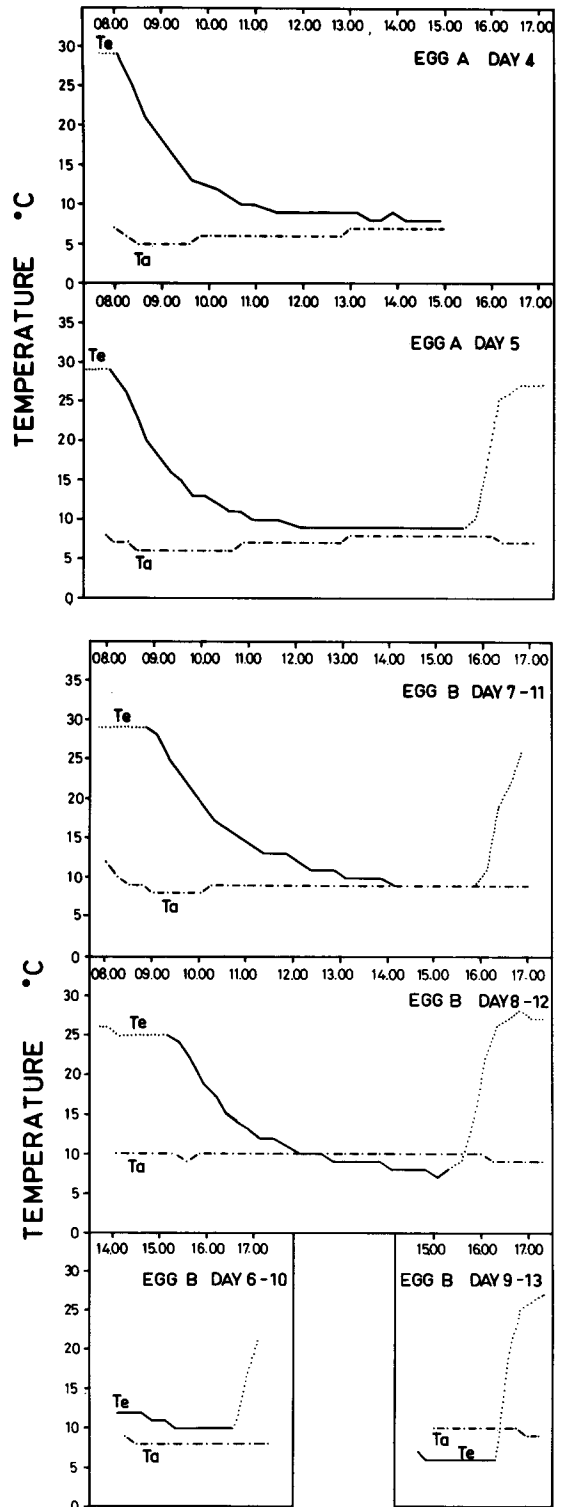


FIGURE 2. The internal temperatures of two eggs during maternal recesses taken on several days in the incomplete incubation phase. ----- $T_a$ near the nest. ······ $T_e$ during incubation. ——— $T_e$ during maternal absence. The laying date of egg B was not exactly determined.

TABLE 1. Duration of maternal recesses in the incubation stage.

| | | Duration (min) of recesses begun[a] | | | Stage of incubation |
|---|---|---|---|---|---|
| | | Forenoon | | Afternoon | |
| Absolute length | | 260; 71.5 | $\bar{x}$ | $57 \pm 24.9$ | Complete incubation regime (Day 19 onwards) |
| | | | R | 35–90 | |
| | | | n | 4 | |
| Minimal length[b] | $\bar{x}^c$ | $174.2 \pm 71.4$ | $\bar{x}$ | $50 \pm 29.8$ | |
| | R | 77–335 | R | 5–85 | |
| | n | 13 | n | 5 | |
| Absolute length | $\bar{x}$ | $412 \pm 45$ | | | Incomplete incubation regime (Days 1–18) |
| | R | $366.5 \pm 456.5$ | | | |
| | n | 3 | | | |
| Minimal length | $\bar{x}$ | $251.3 \pm 128.6$ | $\bar{x}$ | $161.4 \pm 68.9$ | |
| | R | 108–420 | R | 80–270 | |
| | n | 4 | n | 6 | |
| Absolute length | | | | 43.5 | Unknown incubation regime |
| Minimal length | $\bar{x}$ | $192.8 \pm 131.8$ | | 23 | |
| | R | 36–395.5 | | | |
| | n | 8 | | | |

[a] Either recess began (absolute lengths) or timing of recess began (some minimal lengths) pre- or post-12:00.
[b] Beginning and/or end of recess untimed.
[c] $\bar{x}$ = mean ± standard deviation; R = range; n = number of recesses timed. Computed only for samples ≥ 3.

During the complete incubation stage there were usually two recesses per day. Morning recesses lasted from between dawn and 09:30 to early afternoon (Fig. 1); incompletely timed ones ranged up to 335 min duration (Table 1). The second recess generally began between 15:00 and 16:00 and averaged $57 \pm 24.9$ min (range 35–90 min, n = 4). Females usually incubated through the night, beginning one to two hours before dusk. Occasionally this typical regime was varied by the interpolation of an extra incubation bout in the early morning prior to the long recess, or by shortening of the long recess and advancing of the afternoon recess. In the latter case the long recess was still of three to four hours duration. Just before hatching, recesses often became shorter. Thus eggs were usually continuously deserted for three to six hours in the long recess during the complete incubation stage. Mean daily maximum $T_a$'s at this time were 6–12°C in both study areas. The attentive index (mean percentage of the average daylength incubated) for this stage was 45% (Lill, unpubl. data), well below the typical passerine range of 60–80% (Skutch 1962).

INTERNAL EGG TEMPERATURES DURING MATERNAL RECESSES

$T_a$ near ground level was 10°C or less during all six July daytime monitoring sessions. On the two days it was monitored, $T_e$ of egg A dropped from 29°C to 10°C in 2.6–3 h following maternal morning exodus and stabilized within 1–3°C of $T_a$ after 3–3.25 h

(Fig. 2). On the second afternoon, resumption of incubation induced a 0.24°C/min rise in $T_e$ over 75 min. Both whole-day monitoring sessions for egg B yielded similar results to those for egg A except that on the second day initial $T_e$ was 3°C lower and the rate of cooling to $T_a$ much faster. In two further afternoon monitoring sessions, $T_e$ of egg B rose 0.35 and 0.37°C/min respectively when the female resumed incubation. The results show that in the incomplete incubation phase embryos were extensively exposed to low temperatures each day. Egg cooling rates ranged from 0.065 to 0.1°C/min (mean 0.081°C/min, n = 4) and heating rates from 0.222 to 0.367°C/min (mean 0.292°C/min, n = 5). Over the same temperature range, both eggs heated up much faster when incubation resumed than they cooled down after maternal exodus (Table 2).

THE BROODING REGIME

Eggs hatched in August and September. There was no obvious, consistent daytime brooding rhythm and daytime brooding

TABLE 2. Cooling and reheating times of two eggs with implanted transmitters.

| Egg/day measured | Cooling or heating temperature range[a] | Minutes taken to cool | Minutes taken to reheat |
|---|---|---|---|
| A; Day 5 | 9–28°C | 225 | 75 |
| B; Day 7–11 | 9–26°C | 290 | 60 |
| B; Day 8–12 | 8–25°C | 275 | 55 |

[a] These ranges are the closest possible approximations to the ranges between incubation temperature and the lowest $T_e$ recorded during maternal absence.
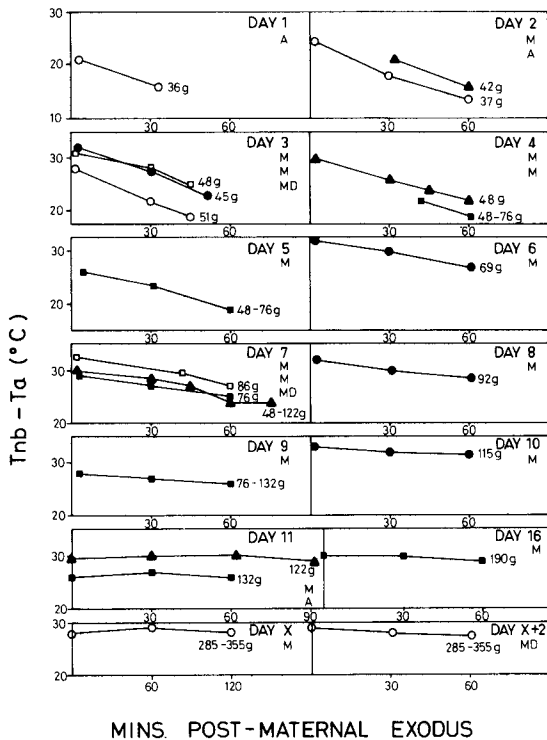
MINS. POST-MATERNAL EXODUS

FIGURE 3. $T_{nb} - T_a$ (°C) at intervals following maternal post-brooding departure. Exact or approximate nestling weight shown for each curve. Five nestlings (solid triangle, solid circle, solid square, crossed circle and open square) were measured on more than one day. Curves marked with open circles are for nestlings measured on only one day. Day 1 was hatching day. Readings taken on day X and X + 2 were for an unaged, mid-term nestling. Readings for Day 11 onwards commenced at an arbitrary time as there was no daytime brooding. The curve for a 51 g nestling on Day 3 was obtained after flushing the mother following four hours of continual brooding from first light on a rainy day. Time of day at which each set of readings was begun is shown as M (pre-10:00), MD (10:00–14:00) or A (post-14:00) to the right of each cell; the vertical order of these symbols corresponds with the vertical order of their associated cooling curves.

gradually decreased and ended on day 10 when nestlings averaged 128 g (Lill, unpubl. data).

Twenty-nine brooding sessions spread over most daylight hours and recorded for nestlings up to nine days old averaged 37 ± 21 min in length (range 13.5–126 min). Mean duration of thirty-two maternal recesses was 39 ± 20 min (range 14–104 min), and several far longer recesses were recorded throughout the daytime brooding phase (Table 3). Mean daily maximal $T_a$'s in the two study areas at this time range from 9–15°C. Brooding constancy (percentage of the average daylength spent brooding) averaged 42.1% over the ten days of daytime brooding.

TABLE 3. Duration of maternal daytime recesses in the daytime-brooding nestling stage.

| Nestling age (days post-hatching) | | Duration of recesses (min) | |
|---|---|---|---|
| | | Absolute length | Minimal[a] length |
| 1 | | 35 | |
| 2 | $\bar{x}$ | 16.6 ± 2.4[c] | |
| | R | 14–19.5 | |
| | n | 4 | |
| 3 | $\bar{x}$ | 40.3 ± 11.5 | |
| | R | 29.5–60 | |
| | n | 6 | |
| 4 | | 26.5; 53 | 20; 28.5 |
| 5 | $\bar{x}$ | 54.2 ± 43.3 | 38; 55.5 |
| | R | 25.5–104 | |
| | n | 3 | |
| 6 | | 53.5; 77 | |
| 7 | | | 4.5; 25 |
| 8 | R | | 46–118 |
| | n | | 3 |
| 9 | | 35.5; 42 R | 5–182 |
| | | n | 4 |
| 10 | | | 72; 67 |
| 1–4[b] | | 34; 38 | 2.5 |
| 1–6 | $\bar{x}$ | 38.9 ± 19.5 R | 6–31 |
| | R | 20–76 n | 3 |
| | n | 7 | |
| 5–8 | $\bar{x}$ | 32 ± 12.5 | 20.5; 31.5 |
| | R | 20–45 | |
| | n | 3 | |

[a] Beginning and/or end untimed.
[b] Nestling ages only approximately known.
[c] For samples of three or more absolute lengths, mean ± standard deviation, range (R) and sample size (n) are given. For samples of three or more minimal lengths, range and sample size are given.

## NESTLING TEMPERATURES DURING MATERNAL ABSENCES

The slopes of the cooling curves obtained for seven nestlings (Fig. 3) show a gradual improvement in thermoregulation up to day 10 when nestlings were effectively endothermic and daytime brooding ceased. At $T_a$'s of 2–12°C, $T_{nb}$ fell 6–9°C after 30 min post-brooding exposure on days 1–4 and 10–13°C after 60 min exposure on days 2, 4, 5, and 6. An hour's exposure on days 9 and 10, however, induced only a 2°C drop. Given the duration of maternal recesses (Table 3), 4–8°C drops in $T_{nb}$ must have been common on days 1–6 and 12–13°C drops probably occurred during the longest recesses noted for this nestling age.

## NESTLING GROWTH RATES

The nestling period ranged from 41–44 to 54–55 days (best mean estimate 47 days). Mean hatching weight was 46 ± 6 g (n = 11) and mean fledging weight was 571 ± 63 g (n = 11) or 63% of the average adult (female) body weight. Since the converted growth curves of five known-age nestlings which fledged are essentially linear (Fig. 4),
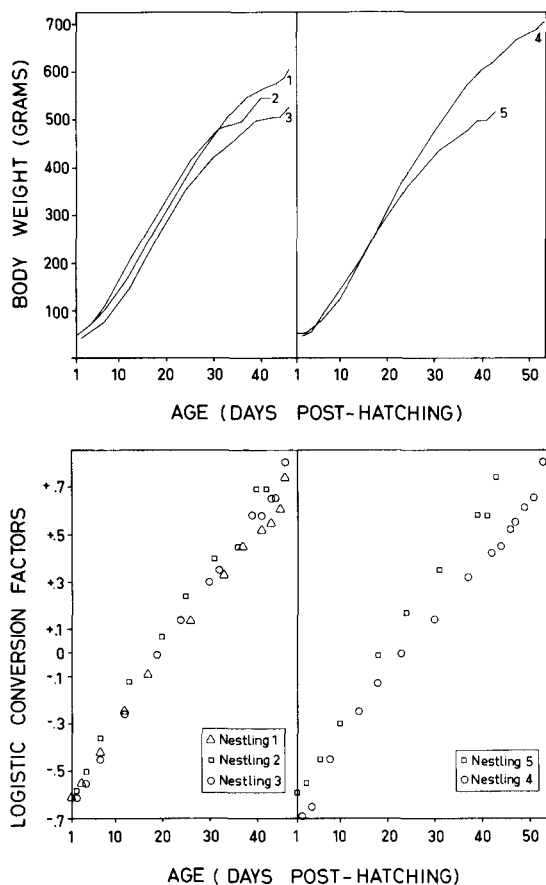
FIGURE 4. Actual and converted growth curves for five exactly-aged nestlings which fledged at Healesville (1976–1977). Curves divided into two sets to facilitate reading. Day 1 = day of emergence from egg.

growth, though slow, was clearly logistic in form (Ricklefs 1967). K, the growth constant of the logistic equation, ranged from 0.105–0.122 (mean 0.117) for the five growth curves; $t_{10-90}$ ranged from 35.4–41.9 days, with a mean of 37.6.

## DISCUSSION

### THE INCUBATION REGIME AND EMBRYONIC TEMPERATURES

$T_e$'s of 25–29°C recorded towards the end of nocturnal incubation are well below the 33–38°C range documented for other species during continuous egg contact by the incubating parent(s) (Drent 1970). The discrepancy probably stems from the transmitter's weight, which must have ensured that it was always at the base of the egg, which is probably significantly cooler than at the early embryo's topical position (Drent 1972).

The 3–6 h morning recess during the full incubation stage clearly leads to extreme lowering of embryonic temperature, even if $T_e$ is a little higher than indicated by pres-

ent measurements. Increased embryonic thermogenesis later in the incubation period is probably insufficient to significantly counteract the degree of exposure recorded (MacMullan and Eberhardt 1953, Drent 1970). The Superb Lyrebird's attentiveness index is far lower than those of most passerines, tropical hole-nesters and unaided uniparental incubators (Skutch 1962), including many breeding at low $T_a$'s (e.g., Capercaillie, *Tetrao urogallus*, 95%, Lennerstedt 1966; Pink-footed Goose, *Anser fabalis brachyrynchus*, 91.3%, Inglis 1977). High frequencies of predation on nests may also have promoted selection for high levels of attentiveness in many birds, but although lyrebird nests are vulnerable and often depredated (Lill, unpubl. data), the known involvement of ubiquitous, non-endemic nest predators clouds the issue in this species. The incubation regime and embryonic thermal environment of the Superb Lyrebird are unusual but not unique, even among low temperature breeders. Long nest recesses resulting in low embryonic temperatures occur regularly in some procellariiforms and galliforms (Barth 1949, Westerskov 1956, Pefaur 1974).

Moderate exposure at 0–25°C slows development without inducing growth abnormalities in chicken and possibly other avian embryos, but significant exposure between 37°C (incubation temperature) and 27–25°C [physiological zero temperature (PZT) below which development ceases] causes abnormal growth (Lundy 1969). If chicken and lyrebird PZTs are similar, Figure 1 indicates that daily exposure in this critical range is fairly restricted and, by analogy, delayed development is probably the main effect of egg neglect in lyrebirds.

In birds, egg weight is positively correlated with duration of incubation period (Rahn and Ar 1974) and adult body size (Huxley 1927), which in turn is inversely correlated with growth rate (Ricklefs 1968, 1973). Thus lyrebirds should have a long incubation period irrespective of daily embryonic cooling. However, the larger corvids, the passerines closest to lyrebird size, have only approximately three-week incubation periods (Witherby et al. 1938, Rowley 1973). Moreover, from the relationship between egg weight and incubation period in birds (Rahn and Ar 1974), a 29–30 day incubation period rather than the 50 days observed (Lill, unpubl. data) would be predicted for the 62.9 g lyrebird egg. Significantly, Ward (1940) reported that a newly laid lyrebird egg which was contin-

uously incubated by a domestic hen hatched after 28 days. This critical experiment should be replicated on a larger scale.

Lyrebird eggs cooled more slowly during maternal recesses than 100-g Herring Gull (*Larus argentatus*) eggs exposed at similar $T_a$'s (Drent 1973). It is doubtful whether nest insulation causes this slower cooling rate, since air temperature in the nest chamber is within 1°C of $T_a$ during incubation and daytime brooding of nestlings (Lill, unpubl. data). Incubating females spent nearly all their recess time foraging. Given the necessity of six to seven hours foraging daily, taking one long recess might keep $T_e$ outside the detrimental intermediate temperatures for a greater percentage of the day than several shorter recesses. This incubation rhythm would be particularly adaptive when rates of egg cooling are relatively slow.

THE BROODING REGIME AND EARLY
NESTLING TEMPERATURES

The considerable exposure of ectothermal lyrebird nestlings to low temperatures during maternal recesses should reduce their growth rate. The additional insulation provided by the domed and burrow nests of some species somewhat buffers nestlings against low $T_a$'s during recesses and advances the age of effective endothermy (e.g., Roberts 1940, Dunn 1976). But such buffering does not seem to occur in lyrebirds as indicated above, probably due to the size of the nest entrance. As nestling exposure is less extreme than embryonic exposure and endothermy is attained by day 10, the effect of cooling on growth should be far less than in the incubation period. This prediction is supported by Drent's (1975) analysis of the nestling growth rate–incubation period relationship in birds. The lyrebird's mean growth rate ($K = 0.117$) is unusually slow among passerines. Nestling growth rate and adult body size are inversely correlated in birds, but comparing the lyrebird values with those for other passerines (Ricklefs 1968, 1969) indicates that large body size does not entirely account for the slowness of nestling growth in this species. Similar growth rates occur mainly among raptors and seabirds.

The impact of chilling on growth rate is harder to assess for the nestling than the embryo. Ectothermal nestlings of many species can tolerate considerable experimental exposure to low temperatures (Dawson and Evans 1960) and marked lowering of $T_{nb}$ during natural parental recesses has

been recorded in a few species (e.g., Wilson's Storm-Petrel, *Oceanites oceanicus*; Pefaur 1974; Snowy Owl, *Nyctea scandiaca*; Barth 1949). However, too few studies have combined detailed documentation of the brooding rhythm with measurement of $T_{nb}$ for us to know whether natural exposure of young nestlings to a low $T_a$ is common. While the degree of exposure documented here may reduce the nestling's growth rate, it seems insufficient to account entirely for the extreme length of the lyrebird's nestling period. Possibly the slow nestling growth rate evolved partly because it spreads out the parental energetic load in a species where brood reduction is not possible (Ricklefs 1968, 1973).

SUMMARY

Incubation and brooding regimes of Superb Lyrebird females were studied over six winter breeding seasons at two wet sclerophyll forest sites in southeastern Australia. Internal temperatures of two eggs were monitored telemetrically over several days soon after laying. Core temperatures of young nestlings were measured at intervals after maternal exodus during the first ten days post-hatching, and some similar readings were obtained for older, endothermic nestlings. Growth curves were obtained and growth rates determined for five known-age nestlings.

The full incubation rhythm developed gradually and was characterized by a low (45%) attentive index and a three to six hour morning recess. Internal egg temperatures fell and stabilized around ambient levels (approx. 10°C) for several hours daily during these long maternal absences. When incubation resumed, the egg reheated much faster than it had cooled.

Daytime brooding ceased ten days after hatching when nestlings became endothermic. Mean recess duration during this brooding period was 39 min, but 45–60 min recesses were common on days 1–6. Nestling temperature measurements showed that 4–8°C drops must have been common during maternal absences and drops of 12–13°C characteristic of longer recesses early in the ectothermic period. Nestling growth curves were logistic, mean K being 0.117 and mean $t_{10-90}$ 37.6 days.

Comparative evidence suggests that retardation of embryonic growth is the main effect of daily egg neglect. One possible adaptive value of a single long recess rather than several shorter daily recesses is advanced. The effect of cooling on nestling

growth rate is harder to assess and probably less pronounced.

## ACKNOWLEDGMENTS

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Departments of Zoology and Psychology, Monash University, Clayton, Victoria, Australia 3168. Accepted for publication 18 September 1978.