



## EMBRYONIC THERMAL TOLERANCE AND TEMPERATURE VARIATION IN MOUNDS OF THE AUSTRALIAN BRUSH-TURKEY (*ALECTURA LATHAMI*)

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**ABSTRACT.**—In oviparous reptiles, incubation temperature has been shown to have profound effects on embryonic development and hatchling phenotypes. However, these effects are not well studied in birds, because they typically brood their eggs within a narrow range of temperatures. The Australian Brush-turkey (*Alectura lathami*) is a megapode that constructs incubation mounds and relies on the heat produced by respiring microorganisms in these mounds to incubate its eggs and is, therefore, a useful comparative model. We developed a new method for monitoring mound and egg temperature to determine both mound thermal variability and the thermal tolerance of embryos. All mounds exhibited greater temperature fluctuations than previously reported or predicted by modeling. Furthermore, all Australian Brush-turkey embryos were exposed to suboptimal temperatures for prolonged periods during development, some experiencing temperatures 6°C above or 9°C below the optimum (34°C) for 12 h. This is the first evidence of bird embryos developing during long-term exposure to suboptimal temperatures. Notably, natural incubation periods were 2–6 days shorter than previously reported for this species. *Received 24 May 2007, accepted 17 November 2007.*

**Key words:** *Alectura lathami*, Australian Brush-turkey, body temperature, embryos, thermal tolerance.

### **Tolerancia Térmica del Embrión y Variación de la Temperatura en Montículos de *Alectura lathami***

**RESUMEN.**—En los reptiles ovíparos, la temperatura de incubación tiene profundos efectos en el desarrollo del embrión y en el fenotipo de las crías. Sin embargo, estos efectos no están bien estudiados en las aves, porque típicamente éstas incuban a sus huevos en un rango estrecho de temperaturas. *Alectura lathami* es una especie de megápodo que es un modelo comparativo útil debido a que construye montículos de incubación y depende del calor producido por microorganismos aeróbicos en estos montículos para incubar sus huevos. Desarrollamos un nuevo método para monitorear la temperatura de los montículos y de los huevos para determinar la variabilidad térmica de los montículos y la tolerancia térmica de los embriones. Todos los montículos mostraron mayores fluctuaciones de temperatura que las previamente registradas o predichas por los modelos. Más aún, todos los embriones de *A. lathami* fueron expuestos a temperaturas subóptimas por períodos prolongados durante el desarrollo, e incluso algunos experimentaron temperaturas de 6°C por arriba o 9°C por debajo del óptimo (34°C) por 12 h. Esta es la primera evidencia de embriones de aves que se desarrollan durante una exposición prolongada a temperaturas subóptimas. Llamativamente, los períodos de incubación natural fueron de 2 a 6 días más cortos que los registrados anteriormente para esta especie.

BIRD EGGS REQUIRE external heat to complete embryonic development. Most birds are brood incubators and use parental body heat for this purpose, but megapodes are unique among birds because they use environmental heat—solar, geothermal, and the heat released by decomposing organic matter—to incubate their eggs. These sources are more difficult to regulate than the heat provided by brood-incubating birds; thus, megapode embryos may be exposed to a wider range of incubation temperatures than other bird embryos.

However, theoretical models (hereafter “the Seymour mound model”) of incubation mounds constructed of soil and leaf litter, such as those built by Australian Brush-turkeys (*Alectura*

*lathami*), predict that a stable equilibrium temperature will be reached and maintained, provided that certain conditions are met (Seymour 1985, Seymour and Bradford 1992). These conditions are (1) a critical mass of fresh litter (~3,000 kg, approximately 0.75 m high × 2.0 m in diameter), (2) sufficient water content (>0.2 mL g<sup>-1</sup> dry material), and (3) occasional mixing of the litter.

The Australian Brush-turkey (hereafter “brush-turkey”), a megapode that inhabits the coastal belt of eastern Australian as far south as Sydney (34°00'S, 151°00'E), incubates its eggs in mounds built from soil and leaf litter (Jones 1995). Heat produced by respiring microorganisms within decomposing material is the sole source of heat for incubation (Frith 1956). But because of the

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large size (~200 g) of brush-turkey eggs compared with those of most other birds, heat produced by the developing embryo in the latter stages of development may appreciably alter incubation temperatures. Unlike most birds, neither sex of brush-turkeys provides parental care beyond the maintenance of the mound by the male (Jones 1995). The super-precocial chicks dig themselves out of the mound after hatching and must be competent at thermoregulating, finding food, and avoiding predation if they are to survive (Frith 1956).

Artificial incubation experiments (Göth and Booth 2005) and spot measurements of natural incubation-mound temperatures (Seymour 1985, Jones 1988, Seymour and Bradford 1992) have provided preliminary support for the Seymour mound model and suggested an optimum incubation temperature of ~34°C for brush-turkey eggs. Also, other investigations of brush-turkey mounds have found temperatures to be fairly stable at the position in the mound where eggs are typically laid (Frith 1956, Seymour 1985, Jones 1988). However, these studies have relied on opportunistic rather than systematic measurements of mound temperature. Furthermore, studies of the mating system of this species have shown that not all females have access to mounds or mound depths that would provide the optimal temperature for incubation and must resort to laying eggs in suboptimal positions or mounds. Therefore, the prediction of the Seymour mound model, that eggs experience optimal and stable temperatures throughout development, needs to be tested empirically by continuous monitoring of egg temperature within natural mounds.

Because megapodes use environmental heat to incubate their eggs and produce super-precocial chicks, their incubation strategy is remarkably similar to that of oviparous reptiles that incubate their eggs in underground nests or mounds. Direct comparisons can be made with reptilian embryos incubated by environmental heat that may experience relatively large fluctuations in temperature throughout incubation and are, therefore, able to develop successfully over a broad range of temperatures (Deeming and Ferguson 1991, Birks 1996, Deeming 2004). For example, the eggs of many reptile species experience daily and seasonal fluctuations of up to 10°C throughout development, and development continues normally over these temperature changes. However, in most reptiles, even minor differences in temperature experienced during development can affect ecologically important hatching traits, such as sex, size, energy reserves, and locomotor performance (Deeming 2004). By contrast, most avian embryos are brood-incubated by body heat, the parents adjusting their behavior to regulate incubation temperatures within a narrow range (Webb 1987). Most avian embryos can tolerate relatively large (>10°C) and prolonged (a few days) decreases in incubation temperature by ceasing development when cooled and recommencing when temperatures return to optimal. However, if these same embryos are exposed to suboptimal temperatures (2–5°C above or below optimal), development continues and typically results in teratogenic abnormalities. As a result, most bird embryos cannot tolerate prolonged exposure to suboptimal incubation temperatures (Webb 1987). Conversely, because of their nesting biology, megapode embryos are potentially exposed to a wider and more variable range of incubation temperatures; temperatures may be just a few degrees above or below the optimum, and their eggs may experience significant heating because of increased metabolic

heat production during the latter third of incubation. We predict that if natural mound temperatures are found to be more variable than the Seymour mound model predicts, megapode embryonic thermal tolerances may be more closely akin to those of oviparous reptiles than to those of other avian species.

To test the thermal tolerance of naturally developing brush-turkey embryos and the Seymour mound model's prediction of naturally built incubation mounds, we determined (1) the temperatures experienced by brush-turkey eggs within natural incubation mounds, (2) the thermal tolerance of embryos developing successfully to hatching, (3) the influence of metabolic heat on egg temperature, and (4) the incubation period of eggs in natural mounds.

## METHODS

*Study population and detection of newly laid eggs.*—During the 2004–2005 and 2005–2006 breeding seasons (August–January), 7–12 adult brush-turkeys inhabited the St. Lucia campus of the University of Queensland, Brisbane, Australia (27°32'S, 153°00'E), and the four breeding males constructed 14 and 12 functioning incubation mounds in 2004–2005 and 2005–2006, respectively. Eggs from nine of these mounds were monitored. For the 3 h following dawn, mounds were monitored for females displaying laying behaviors (for a full description, see Jones 1990), because most eggs are laid during this period. If a male is present at the time of laying, he typically chases the female away from the mound area once the egg has been half buried by the female, before completing the burying process himself. To gain access to the eggs without harassing the female (to ensure that she would not abandon laying into the mound) but before complete burial, data loggers were placed on the half-buried eggs and in the mound immediately adjacent to the egg when the male chased the female from the vicinity. Occasionally, females lay with no male present. In such cases, we flushed the female from the vicinity of the mound when the egg was half buried. This method ensured the least disturbance to the brush-turkeys and the mound's structural integrity while allowing access to freshly laid eggs at naturally occurring positions within the mound. On one occasion, an egg (no. 101) was discovered in a mound, but the exact laying date was not known. A data logger was placed on this egg, but because the laying date was not known, it could not be used to measure the incubation period or to calculate a mean incubation temperature for the entire incubation period.

*Temperature monitoring.*—Eggs were exposed but not removed from the mound. An iButton (Dallas Technologies, Cedar Hill, Texas) temperature data logger recorded eggshell surface temperature and, in the 2004–2005 season, another iButton measured mound temperature adjacent to the egg. In the 2005–2006 breeding season, the eggshell surface temperature, but not adjacent mound temperature, of a further nine eggs was monitored using the same method. The iButton was attached to the eggshell surface using a 25 × 25 mm section of adhesive tape and connected to the second data logger by 100 mm of nylon monofilament line. Loggers were programmed to record temperature every 2 h throughout incubation. To ensure that eggs could be located later, egg position within the mound was mapped. We then buried the egg, compacting the mound material in a way similar to that

TABLE 1. Thermal tolerance of Australian Brush-turkey (*Alectura lathami*) embryos in natural incubation mounds ("12-h min-max" and "24-h min-max" are the minimum and maximum temperatures recorded for a continuous 12-h and 24-h period; *n* is the total temperature readings recorded; "failed" = embryos died during incubation).

Egg	Mound	Male	Lay date	Eggshell surface temperature (°C)				<i>n</i>	Incubation period (days)
				Min-max	Mean $\pm$ SD	12-h min-max	24-h min-max		
704	7	1	5 December 2004	31.0–37.5	35.2 $\pm$ 1.4	31.5–37.5	31.5–37.5	554	46.2
802	8	2	1 December 2004	29.5–37.0	34.9 $\pm$ 1.6	30.5–37.0	31.5–37.0	545	45.4
803	8	2	5 December 2004	28.5–37.0	34.6 $\pm$ 1.8	29.5–37.0	31.0–36.5	554	46.2
901	9	3	3 December 2004	29.5–40.0	34.7 $\pm$ 2.5	32.0–39.5	33.0–39.5	547	45.6
1,001	10	3	3 December 2004	29.5–40.0	35.3 $\pm$ 2.0	30.5–39.0	31.0–38.5	528	44.0
1,002	10	3	6 December 2004	30.5–38.5	34.5 $\pm$ 1.7	32.5–37.5	32.5–37.0	509	42.4
1,007	10	3	7 December 2004	27.5–37.0	34.6 $\pm$ 1.6	30.5–36.5	31.5–36.5	543	45.3
101	1	4	September 2004	24.5–38.5	n/a	25.0–38.5	25.5–38.2	294	(24.5)
717	7	5	8 September 2005	30.7–39.0	35.0 $\pm$ 1.8	31.5–38.4	31.9–37.6	555	46.3
1,403	14	6	15 September 2005	31.9–40.7	35.7 $\pm$ 1.9	32.4–40.7	32.5–40.2	519	43.3
718	7	5	14 October 2005	32.4–38.2	35.6 $\pm$ 1.1	33.6–38.2	33.4–37.9	529	44.1
1,901	19	7	17 October 2005	31.9–38.2	36.0 $\pm$ 1.0	35.4–38.0	34.8–37.9	511	42.6
806	8	8	7 November 2005	30.3–38.2	35.4 $\pm$ 1.3	33.0–37.9	34.2–37.4	528	44.0
1,401	14	6	8 September 2005	30.5–42.6	34.3 $\pm$ 2.4	30.6–42.0	31.0–41.4	552	Failed
1,909	19	7	23 January 2006	28.8–36.0	33.4 $\pm$ 2.0	29.0–35.9	29.2–35.9	552	Failed

of an adult burying an egg. The data loggers were retrieved 65 days after the eggs were laid. Hatching was indicated by the presence of eggshell pieces and the absence of a buried chick. The day of hatch was determined from the temperature traces by noting a sudden drop in eggshell surface temperature, which then closely matched the adjacent mound temperature.

For each egg, a 12-h and a 24-h period of minimum and maximum eggshell surface temperatures was determined from the entire course of the incubation period, excluding the first 48 h of incubation (Table 1). For example, the 12-h minimum was the lowest temperature the eggshell surface was at or below for a continuous period of 12 h. The periods of 12 h and 24 h were arbitrarily selected to represent periods of prolonged exposure. The first 48 h were excluded because the opening of the mound to lay eggs resulted in a drop in mound temperature at the site of egg laying, and this temperature was returned to general mound temperatures within 48 h.

Rainfall measurements were recorded on the St. Lucia campus by the School of Geography, Planning and Architecture. The relationship between eggshell surface temperature and incubation period was examined using Pearson correlation analysis.

## RESULTS

**Mound temperatures and embryonic thermal tolerance.**—All mounds were considered to meet the conditions of the Seymour mound model; that is, they were larger than  $0.75 \times 2.0$  m and were mixed regularly by the males, which typically visited mounds every day and spent 0.5–2.0 h working each mound. We did not measure the water content of mound material, but the

litter material was moist to the touch, which suggested that the water content was high. Mound temperatures adjacent to eggs averaged  $33.8 \pm 1.9^\circ\text{C}$  (SD; 4,074 data points from 7 eggs) and ranged from 24.5 to  $37.5^\circ\text{C}$ . Periods of heavy rain typically reduced mound temperatures by 4– $10^\circ\text{C}$  for 2–10 days. The sharpest drop in mound temperature was recorded for egg no. 803, where heavy rain (47 mm in 2 h) caused an immediate  $10^\circ\text{C}$  drop in mound temperature and a corresponding  $6^\circ\text{C}$  fall in eggshell surface temperature (Fig. 1).

Fifteen eggs were monitored in all, eight from five mounds in the 2004–2005 breeding season and seven from four mounds in the 2005–2006 season. Hatching success was 87%. For eggs that hatched, eggshell surface temperatures for the entire incubation period averaged  $34.8 \pm 1.9^\circ\text{C}$  (6,422 data points from 12 eggs) and ranged from 24.5 to  $40.7^\circ\text{C}$ . Typically, eggshell temperature varied greatly during the course of incubation and changed by as much as  $8^\circ\text{C}$  over a five-day period (Fig. 2). Hatching occurred after prolonged periods of exposure to high and low temperatures (Table 1). For example, egg no. 101 hatched after exposure to temperatures below  $25.0^\circ\text{C}$  for 12 h and below  $25.5^\circ\text{C}$  for 24 h, whereas egg no. 1,403 hatched after exposure to  $40.2^\circ\text{C}$  for 24 h.

**Metabolic heat production and incubation period.**—From about half-way through the incubation period, egg temperature began to rise above the temperature of the adjacent mound material, and by the final week of incubation this temperature difference reached  $2.5$ – $3.5^\circ\text{C}$  (Fig. 1). The incubation period of naturally incubated eggs averaged  $44.80 \pm 0.38$  (SE) days and varied from 42.4 to 46.3 days. Incubation period was negatively correlated with mean eggshell surface temperature (Fig. 3).

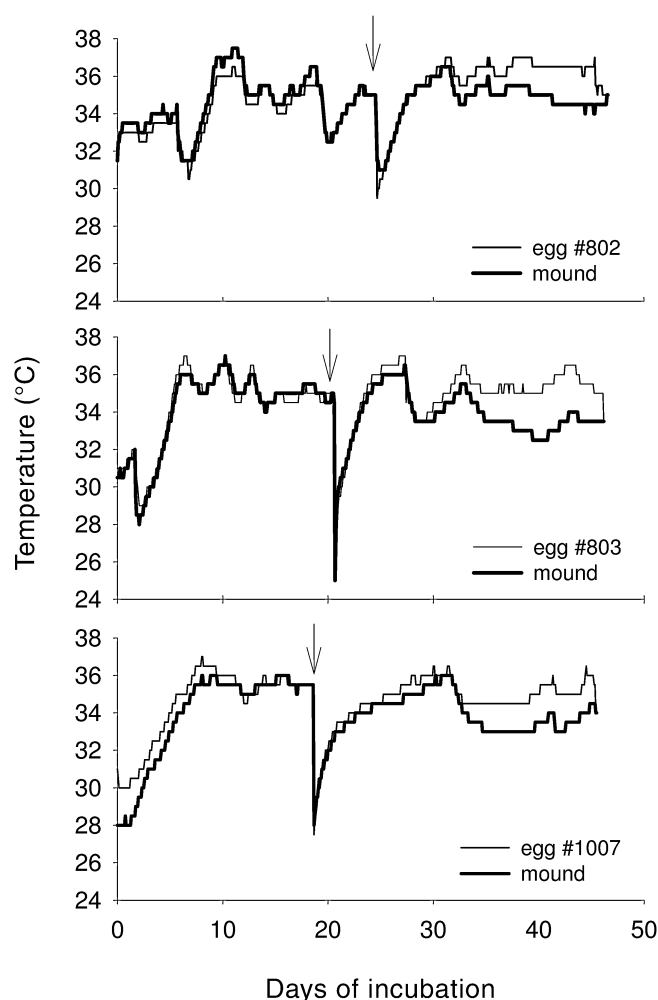


FIG. 1. Temperature of eggshell surfaces and of mound material adjacent to Australian Brush-turkey eggs from the time of laying until hatching. Note that egg temperature increases by several degrees toward the end of incubation because of metabolic heat produced by the large embryos. The rapid drop in eggshell temperature to equality with mound temperature was used to indicate hatching and to calculate the incubation period. Arrows indicate periods of heavy rain. Note that, unlike the prediction of the Seymour mound model, all mounds experienced fluctuations in temperature and failed to reach a stable equilibrium temperature.

## DISCUSSION

*Mound temperatures and the Seymour model prediction.*—The brush-turkey mounds we studied appeared to meet the general assumptions of the Seymour mound model. However, the temperature fluctuations observed in all mounds were greater than the model predicts. Monitored mounds were of sufficient size and were worked regularly by a male (observed on early-morning egg-collection visits), yet they deviated significantly from the targeted temperature of 34°C for prolonged periods. Previous studies (Seymour and Ackerman 1980, Jones 1988) did not detect these continual shifts in temperature (i.e., those not produced by heavy

rainfall), possibly because they used opportunistic or mean measurements of mound temperature at places within the mound that may or may not have contained eggs. Previous studies of brush-turkey mounds found average temperatures of 35.8°C (Frith 1956), 33.3°C (Jones 1988), and 32.9°C (Seymour and Bradford 1992), compared with our 33.8°C. The present study has the advantage of continuous systematic monitoring of eggshell and adjacent mound-material temperatures and, hence, gives a temporally and spatially complete record of natural incubation temperatures. Jones's (1988) study indicated that the only major shifts in mound temperatures were attributable to periods of heavy rain where the temperature dropped dramatically. In the present study, some, but not all, of the major temperature shifts were attributable to heavy rain, and mounds that cooled by  $\leq 10^{\circ}\text{C}$  took 2–10 days to recover their pre-rain temperatures. In summary, although the mean temperature of mounds in the present study was similar to that recorded in other studies, the variations in temperature far exceeded those previously recorded, ranging from 24.5 to 37.5°C.

*Thermal tolerance of embryos.*—Although the mounds were found to deviate significantly from the predictions of the Seymour mound model, the average incubation temperature of eggs in the present study was 34.8°C. A review of avian incubation temperatures by Webb (1987) found the mean egg temperature of most species to be in the low to mid-30s; however, because of the thermal gradients within the egg produced as a result of contact incubation (Turner 2002), the developing embryos typically experience temperatures of 36 to 38°C. By contrast, mound-incubated eggs do not experience thermal gradients within the egg, so their embryos develop at temperatures close to the surrounding mound material except during the last third of incubation, when egg temperature increases because of metabolic heating. So, although most bird embryos develop at a relatively constant 37–38°C, brush-turkeys develop at temperatures several degrees lower during early incubation (32–34°C), but this typically increases to 35–37°C by the end of incubation.

Compared with other avian embryos, brush-turkey embryos show remarkable thermal tolerance and were able to develop successfully to hatching despite prolonged shifts to suboptimal temperatures. The present study shows that brush-turkey eggs commonly experience incubation temperatures as much as 5°C above and 9°C below the optimum for periods of  $\geq 12$  h. For example, one embryo (egg no. 101) developed successfully despite being exposed to temperatures  $\leq 25.5^{\circ}\text{C}$  for a 24-h period,  $>8^{\circ}\text{C}$  below the optimal temperature. Many brooding birds are able to tolerate large ( $>10^{\circ}\text{C}$ ) drops below optimum temperature by ceasing embryonic development during these periods. Most remarkable is that all the brush-turkey eggs monitored experienced temperatures 2–5°C suboptimal for periods of days or weeks when embryos continued to develop without detriment to the embryo. The embryos of brooding birds cannot tolerate more than a few hours in this temperature range, because prolonged development at slightly suboptimal temperatures results in tetragenic deformities (Wheelright and Boersma 1979, Webb 1987).

Although unusual for a bird, the reproductive strategy of megapodes is similar to that of large reptiles, which often deposit eggs in underground nests or in mounds and also tolerate prolonged exposure to suboptimal temperatures. Birds are evolutionarily closest to crocodiles (Carroll 1988), some species of which also build mounds



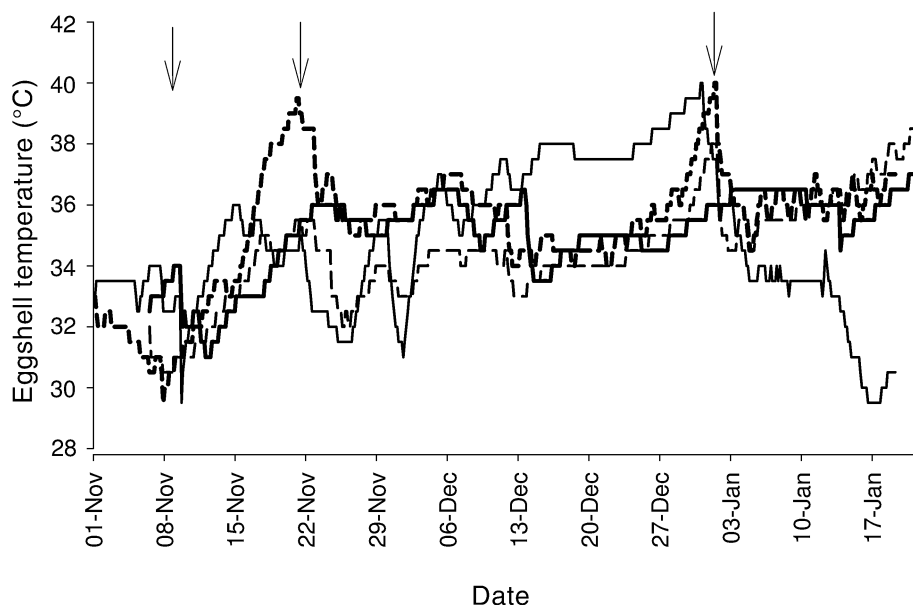


FIG. 2. Eggshell surface temperature of Australian Brush-turkey eggs no. 704 (thick line), 901 (thin line), 1,001 (thick dash), and 1,002 (thin dash) from the day of laying until hatching. Eggs were laid in natural incubation mounds during the 2004–2005 breeding season in St. Lucia, Brisbane. Arrows indicate periods of heavy rain.

of organic matter. It was originally supposed that, because of these similarities, megapodes were a primitive lineage of birds, but recent molecular studies have shown that this group has evolved more recently and that their reproductive strategy is secondarily derived (Jones and Birks 1992). Because of their reliance on environmental heat sources, the embryos of both reptiles and megapodes are tolerant of prolonged periods at suboptimal temperatures. Most

reptiles typically have a lower optimum temperature (25–30°C) for incubation than birds (Seymour and Ackerman 1980), except for crocodilians, which, interestingly, have optimal incubation temperatures intermediate to those of other reptiles and birds (Magnusson et al. 1985). In light of these results, further research is needed to determine whether, as in reptiles, these differences in incubation temperature affect ecologically important traits of brush-turkey hatchlings exposed to different incubation temperature regimes.

**Metabolic heat.**—During the last few weeks of incubation, brush-turkey embryos are sufficiently large to produce considerable metabolic heat, which raises egg temperature above the surrounding mound temperature. By the end of incubation, eggshell surface temperature is typically 2.5–3.5°C above the surrounding mound temperature. Consequently, this alters the thermal experience of the embryo and increases the mean incubation temperature. Also, this temperature difference across the eggshell produces a water-vapor pressure gradient that results in significant water loss from the egg (Seymour et al. 1987). These phenomena, the production of heat and resultant water loss, have also been observed in Malleefowl (*Leipoa ocellata*), another megapode (Booth 1987).

**Incubation period.**—In general, temperature has a strong negative effect on incubation period; thus, substantial variation in incubation periods of brush-turkeys is likely, given the temperature variation of mounds. As expected, incubation period was negatively correlated with mean eggshell temperature, and, although there were significant thermal fluctuations in temperature, the mean incubation temperature of all eggs was surprisingly similar. The incubation period of all eggs that hatched in the present study (42–47 days) was shorter than the previously reported 49 days (Baltin 1969). This difference may be attributable to the fact that Baltin (1969) measured incubation period as the number of days between egg laying and the appearance of the chick on the

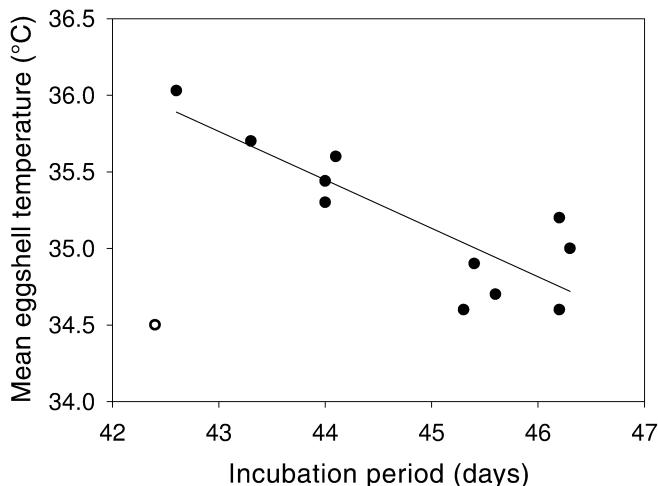


Fig. 3. Correlation between mean eggshell temperature and incubation period for Australian Brush-turkey eggs monitored throughout incubation in natural mounds ( $n \geq 509$ ). Incubation period was weakly and negatively correlated with mean eggshell surface temperature ( $r = -0.469$ ,  $n = 12$ ), but when an outlier (open circle) was removed, the correlation increased significantly ( $r = -0.844$ ,  $y = 125.65 - 2.29x$ ,  $P = 0.001$ ,  $n = 11$ ).

mound's surface, and it is known that brush-turkey chicks take one to two days to dig to the surface of the mound (Göth 2002); alternatively, the mound observed by Baltin (1969) had cooler average temperatures than the mounds we observed.

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