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ENERGETICS OF EMBRYONIC DEVELOPMENT IN THE MEGAPODE BIRDS, MALLEE FOWL *LEIPOA OCELLATA* AND BRUSH TURKEY *ALECTURA LATHAMI*¹

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(Accepted 1/3/84)

Mallee fowl (MF) and brush turkey (BT) lay large, energy-rich eggs (173 g at 10.2 kJ/g contents for MF and 180 g at 9.8 kJ/g contents for BT) that are incubated by burial in mounds of warm earth or decaying vegetation. Their incubation periods of 62 days (MF) and 49 days (BT) are unusually long, and their hatchlings are among the most precocial of any birds. Metabolic rates of embryos of both species just prior to hatching are about 61 cm³ O₂/h, 98% (MF) and 64% (BT) higher than predicted. Metabolism is supported solely by chorioallantoic respiration until hatching, and pulmonary respiration begins suddenly when the shell membranes are torn. Estimates of total energy expenditure during incubation prior to hatching (E_i) based on O₂ consumption closely approximate estimates based on energy content of fresh eggs and hatchlings. The E_i are high (~600 kJ for MF and ~475 kJ for BT) because of the long incubation periods. Hatchlings must dig out of the incubation mounds, and costs of this may add 8% (MF) to 33% (BT) to the E_i before hatchlings reach the surface. Lower emergence costs and larger initial energy stores of MF eggs partly compensate for higher developmental costs, so chicks of both species begin life on the surface with similar energy reserves. The large yolks (>50% of egg contents) and high energy content of megapode eggs were essential adaptations in the evolution of a reproductive system in which embryonic development and hatchling behavior are energetically expensive.

INTRODUCTION

The mound builders (Megapodiidae) are galliform birds endemic to Australasia. Megapodes are unique among birds because they incubate their eggs in pits or in mounds where heat is supplied by microbial respiration, the sun, or geothermal activity (Frith 1956). They are also unusual in producing the most precocial hatchlings of any birds (Nice 1962) and in having extremely long incubation periods (Frith 1956; Nice 1962). Chicks are totally independent after hatching, neither requiring nor receiving any parental care (Campbell 1901; Frith 1955, 1956; Bergman 1963; Baltin 1969). Hatchling mallee fowl (*Leipoa ocellata*), for

example, emerge from the mound unassisted, are fully homeothermic, and are capable of flight within a day or two (Frith 1959; Booth 1984). In the three Australian megapodes for which data are available, reported incubation periods range from 45 to more than 90 days (Bellchambers 1916; Meyer 1930; Fleay 1937; Frith 1956; Baltin 1969).

In this study we report on the energetics of development in two Australian megapodes, mallee fowl and brush turkeys (*Alectura lathami*). We examine the relationships among incubation period, extreme precocity, energy utilization, and the consequent requirements for provisioning in the eggs.

MATERIAL AND METHODS

SOURCE OF EGGS

Mallee fowl eggs were collected (under National Parks and Wildlife Service permits) from eight mounds on Calperum Station, near Berri, South Australia, and brush turkey eggs from five mounds in Flinders Chase National Park, Kangaroo Island, South Australia. Kangaroo Island is not

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part of the natural range of brush turkeys but supports a healthy population derived from a pair of birds introduced in 1948 (Ford 1979). On each visit to a mound we recorded the total number of eggs and chicks present, if any, and marked each egg for future identification. Collected eggs were packed in warm mound material in an insulated container and transported to the laboratory within 6 h. Eggs held in the laboratory were buried to a depth of about 5 cm in natural mound material and maintained at a temperature of 34 ± 0.5 C and a relative humidity near 100%. These conditions of temperature and humidity mimic those found near eggs in natural mounds (Seymour and Ackerman 1980; Vleck, unpublished data). Eggs were not turned but were kept in the same orientation they had in their natural mounds.

OXYGEN CONSUMPTION

Rates of oxygen consumption ($\dot{V}O_2$) of developing embryos were measured in closed, constant-volume systems or in open, flow-through systems. For the former method, each egg was transferred from the incubator to a chamber (approximately 1,100 cm³ in volume) immersed in a water bath at 34 C. Humidity in the chamber was maintained at near 100% by enclosing in it a shallow pan of distilled water. The chamber was sealed, and a gas sample was taken by injecting approximately 60 cm³ of saturated air at 34 C from a syringe, mixing by withdrawing and reinjecting the sample twice, then withdrawing a 50 cm³ sample. The chamber was then vented to atmospheric pressure and resealed. Chamber temperature was measured to 0.1 C with a mercury thermometer inserted through a rubber stopper in the lid. After an interval, a second sample was obtained by aspirating about 60 cm³ through a stopcock into a syringe. After sealing each sample in its syringe, we depressed the plunger so that room air could never be aspirated into the sample. Oxygen concentrations were measured by injecting the samples through a desiccant (Drierite) and a CO₂ absorber (Ascarite) into a Taylor Servomex paramagnetic O₂ analyzer accurate to 0.005% O₂. $\dot{V}O_2$ was calculated as $\dot{V}O_2 = V/t \cdot (F_I - F_E)/(1 - F_E) \cdot (PB - PH_2O)/PB$; where V is the gas volume in the chamber

(= chamber minus egg volume), t is the time between samples, PB is the barometric pressure, PH_2O is the water vapor pressure (saturated) at chamber temperature, and F_I and F_E are the initial and end fractional O₂ concentrations in dry, CO₂-free gas samples. All gas volumes are reported at standard temperature (0 C) and pressure (760 Torr = 101.3 kPa). The factor $(PB - PH_2O)/PB$ corrects the chamber gas volume to a dry volume. We did not correct for CO₂ initially present in the chamber, but this never exceeded 0.5% and would have led at most to a 0.5% overestimate of $\dot{V}O_2$.

For the open-flow measurements we used a two-channel system. In one channel the chamber contained an egg or hatchling, and in the other channel the chamber was left empty. In each channel, air under pressure passed through Ascarite and Drierite, then through a Fisher-Porter flowmeter, an air-stone humidifier, and a metabolic chamber. The excurrent air from each chamber was bubbled through a saturated KOH solution to remove CO₂, then passed through desiccants to a two-channel Taylor Servomex O₂ analyzer, which measured the difference in fractional oxygen content between the two channels. Flow rates to the chambers were adjusted to keep the difference less than 1%. Flowmeters were calibrated against a soap-bubble flowmeter, and data were recorded on a Perkin-Elmer flatbed recorder. The $\dot{V}O_2$ was calculated using equation 2 of Hill (1972).

We express $\dot{V}O_2$ as a function of days before hatching rather than days incubated because we usually did not know how long eggs had been incubated before we collected them. These data can be converted to days incubated by subtracting them from the reported incubation period of 49 days for brush turkey (Baltin 1969) and 62 days for mallee fowl (Frith 1959).

HATCHING AND EMERGENCE FROM THE MOUND

Open-flow respirometry was also used to measure $\dot{V}O_2$ continuously during hatching and burrowing of the chick through mound material. Eggs that were close to hatching were placed at the bottom of 25–30 cm of mound material in a Lucite cylinder (i.d. = 11.3 cm) which replaced the metabolism chamber in the system described above.

Progress of a hatchling could be viewed whenever it was near the clear wall of the cylinder. Metabolic rates were corrected for oxygen consumption by mound material.

PHYSICAL CHARACTERISTICS OF EGGS

Egg length and breadth and shell thickness were measured to 0.01 mm with a micrometer. Shell-thickness measurements are the mean of at least six measurements on each shell. Egg volumes were measured by weighing eggs first suspended in air and then suspended in water (Hoyt, Vleck, and Vleck 1978). There was no measureable change in mass after immersion in water. Initial densities of some eggs were determined by weighing eggs of known volume after refilling any airspaces within the eggs with water (Ar and Rahn 1980). Initial masses of other eggs were calculated as the product of measured volume and average initial density. Albumen and yolk content were measured by carefully separating the components of fresh or hard-boiled eggs. Water loss during boiling was assumed to be entirely from the albumen. There were no significant differences between the results for fresh and hard-boiled eggs. Water content of egg components and hatchlings

was determined by drying to constant mass at 60 C, lipid content by chloroform-methanol extraction, ash content by combustion in a muffle furnace at 500 C, and caloric content by combustion of three dried and pulverized subsamples in a Gallenkamp ballistic bomb calorimeter calibrated with certified standard benzoic acid (National Chemical Laboratories, Great Britain).

RESULTS

ONTOGENY OF OXYGEN CONSUMPTION

The $\dot{V}O_2$ in both species increased throughout incubation until about the last 5–8 days before hatching (figs. 1, 2). During this final period, there was increased variation within and between eggs but no significant changes in mean $\dot{V}O_2$. The mean $\dot{V}O_2$ on the day before pipping and hatching was 61.0 cm³/h (SD = 8.4) in 13 mallee fowl eggs and 60.9 cm³/h (SD = 4.7) in seven brush turkey eggs.

Total oxygen consumption throughout incubation, calculated by integrating mean daily $\dot{V}O_2$ over time, was 31.2 liters O₂ for mallee fowl and 24.1 liters O₂ for brush turkeys. With the assumption of an energy equivalent of 19.64 kJ/liter O₂ (D. Vleck,

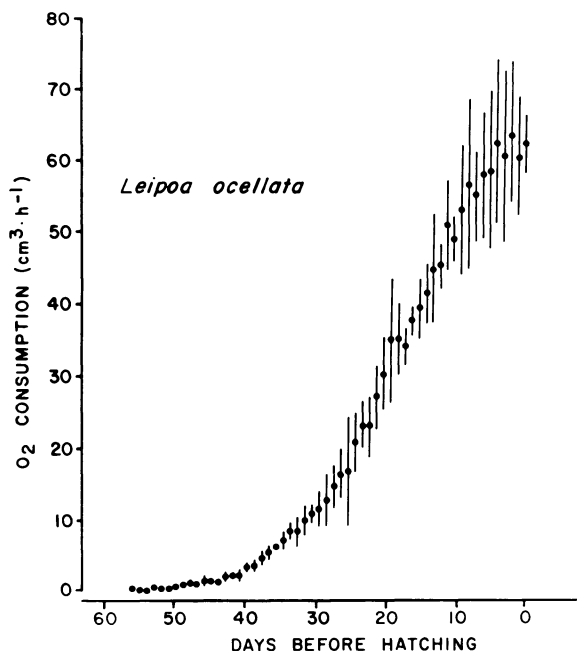


FIG. 1.—Rates of oxygen consumption during incubation of mallee fowl embryos. Symbols are mean \pm SD. Sample sizes ranged from one to 13 and averaged 6.7. Data are plotted against number of days before hatching because in almost all cases the date of laying was unknown.

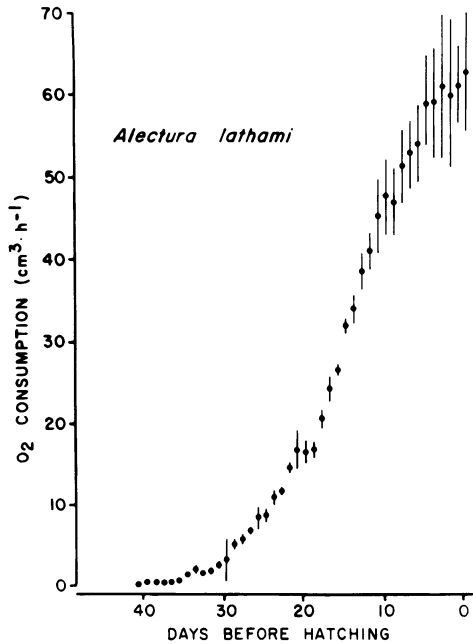


FIG. 2.—Rates of oxygen consumption during incubation of brush turkey embryos. Sample sizes ranged from one to nine and averaged 3.8. Symbols as in fig. 1.

Vleck, and Hoyt 1980), this corresponds to total energy expenditures during development in the egg of 613 kJ for mallee fowl and 474 kJ for brush turkeys.

HATCHING AND EMERGENCE FROM THE MOUND

At the end of incubation, megapode embryos have neither a functional egg tooth nor a well-developed *Musculus complexus* ("hatching muscle") (Clark 1964; Vleck, unpublished data), which in other bird species functions to elevate the beak and puncture the shell during hatching. Megapodes do not pip the eggshell with their beak and gradually work their way out of the shell; instead, they quickly break the thin shell apart with their powerful legs (Frith 1959; Baltin 1969; Vleck, unpublished data). Hatching is almost explosive and usually requires only a few minutes from the first break in the shell to complete emergence.

By the time hatching is complete, avian embryos must have made the transition from chorioallantoic respiration to pulmonary respiration. In most species this transition begins well before hatching is complete and sometimes even before pipping (Visschedijk 1968). Water loss from

eggs of most birds results in formation of an airspace between the shell membranes into which embryos may penetrate ("internal pipping") and breathe prior to hatching (Freeman and Vince 1974). As Seymour and Rahn (1978) point out, hatching in megapode eggs must follow a markedly different pattern because these eggs do not have such an air cell (Baltin 1969; Vleck, unpublished data).

Our observations of hatching in four brush turkeys indicate that, in this species at least, pulmonary respiration does not begin until the extra-embryonic and shell membranes are ruptured and fluid drains from the egg. In one hatching the shell was fractured into several pieces yet the shell membrane was not broken, so we were able to watch the embryo closely while it was encased by only a shell membrane. Pulsations of blood vessels in the chorioallantoic membrane were obvious, but there was no sign of any movement that could be construed as pulmonary ventilation. About 60–90 s after breaking the shell, the bird tore the shell membrane and emerged. The chorioallantoic circulation closed down with such rapidity that there was almost no blood loss, and pulmonary ventilation began within seconds of the tearing of the membrane. The transition from chorioallantoic to pulmonary respiration in this chick was rapid and essentially synchronous with the emergence of the hatchling from the shell membrane. An immediate increase in $\dot{V}O_2$ was associated with this transition, and metabolic rate increased two- to fourfold during the first hour after hatching (fig. 3).

The eggshell is neither the only nor the most significant barrier between a megapode embryo and the surface world. In both mallee fowl and brush turkeys, eggs are buried 40–80 cm below the surface during incubation (see Frith [1956] for a review of breeding biology of megapodes), and after hatching chicks must dig their way up to the surface. To estimate the energy costs of escaping from the mound, we made continuous recordings of the $\dot{V}O_2$ of one brush turkey and two mallee fowl chicks as they hatched and then dug their way up through 25–30 cm of natural mound material (sand for mallee fowl, plant detritus for the brush turkey).

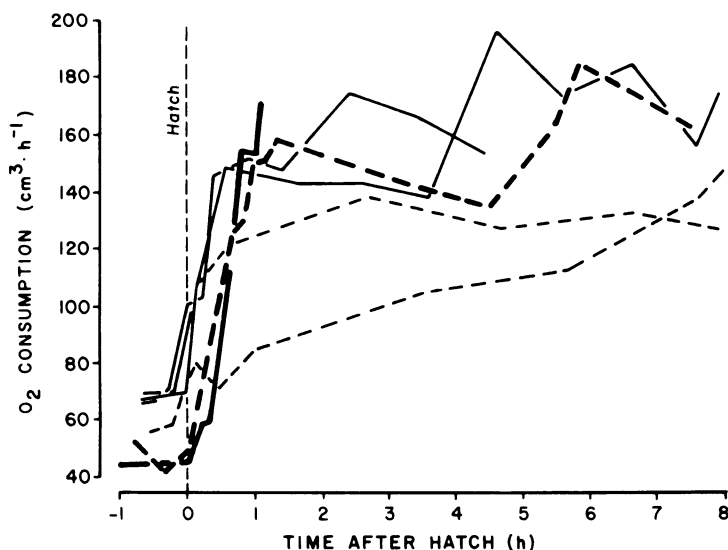


FIG. 3.—Rates of oxygen consumption of two brush turkeys (thick lines) and four mallee fowl (thin lines) during and after hatching. The dashed lines are for chicks that were burrowing up through mound material (see text).

For the first 3–4 h after hatching, chicks did not move much and made little progress toward the surface. Thereafter, 5–10-min bursts of activity were separated by 10–80-min periods of rest. The brush turkey emerged on the surface after 18.2 h, and the mallee fowl after 10.9 and 23.3 h. During this time the brush turkey consumed 2.5 liters O_2 (=49 kJ) and the mallee fowl 1.4 and 2.7 liters O_2 (=27 and 53 kJ, respectively). Burial in mound material per se did not increase mean rate of energy expenditure of chicks. Average $\dot{V}O_2$ of chicks buried in mound material ($127 \text{ cm}^3/$

h, SD = 11) did not differ from that of chicks of the same age that were not buried (fig. 3) but was higher than the rates of about $90 \text{ cm}^3/\text{h}$ that Booth (1984) reports for dry, resting mallee fowl hatchlings at the same ambient temperature (34 C).

PHYSICAL CHARACTERISTICS OF THE EGGS

Dimensions and shell characteristics of brush turkey and mallee fowl eggs are summarized in table 1. Initial masses of mallee fowl eggs ranged from 148 to 195 g with a mean of 173 g. Frith (1959) reported a mean mass of 187 g in a much larger sample

TABLE 1

DIMENSIONS OF MALLEE FOWL AND BRUSH TURKEY EGGS AND INCUBATION PERIOD

Dimension	Mallee Fowl	Brush Turkey
Length (mm)	91.0 ± 2.5 (43)	93.8 ± 3.2 (25)
Breadth (mm)	58.5 ± 1.2 (43)	59.1 ± 1.9 (25)
Volume (cm^3)	163 ± 8.5 (30)	169 ± 14.7 (24)
Initial density (g/cm^3)	1.063 ± .011 (6)	1.069 ± .001 (5)
Initial mass (g)	173	180
Shell mass (g)	9.7 ± .80 (12)	11.3 ± .23 (11)
Shell thickness:		
With membranes (mm)305 ± .060 (7)	.368 ± .026 (5)
Without membranes (mm)271 ± .029 (6)	.329 ± .020 (4)
Incubation period (days)	62	49

NOTE.—Results are given as mean ± SD; numbers in parentheses are sample sizes. Initial mass was calculated as the product of volume and initial density, not measured directly. Shell mass is a dry mass, but includes shell membranes. Incubation periods are from Frith (1959) and Baltin (1969).

of eggs from New South Wales. Brush turkey eggs we collected from five different mounds had a mean mass of 180 g (range = 151–221 g). Eggs from zoo birds average over 200 g (Baltin 1969; Seymour and Rahn 1978), but eggs from free-living brush turkeys are smaller. Heinroth (1922) and Fleay (1937) reported egg masses near 180 g, and 19 brush turkey eggshells in the South Australian Museum collected from within the natural range of the species did not differ significantly in length or breadth (*t*-test, $P < .01$) from the eggs we collected on Kangaroo Island.

The eggs of megapodes are remarkably large relative to the adult body mass of about 1.8 kg. The allometric relationship between adult and egg mass in the Galliformes predicts that a 1.8-kg female should produce a 60-g egg (Lack 1968). Megapode eggs are about three times this mass.

Both mallee fowl and brush turkey eggs have large yolks that are rich in lipid and energy (table 2). Yolk comprises 52.6% (SD = 1.1, $N = 4$) of the egg contents in mallee fowl and 50.1% (SD = 1.4, $N = 4$) in brush turkey eggs. These percentages are lower than the 67% reported for *Megapodius eremita* (= *freycinet*) eggs by Meyer (1930) and the 60%–64% yolk in *Talegalla* eggs reported by Mayr (1930) but are higher

percentages than in all but five of the 149 species of birds for which such data are available (Carey, Rahn, and Parisi 1980). The energy density of the egg contents is about 10 kJ/g wet mass in both species (table 2). Eggs of only two of the 59 other species listed by Carey et al. (1980) have higher energy densities.

Because of the large yolk and high lipid content, the megapode eggs have a very low water content. Contents of mallee fowl eggs are 66.5% (SD = 0.8, $N = 4$) water, and contents of brush turkey eggs are 68.4% (SD = 0.7, $N = 4$) water. The only bird known to have a drier egg is the brown kiwi, *Apteryx australis*. The contents of kiwi eggs are only about 61% water (Calder, Parr, and Karl 1978).

Composition and energy content of three hatchlings of each species we studied are listed in table 3. Residual yolk amounts to 11%–13% of hatchling mass, and yolk-free hatchling mass is 54%–59% of initial egg mass. Both of these values are close to those for other nonmegapode galliforms and for birds in general (Romanoff 1944; Schmekel 1960; D. Vleck et al. 1980). As in other birds (Ar and Rahn 1980), the percentage water content is similar in the fresh egg and in the hatchling (tables 2, 3).

Energy cost of development through

TABLE 2

INITIAL COMPOSITION AND ENERGY CONTENT OF FOUR MALLEE FOWL AND FOUR BRUSH TURKEY EGGS

	Mallee Fowl	Brush Turkey
Mass of components (g):		
Whole egg	179.4 ± 8.9	169.2 ± 17.1
Shell and shell membranes	9.9 ± .5	11.4 ± .2
Total contents	169.5 ± 8.5	157.1 ± 15.9
Yolk	89.1 ± 3.9	78.6 ± 5.7
Albumen	80.5 ± 5.2	78.5 ± 10.2
Yolk composition (%):		
Water	47.3 ± 1.0	49.4 ± 2.1
Lipid	28.9 ± 1.6	28.7 ± 4.0
Ash	2.4 ± .4	2.4 ± .6
Albumen composition (%):		
Water	88.1 ± .8	87.4 ± .9
Lipid	.1 ± .1	.1 ± .04
Ash	.8 ± .05	.8 ± .06
Energy density (kJ/g wet mass):		
Yolk	16.8 ± .2	16.3 ± .9
Albumen	2.8 ± .2	3.0 ± .2
Total contents	10.2 ± .1	9.8 ± .2

NOTE.—Results are given as mean ± SD.

TABLE 3
COMPOSITION AND ENERGY CONTENT OF THREE NEWLY HATCHED
MALLEE FOWL AND THREE NEWLY HATCHED BRUSH TURKEYS

	Mallee Fowl	Brush Turkey
Initial mass of eggs (g)	166 ± 3.2	181 ± 7.2
Yolk-free hatchlings:		
Mass (g)	98 ± 11.2	98 ± 3.1
Water (%)	68 ± 2.6	64 ± 3.5
Lipid (%)	8.8 ± .9	11 ± 1.0
Ash (%)	2.7 ± .3	2.8 ± .3
Energy density (kJ/g)	8.7 ± .8	10.2 ± 1.0
Residual yolk:		
Mass (g)	15 ± 2.5	12 ± 3.1
Water (%)	62 ± 7.2	46 ± 1.1
Lipid (%)	16.4 ± 3.1	25.4 ± .4
Ash (%)	2.0 ± .4	2.3 ± .1
Energy density (kJ/g)	11.2 ± 2.0	16.5 ± .2

NOTE.—Results are given as mean ± SD.

hatching, calculated as the difference between energy content of eggs and of hatchlings, is very close to that calculated from $\dot{V}O_2$ measurements. We estimated initial energy content of eggs that produced the hatchlings in table 3 by multiplying the initial egg mass of their eggs (less shell mass) by the energy density of egg contents for that species from table 2. For the three mallee fowl, the average energy expenditure during incubation was 583 kJ (SD = 91), and for the three brush turkeys it was 471 kJ (SD = 114). These are 95% and 99%, respectively, of the values calculated from respirometry and are not significantly different from these values.

We also recorded mass and energy content of the yolk and yolk-free bodies of 15 mallee fowl embryos and hatchlings of different ages (figs. 4, 5). Ages of these embryos were estimated by measuring $\dot{V}O_2$ for several days before they were killed. Because of the low variance in $\dot{V}O_2$ between eggs of the same age prior to the last week of incubation, superimposing these measurements on the curve in figure 1 allowed us to estimate the age of the embryos to within 1 or 2 days.

As in other precocial birds (C. M. Vleck, Vleck, and Hoyt 1980), embryo growth in the megapodes is a sigmoidal function of time (fig. 4). Yolk mass and energy content decline as embryo mass and energy content increase. Because of its higher water content (tables 2, 3), the wet mass of the embryo eventually exceeds the wet mass of the yolk.

Most of the energy contained in the yolk is transferred to the embryo during the last 20% of incubation (fig. 5). A substantial part of this transferred energy ends up as peritoneal and subcutaneous fat in the term embryo. Hatchlings and term embryos of both species have conspicuous fat depots

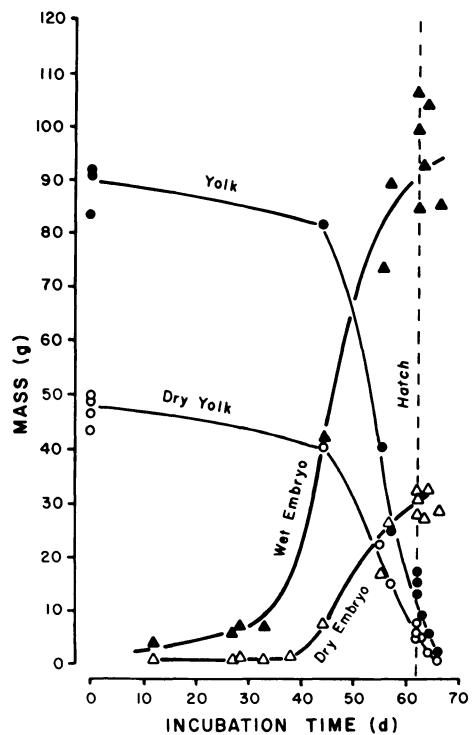


FIG. 4.—Mass of yolk (circles) and embryos (triangles) during incubation in mallee fowl. Solid symbols are wet masses, open symbols are dry masses.

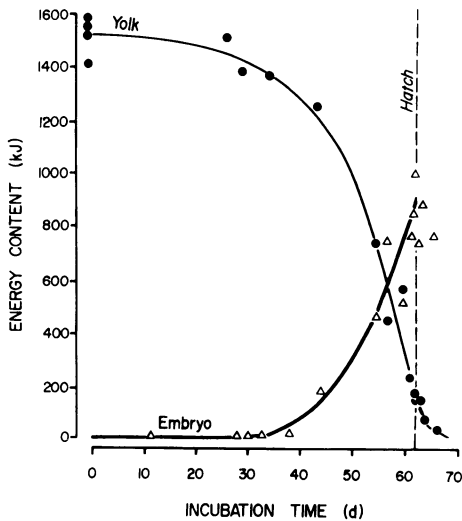


FIG. 5.—Total energy content of yolk (circles) and embryo (triangles) during incubation in mallee fowl.

that are absent in younger embryos. In mallee fowl, lipids average 26.5% (SD = 3.4, $N = 5$) of the dry mass in hatchlings and embryos within 5 days of hatching. Lipid content of younger embryos is significantly lower ($t = 3.76$, $P < .01$), averaging 18.0% of dry mass (SD = 2.3, $N = 3$).

DISCUSSION

ONTOGENY OF OXYGEN CONSUMPTION

The pattern of increase in $\dot{V}O_2$ in the megapodes (figs. 1, 2) is similar to that of other precocial species: a relatively rapid increase early in incubation and a period of more or less constant $\dot{V}O_2$ in the few days before hatching (Vleck, Hoyt, and Vleck 1979). We have suggested elsewhere that during this final period there is a reduction in energy-expensive tissue growth and a maturation of the physiological systems important in precocial behavior (D. Vleck et al. 1980). Our limited data on embryo growth (fig. 4) are consistent with the hypothesis that growth rate and therefore energy cost of growth decline in the last few days of incubation. There is a considerable amount of movement by the embryos during the last week of incubation, presumably facilitating development of the neuromuscular control essential for digging out of the mound, walking, and flying. The irregular variation in $\dot{V}O_2$ both within and between eggs during the last 5–8 days of

incubation may be a consequence of this muscular activity.

The metabolic rate of embryos at the end of incubation just prior to increases in $\dot{V}O_2$ associated with pipping and hatching has been used for between-species comparisons. There is no internal pipping or pipping stage in megapodes, and, in late incubation, no significant increase in metabolic rate until minutes before hatching (fig. 3). Consequently, we use $\dot{V}O_2$ measured on the last day before hatching to compare with “pre-pipping” or “pre-internal pipping” metabolic rates of other birds.

Both mallee fowl and brush turkeys have high metabolic rates just prior to hatching. Hoyt (1980) described the relation between pre-pipping $\dot{V}O_2$, egg mass (M), and incubation period (I) for 34 species of birds with the equation $\text{cm}^3 \text{O}_2/\text{day} = 139M^{.848}/I^{.654}$. The measured rates for brush turkey and mallee fowl are 64% and 98% higher, respectively, than predicted from this equation. Measured values are closer (31% higher for brush turkey and 35% higher for mallee fowl) to predictions of the simple allometric equation $\text{cm}^3 \text{O}_2/\text{day} = 25.2M^{.73}$ (Hoyt et al. 1978). Equations based largely on bird species with relatively short incubation periods may have little utility for predicting values for birds with very long incubation periods.

ENERGETICS OF DEVELOPMENT

The long incubation periods of megapode eggs are associated with high total expenditures of energy (E_i) during incubation (fig. 6). In birds, both incubation period and E_i vary with initial egg mass. The megapodes have incubation periods much longer than predicted for eggs of their masses. Their E_i are correspondingly high when compared with predictions based on other precocial birds, most of which have incubation periods less than or equal to values predicted on the basis of egg mass. Other bird species with incubation periods much longer than predicted on the basis of egg mass—notably, the Procellariiformes and Psittaciformes—also have high E_i (Ackerman et al. 1980; Vleck and Kenagy 1980; Bucher 1983).

These high E_i 's presumably result from the high cost of maintaining embryo tissue over a long incubation period (C. M. Vleck

et al. 1980). Metabolism of embryos can be apportioned between expenditures for maintenance of existing tissue and those for growth of new tissue. Growth costs, or the costs of biosynthesis of a chick from materials in the yolk and albumen, probably do not depend on growth rates. Maintenance costs, however, must increase as incubation time increases.

It is tempting to attribute the exceptionally high E_i in megapodes, at least in part, to their extreme precocity. Precocial birds in general have higher E_i than do altricial species hatching from eggs of the same size (Ar and Rahn 1980; C. M. Vleck et al. 1980). This does not, however, necessarily mean that growth of a precocial chick is more expensive than growth of an altricial chick of the same body size. Instead, it can be attributed to more rapid growth earlier in development, and the consequent higher maintenance costs, in precocial species

(C. M. Vleck et al. 1980). Growth patterns of mallee fowl embryos (fig. 4) do not appear to differ from those of other precocial species when normalized for egg size and incubation period. At the present, we have no basis for attributing high costs of development to extreme precocity per se.

Long incubation periods appear to be the proximate cause for the high E_i in mallee fowl and brush turkeys. It is, of course, possible that extreme precocity requires more time for development and thus could be an ultimate cause, but interspecific comparisons do not support this view. In mallee fowl and brush turkeys, egg mass (table 1), energy density of the eggs (table 2), and hatchling mass (table 3) are similar, but the incubation periods (62 and 49 days for mallee fowl and brush turkey, respectively) are very different. Mallee fowl, with a 27% longer incubation period, have a 29% greater E_i than do brush turkeys. Hatchlings

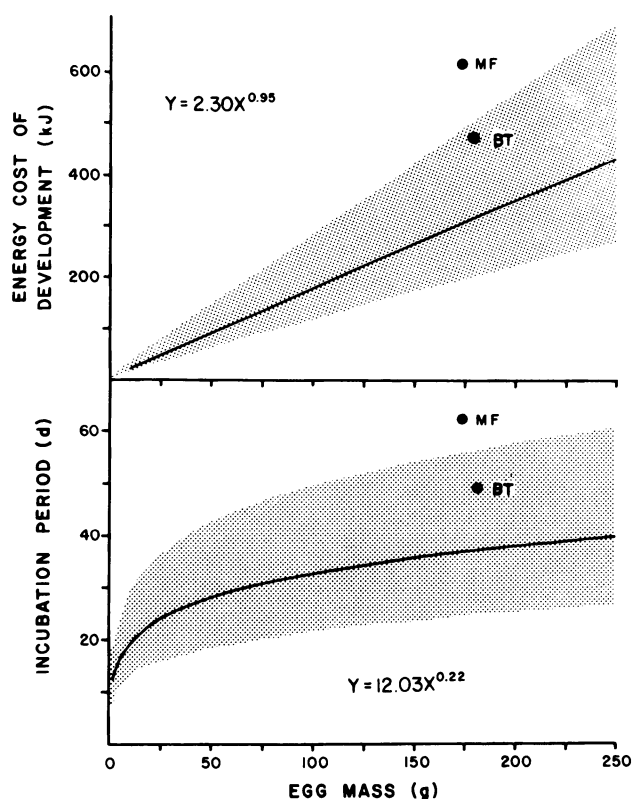


FIG. 6.—Total energy (E_i) used during embryonic development (*top*) and length of incubation (*bottom*) in mallee fowl (*MF*) and brush turkey (*BT*). Curves are predicted values based on allometric equations from C. M. Vleck et al. (1980) for energy and Rahn and Ar (1974) for incubation period. The shaded areas are 95% confidence intervals for predictions of individual values of energy cost or incubation period from egg mass. They are asymmetrical because statistical analyses were carried out using log-transformed data.

of the two species appear superficially to be equally mature both physically and physiologically. Because of their more rapid development and lower E_i , brush turkey hatchlings have both a higher energy density and more energy in residual yolk than do mallee fowl (table 3), in spite of the fact that their eggs initially contain slightly less energy. Degree of precocity is not closely tied with incubation period for bird species in general (Rahn and Ar 1974). Many procellariiforms have incubation periods as long as the megapodes (Ar and Rahn 1980) but are much less precocial at hatching, and many anseriform and galliform species with hatchlings second only to the megapodes in precocity have incubation periods only one-third to one-half as long.

EMERGENCE FROM THE MOUND

The process of escaping from the mound is energetically expensive. The three hatchlings (one brush turkey and two mallee fowl) that we studied started only 25–30 cm below the surface, yet the total energy that they expended between hatching and emergence averaged about 8% of the total used prior to hatching. This amounts to 16%–25% of the energy remaining in the yolk at the time of hatching. In natural mounds hatchlings may be buried much deeper than in our experiments, so those experiments alone do not allow us to estimate how much energy hatchlings use to dig out of natural mounds. We estimated total cost of emergence from natural mounds by multiplying the average metabolic rate of buried chicks in the lab by the average time it takes hatchlings to dig out of natural mounds. We calculated this average residence time as described below.

Megapodes lay eggs at intervals of several days throughout a lengthy breeding season (Frith 1956). Because development starts as soon as an egg is laid, chicks hatch at similar intervals. We used this information as the basis for an estimate of the time it took hatchlings to emerge from the mound. The ratio of number of chicks (C) to number of live eggs (E) in mounds should be approximately equal to the ratio of residence time (R) of a hatchling in the mound to the residence time of an egg in the mound, that is, incubation period (I). An estimate of residence time of hatchlings is

then given by the equation $R = I \cdot C/E$. This assertion will be most nearly correct when mound censuses are restricted to that portion of the breeding season when chicks are hatching and eggs are still being laid and when every living egg and no dead ones are counted each time a mound is opened.

Mallee fowl have an average incubation period of 62 days, and over three breeding seasons we encountered two live chicks and 156 live eggs in mounds. Brush turkeys have an incubation period of 49 days, and we found six chicks and 110 live eggs in natural mounds. For mallee fowl hatchlings we estimate residence time in mound as $R = 62 \cdot 2/156 = 0.79$ days, and for brush turkeys $R = 49 \cdot 6/110 = 2.67$ days. Our estimates are close to estimates based on direct observations. Frith (1959) reported that 2–15 h elapse between hatching and emergence in mallee fowl, and Fleay (1937) and Baltin (1969) reported that it takes brush turkeys hatchlings 1–2 days to emerge from mounds in zoos.

Using our estimates of residence time, we determine that total cost of emergence from natural mounds is about 48 kJ in mallee fowl and 158 kJ in brush turkeys. For mallee fowl this amounts to 8% and for brush turkeys 33% of the energy they use up to the time of hatching. The long residence times and high costs of emergence for brush turkey chicks in the field may be due to the differences between their mounds and those of mallee fowl. Brush turkey chicks must force their way up through an interlocking mass of plant detritus, while mallee fowl face a barrier that is primarily composed of loose, dry sand. In addition, during much of the breeding season mallee fowl open their mounds daily, sometimes to within a few centimeters of eggs, to increase solar heat input (Frith 1962). This also keeps the mound material friable, which must facilitate escape of mallee fowl chicks from the mound. If our estimates are accurate, brush turkeys should emerge on the surface with a total energy content of about 1,100 kJ, and the mallee fowl with about 1,000 kJ. Lower costs of emergence from the mound for mallee fowl partially compensate for their lower energy stores at the time of hatching (table 2).

The long incubation period and burial

of the eggs of megapodes make development from a fertilized egg to an independent chick a relatively expensive process. Energy reserves in the egg must be sufficient to meet demands of embryo and hatchling throughout this process. The unusually large yolk and high energy density of megapode eggs (table 2) represent essential adaptations in the evolution of such a system.

ENERGETICS OF REPRODUCTION IN
ADULT MEGAPODES

For a parent bird, the energy cost of reproduction includes not only the energy it invests in the eggs themselves but also the energy that it must invest in providing appropriate incubation conditions, as well as any other necessary parental care (Vleck 1981). Although megapode parents supply no parental care after hatching and do not expend metabolically derived heat to warm their eggs, the energy expenditure involved in egg laying, mound construction, and mound maintenance is considerable. We estimated that the mounds of both species we studied contained an average mass of about 3,400 kg of material collected by the adult birds. To open a mound for egg laying or to test its temperature, a mallee fowl must remove and replace about 850 kg of sand. Male mallee fowl spend an average of 5.3 h/day working on their mounds during a 6–9-mo breeding season (Frith 1962). Scrub fowl, *Megapodius reinwardt*, spend a large proportion of their time tending their mounds throughout the year (Crome and Brown 1979). Brush turkeys may work less regularly; once a mound is constructed, it may remain unattended for several days at a time. Of course, some megapode species, especially in more tropical regions, do not construct mounds and spend little or no energy caring for their eggs, although some of these species travel long distances to reach suitable laying sites (Frith 1956).

Because megapodes lay many large and energy-rich eggs each year, the total energy they invest in eggs is greater than in other birds of the same body size. Mallee fowl, for example, lay 15–24 eggs/yr (Frith 1959) which add up to 150%–250% of an adult's body mass. This high investment is possible because the incubation biology of megapodes releases them from physical and

temporal constraints that apply to birds which must sit on their eggs and care for their hatchlings.

For most birds reproductive output is determined by clutch size and number of clutches per year. Most birds lay eggs at 1-day intervals until their clutch is complete. Clutch size may be limited by the rate at which a female's reserves of energy, protein, or calcium are depleted (Drent and Daan 1980). Additional clutches usually cannot be started until fledglings from the first clutch become independent. Female megapodes, however, can lay eggs at any time over a 5-mo (brush turkey) to 8-mo (mallee fowl) breeding season. Mallee fowl lay eggs at intervals of 5–9 days (Frith 1959; present study), and brush turkeys lay eggs at intervals of 2–5 days (Baltin 1969; present study). This presumably permits females to maintain resource balance and continue egg production as long as incubation conditions remain suitable.

Birds that sit on their eggs gain nothing by laying more eggs than they can keep warm, and most birds lay considerably fewer than they can keep warm (Lack 1968). A megapode mound can incubate a much larger volume of eggs than could an incubating adult. With a laying interval of 3 days and an incubation period of 49 days, a brush turkey mound would contain 16 eggs at once, totaling almost 3 kg. A 1.8-kg female could never keep that many eggs warm by sitting on them!

Total clutch size averages 15–24 eggs/yr in mallee fowl (Frith 1959) and 18–24 eggs/yr in brush turkey (Fleay 1937). Total hatchlings per year, ignoring losses to introduced predators, are about 15 in both mallee fowl and brush turkey. Hatching success of some other galliform species may be this high (Lack 1947; Johnsgard 1973), but in few other bird species does a pair rear this many chicks to the point of independence. This high effective fecundity is probably offset by high mortality sometime after the chick emerges from the mound, possibly in the first year of life when the birds are small. Little is known about the life history of nonbreeding megapodes. Although older mallee fowl and brush turkeys can run quickly, younger birds are relatively weak runners and flyers. If they feed in open areas during the day as do the

adults, the young birds are probably exposed to a wide range of predators. For example, the night heron (*Nycticorax caledonicus*) preys on some megapode hatchlings (Diamond 1983).

An extended laying season has an additional advantage from the viewpoint of predation risk (Frith 1956). Unlike most birds, megapodes do not put all their eggs in one temporal basket. Complete predation of a clutch requires that the predator visit the egg-laying site repeatedly and, in the case of brush turkeys and mallee fowl, expend a great deal of energy in digging through the mound each time.

The extended egg-laying period of megapodes is necessary to produce a large clutch

of energy-rich eggs. However, this necessitates prolonged maintenance of appropriate incubation conditions which may be possible only for birds that do not brood their eggs. Highly precocial young would seem to be an essential part of such an adaptive suite. In species that brood their eggs, the parents are generally present when eggs hatch, but this is not the case among megapodes, some of which may never return to the area after eggs are laid (Frith 1956). The large size of megapode eggs may be a consequence of the necessity of producing a relatively large and completely independent hatchling, while the high energy content of eggs is necessary because of the long incubation period.

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