waters *Puffinus puffinus* in relation to their presumed date of hatching. Ibis 108:132–135.

PERRINS, C. M. 1970. The timing of birds' breeding season. Ibis 112:242–255.

SCHULTZ, E. T. 1991. The effect of energy reserves on breeding schedule: is there a saturation point? Funct. Ecol. 5:819–824.

TAITT, M. J. 1973. Winter food and feeding requirements of the Starling. Bird Study 20:226–236.

WALSBERG, G. E. 1980. Energy expenditure in free-living birds: patterns and diversity. Acta Congr. Int. Orn. 17:300–305.

YOM-TOV, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). J. Anim. Ecol. 43:479–498.

SEXUAL DIMORPHISM IN BASAL METABOLISM AND BODY TEMPERATURE OF A LARGE BIRD, THE EMU[1]

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The relationship between body mass and basal metabolic rate (BMR) for birds has had many revisions since Kleiber (1932) included three birds in his initial examination of this relationship for homeotherms. Lasiewski and Dawson (1967) calculated separate relationships for the passerines and non-passerines. Later, Aschoff and Pohl (1970) showed significant differences between the BMR measurements of birds in their normal quiet phase (ρ), as opposed to the active phase (α), of the daily activity cycle. Dann et al. (1989) recently presented an equation based on the ρ-phase BMR measurements of 263 species. They demonstrate that some orders, such as Falconiformes, diverge from the general relationship. This also appears to be so for ratites. Withers (1983) found the BMR of the Ostrich (*Struthio camelus*) to be about 40% lower than usual for birds. Calder and Dawson (1978) also reported similar low BMRs for three species of kiwi (*Apteryx oweni, A. australis,* and *A. haasti*). They also obtained low values for the Emu (*Dromaius novaehollandiae*), but an earlier study by Crawford and Lasiewski (1968) suggested that the BMR of the Emu was not different from other non-passerine species. There are problems with both studies of the Emu; in the 1968 study, Emus were hooded and restrained, and the 1978 measurements were made in the late afternoon on birds with little experience of the procedures. We re-examined the BMR and resting body temperature of the Emu. We also examined the possibility of differences in BMR due to sex and time of year because of the long inactive period (eight weeks)

that males face during their incubation fast in winter (Davies 1974).

MATERIALS AND METHODS

Five Emus of each sex were examined, sex being determined by cloacal examination. Experiments were carried out in winter (July–September) and summer (November–February). None of the Emus were laying or incubating during the study. Birds were familiarized with the experimental procedure for at least two weeks before data collection began.

Experiments were carried out at night during the quiet phase of the Emu's diurnal cycle between 18:00 and 03:30 local time. After 24 hr without food, an animal was placed in a large lexan chamber (1.8 × 1.0 × 0.6 m). This chamber was in a temperature-controlled room in which air temperature was controlled at 25 ± 0.5°C.

Dry air, which flowed into the chamber at approximately 150 liters/min, was measured with a Hastings Mass Flowmeter (Model HFM-201). A 125 ml/min sample of excurrent air was dried, scrubbed of CO_2 with ascarite®, redried and passed through an Applied Electrochemistry S3A-II oxygen analyzer. Five-second averages from the sensors measuring mass flow and O_2 concentration were logged on a personal computer via a 12-bit analog/digital converter (Sable Systems, USA) resulting in a maximum resolution of 0.001% O_2. The system was calibrated several times in each season by the Iron-burn method of Young et al. (1984). Calibration factors varied between 0.97 and 1.02.

Before being placed in the metabolism chamber, each Emu was weighed to the nearest 0.1 kg. After 1–2 hr, data collection was initiated and lasted for an additional 2–3 hr. Body temperature (T_b; measured 10 cm into the cloaca) was taken within 5 min of completion of metabolic measurements with a Jenco electronic thermometer, calibrated against a mercury-in-glass
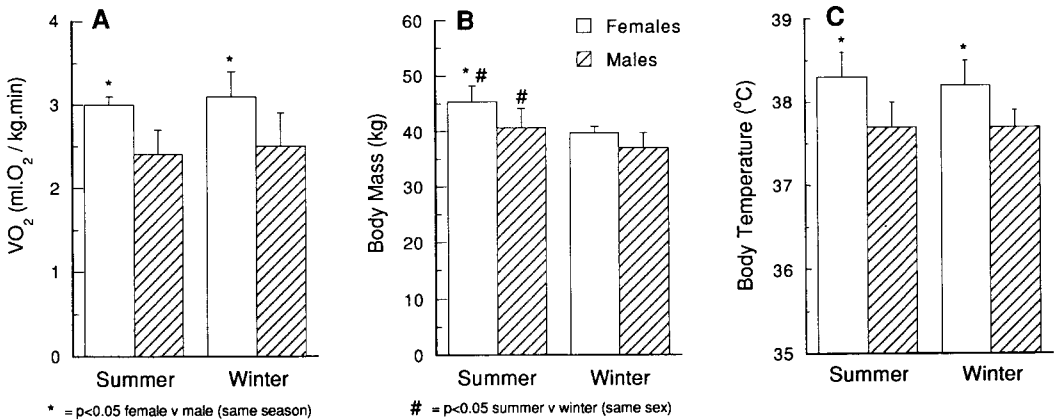
FIGURE 1. A. Basal metabolic rate, B. body mass, and C. body temperature, for female and male Emus in summer and winter. Figures show mean ± SD.

thermometer certified by the National Association of Testing Authorities, Australia.

$\dot{V}O_2$ was calculated using equation 2 from Hill (1972) for a system measuring flow upstream of the chamber, and using dry, CO_2-free air as the reference: $\dot{V}O_2 = \dot{V} \cdot (FIO_2 - FEO_2)/(1 - FEO_2)$, where $\dot{V}$ = flow rate (STPD), and FIO_2 and FEO_2 = fractional concentration of oxygen in dry, CO_2-free inlet and outlet air, respectively. Basal metabolic rate was defined as the lowest continuous ten minutes of $\dot{V}O_2$ in any collection period.

Body temperatures of nine Emus (five male, four female) were measured over 48 hr while the birds were in their pens at the university with food and water available. A thermistor attached to a temperature transmitter (J. Stuart Enterprises, U.S.) was inserted 10 cm into an Emu's cloaca. The transmitter was taped to tail feathers. Signals were received by a Telonics receiver/scanner. Pulse period of the signal was measured with a Telonics TDP-2 processor and a voltage output from the processor monitored by a personal computer via an analog/digital converter (ADC1, Remote Measurements, Washington, U.S.). Each transmitter's pulse period was averaged for 1 min every 10 min. Before and after each use of the transmitters they were calibrated against a certified mercury-in-glass thermometer. No changes in calibrations of transmitters were found.

Metabolism, T_b at the end of the experiment, and mass, were analyzed using Student's t-tests for males versus females. Paired t-tests were used to compare summer to winter data for each sex. Continuous T_b data were reduced to an average temperature for each animal for each 60 min interval in 24 hr. A two-way repeated measures analysis of variance (ANOVA) was used to test for effects of sex and time on T_b. A Student-Newman-Keuls multiple-range test was applied to compare individual means. Values are expressed as mean ± SD.

RESULTS

The BMR of male Emus was significantly lower than that of females in both summer ($P = 0.004$) and winter

($P = 0.03$). Values were: females in summer 2.95 ± 0.09, females in winter 3.08 ± 0.29; males in summer 2.42 ± 0.29, males in winter 2.53 ± 0.36 ml O_2 $kg^{-1}min^{-1}$ (Fig. 1A). These values are 77% (females) and 61.5% (males) of that predicted by the ρ-phase equation of Aschoff and Pohl (1970) for non-passerines, and similarly low with respect to the equation of Daan et al. (1989). The females were significantly heavier than the males in summer ($P = 0.04$), females being 45.4 ± 2.8 kg and males 40.7 ± 3.4 kg (Fig. 1B). Both sexes were heavier in summer (females $P = 0.02$, males $P = 0.005$); winter females were 39.7 ± 1.2 kg and males 37.0 ± 2.7 kg.

Male T_b was lower than that of females in both seasons (summer $P = 0.005$, winter $P = 0.028$). Values were: females in summer $38.3 \pm 0.2°C$, winter $38.2 \pm 0.3°C$, males in summer $37.7 \pm 0.3°C$, winter $37.7 \pm 0.2°C$ (Fig. 1C). As with BMR, there was no difference between summer and winter. We monitored T_b continuously to see whether the difference persisted for the entire day. Both sex ($P = 0.01$) and time ($P = 0.05$) significantly affected T_b. Comparison of means showed time only had a significant effect for males. Male T_b was significantly lower than females at night (Fig. 2). There was no significant difference in T_b between the sexes for the 4 hr from 15:00 to 18:00.

DISCUSSION

Our most notable result was the 20% lower BMR of male Emus compared to that of females. Sexual dimorphism in BMR has been reported for several avian species. However, this is usually associated with a dimorphism in size, with the larger of the sexes having the lower BMR (Rintamaki et al. 1984, Kaiser and Bucher 1985, Daan et al. 1989, Gorecki and Nowak 1990). In the Emu, there was no difference in mass between the sexes in winter, although the BMR of males was 20% lower than that of females. In summer, the males were smaller than the females and the lower BMR was maintained.

Our value of BMR for the male Emu (2,700 kJ/day) is close to the daily energy expenditure calculated for
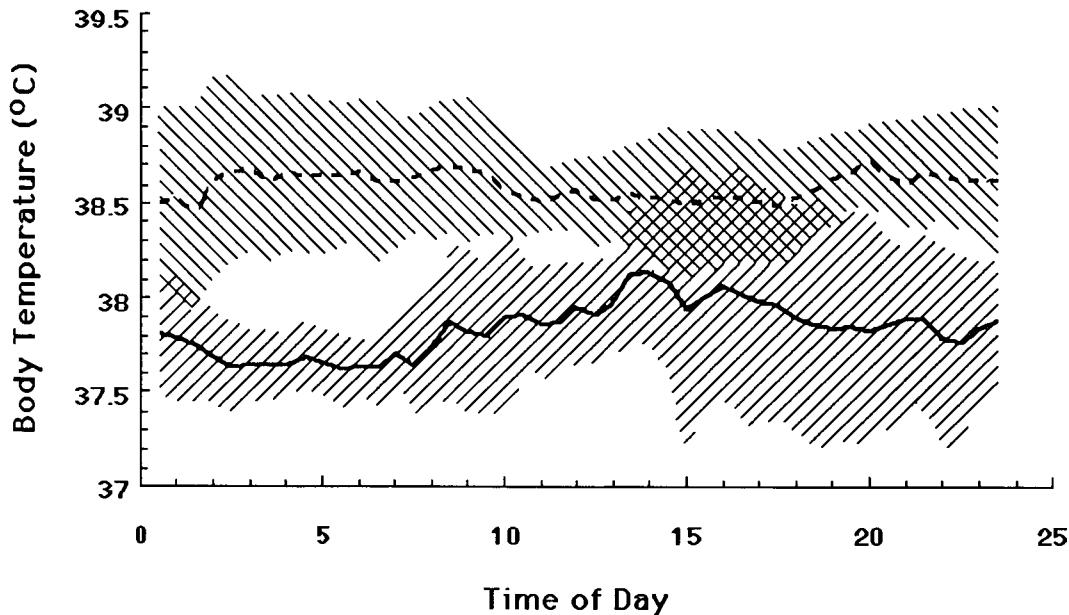
FIGURE 2.   Sixty-minute average body temperatures for female (broken line) and male (solid line) Emus for twenty-four hours. (Shaded areas denote the mean ± SD.)

two male Emus during their eight-week incubation fast (2,525 kJ/day, Buttemer and Dawson 1989). It is tempting to speculate that a low male BMR may result from selection operating via the eight-week incubation fast undertaken by the male. Failure of incubation due to depletion of body reserves at higher resting levels of metabolism may have exerted selection pressure towards the reduction of the BMR of males in a population. Alternatively, the male may need a lower working capacity (Drent and Daan 1980) than the female because of this long inactive period, and can afford a lower BMR than the female.

The T_b of ratites is lower than those seen in other non-passerine birds. However, this does not account for the lower BMR of the Ostrich (Withers 1983). For a Q_{10} of 2.5 to alone account for the observed differences in BMR between the Emu sexes, T_b would have to differ by 2.2°C. The apparent lack of a diurnal cycle in T_b in female Emus (Fig. 2) may be due to the averaging of data; one bird exhibited a drop in T_b during the day, and another was constant except for a rise at 20:30. Female T_b for most of the night is above the 95% upper confidence limit of the post metabolism experiment T_b (38.6°C, Fig. 1C). The Emus had constant access to food during T_b monitoring. The females may have remained active and feeding during the night.

Authors of studies on the BMR of other ratite species, the kiwis (Calder and Dawson 1978) and the Ostrich (Withers 1983) suggested that the metabolism of ratites may be below that of other non-passerine birds. Our measurements on the Emu agree with this hypothesis. If an average value for Emus from this study, and single points for each species of kiwi and the Ostrich are used to obtain a BMR-body mass relationship,

the least-squares regression equation for the log-transformed data is: BMR (ml O_2/hr) = 364 × Mass$^{0.763}$ (SE_{slope} = 0.019, r^2 = 0.998, $P \ll 0.001$). This line is 35% lower than the Aschoff and Pohl non-passerine line. The mass exponent of 0.763 is higher than expected for an analysis of families within a suborder (Bennett and Harvey 1987) and may reflect the small data set. Verification of such a BMR-body mass relationship for all ratites will need the BMR of the cassowary and the rheas. These have been reported (cassowary, Benedict and Fox 1927; *Rhea americana,* Crawford and Lasiewski 1968), but need confirmation. The cassowary result is low for a non-passerine, but only one bird was measured and it may have been a juvenile. The data for rheas is doubtful; the birds were hooded, restrained and measured during the day.

A species closely related to the ratites, the tinamou *Nothoprocta perdicaria,* exhibits a BMR intermediate between this proposed ratite level and that of other non-passerines (Withers et al. 1987). Ratites, along with tinamous, are considered to be one of the earliest offshoots in bird evolution (Cracraft 1974), just as the monotremes represent the oldest mammals. Selection seems to have favored increasing levels of resting metabolism in mammals (Dawson and Hulbert 1970). A similar succession may have occurred in bird metabolism, from the ratites to carinate non-passerines to passerines. This scenario would require either: (1) the tinamou to have increased BMR from the primitive "ratite" level, independently from other carinates, or (2) for the ratites to have reduced metabolism from a primitive "tinamou" level, since the tinamou may be the earliest offshoot from the ratite-tinamou lineage (Cracraft 1974). Ratites becoming flightless could have

led to reductions in their required aerobic capacity. If there is a relationship between BMR and maximum aerobic capacity (see Bennett 1991) this would have enabled the ratites to make economies in BMR.

LITERATURE CITED

ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von vögeln als funktion der tageszeit und der körpergröße. Journal Für Ornithologie. 111:38–47.

BENEDICT, F. G., AND E. L. FOX. 1927. The gaseous metabolism of large wild birds under aviary life. Proc. Am. Philos. Soc. 66:511–534.

BENNETT, P. M. 1991. The evolution of activity capacity. J. Exp. Biol. 160:1–23.

BENNETT, P. M., AND P. H. HARVEY. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. J. Zool. Lond. 213:327–363.

BUTTEMER, W. A., AND T. J. DAWSON. 1989. Body temperature, water flux and estimated energy expenditure of incubating Emus. Comp. Biochem. Physiol. A. Comp. Physiol. 94:21–24.

CALDER, W. A., AND T. J. DAWSON. 1978. Resting metabolic rates of ratite birds: the kiwis and the Emu. Comp. Biochem. Physiol. A. Comp. Physiol. 60:479–481.

CRACRAFT, J. 1974. Phylogeny and evolution of the ratite birds. Ibis 116:494–521.

CRAWFORD, E. C., AND R. C. LASIEWSKI. 1968. Oxygen consumption and respiratory evaporation of the Emu and rhea. Condor 70:333–339.

DAAN, S., D. MASMAN, A. STRIJKSTRA, AND S. VERHULST. 1989. Intraspecific allometry of basal metabolic rate: relations with body size, temperature, composition, and circadian phase in the kestrel, *Falco tinnunculus.* J. Biol. Rhythms 4:267–283.

DAVIES, S.J.J.F. 1974. The natural history of the Emu in comparison with that of other ratites, p. 109–120. *In* Proceedings of the 16th International Ornithological Congress, Canberra, Australia. 1974.

DAWSON, T. J., AND A. J. HULBERT. 1970. Standard metabolism, body temperature, and surface areas of Australian marsupials. Am. J. Physiol. 218:1233–1238.

DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

GORECKI, V. A., AND M. NOWAK. 1990. Durch die jahreszeiten bedingte thermoregulationsveranderungen beim fasan (*Phasianus colchicus.* L.). Z. Jagdwiss. 36:236–243.

HILL, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

KAISER, T. J., AND T. L. BUCHER. 1985. The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation and water loss in relation to ambient temperature in the Prairie Falcon *Falco mexicanus.* Physiol. Zool. 58:748–758.

KLEIBER, M. 1932. Body size and metabolism. Hilgardia 6:315–353.

LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A reexamination of the relation between standard metabolic rate and body rate in birds. Condor 69:13–23.

RINTAMAKI, H., L. KARPLUND, H. LINDEN, AND R. HISSA. 1984. Sexual differences in temperature regulation and energetics in the capercaillie, *Tetrao urogallus.* Ornis. Fenn. 61:69–74.

WITHERS, P. C. 1983. Energy, water and solute balance of the Ostrich, *Struthio camelus.* Physiol. Zool. 56:568–579.

WITHERS, P. C., R. B. FORBES, AND M. S. HEDRICK. 1987. Metabolic, water and thermal relations of the Chilean tinamou. Condor 89:424–426.

YOUNG, B. A., T. W. FENTON, AND J. A. MCLEAN. 1984. Calibration methods in respiratory calorimetry. J. Appl. Physiol. 56:1120–1125.