BODY TEMPERATURES OF INCUBATING VERSUS NON-INCUBATING ROADRUNNERS

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ABSTRACT.—Core temperatures of free-living Roadrunners (*Geococcyx californianus*) were monitored with temperature-sensitive radio transmitters. Breeding males were found to perform all of the nocturnal incubation and to maintain normothermic body temperatures at night. Body temperatures of females and non-breeding males dropped at night to as low as 33°C, depending on the ambient temperature. Facultative, short-term hypothermia appears to be a regular energy-saving feature of this species that is conspicuously not employed by the nocturnal incubator.

Most birds exhibit a circadian pattern of body temperature, involving a reduction of 1 to 3°C during the nighttime hours (Dawson 1954, Aschoff and Pohl 1970). Lower nocturnal body temperatures appear to be due to reduced motor activity and other cyclic phenomena of sleep, since nocturnally active birds show a reversal of the pattern, i.e., lower diurnal body temperatures. Only a handful of species exhibit true hypothermia, defined operationally as a reduction of body temperature below 36°C that may or may not involve torpor (Dawson and Hudson 1970). Facultative hypothermia is generally argued to be an energy-saving adaptation in response to periodic food shortages and/or excessively low ambient temperatures (Calder and King 1974). Species that exhibit hypothermia include nectar-feeding hummingbirds, aerial insectivores such as caprimulgids, swallows and swifts, small passerines overwintering in cold climates, and a few tropical species such as anis and colies (Dawson and Hudson 1970, Calder and King 1974). It has been argued that short-term hypothermia should occur only in small animals due to the theoretically prohibitive effects of thermal inertia and high rewarming cost for large animals (Calder and King 1974), yet vultures are known to lower body temperatures to 34°C. Hypothermia is a complex phenomenon for which the costs and benefits are still poorly understood.

The constraints that hypothermia places on breeding birds have not been explored. In particular, incubation and hypothermia may not be compatible. Incubating hummingbirds have generally been found to maintain normothermic body temperatures at night except during unusual cold (Calder 1971, Vleck 1982). Egg temperatures fall well below normal incubation temperatures during these lapses into hypothermia. It is not clear whether non-incubators under similar conditions would show

the same or different responses. If incubators typically maintain high body temperatures under conditions when non-incubators show hypothermia, then incubation may be metabolically expensive. Furthermore, the female of a facultatively hypothermic species may be energetically constrained during incubation if she has laid a large clutch of eggs and must recuperate depleted reserves via hypothermia. Thus facultative hypothermia may have important implications for both clutch size and the sex that performs the incubation.

The Roadrunner (*Geococcyx californianus*) is a large (350 g) cuckoo that has been reported to lower its body temperature under stressful conditions and to warm up by sunning (Ohmart and Lasiewski 1971). Hypothermic birds have been found to conserve a significant amount of energy compared to normothermic birds at the same ambient temperature. The Roadrunner is also among the few species in which the male performs most of the incubation, especially at night (Calder 1967, Ohmart 1973, Skutch 1976). In order to obtain a better understanding of the breeding energetics of this unusual bird, I monitored the body temperatures of free-living Roadrunners using radio-telemetry techniques while simultaneously following breeding activities. I here report significant differences in body temperature for Roadrunners as a function of sex and stage of breeding.

METHODS

I studied a population of Roadrunners at the Camp Pendleton Marine Corps Reserve, approximately 15 km north of Oceanside, San Diego County, California. The study site consisted of a 10 km transect running parallel to the coast and ½ km inland along old Highway 101 between Las Pulgas Road and the San Onofre nuclear power plant. The habitat consisted of fairly undisturbed coastal sage scrub

and chaparral on the steeper hillsides, and semi-grazed pasture on the flatter areas. A system of jeep trails (maintained by military training activities) allowed access to much of the area by car.

Birds were captured in standard raptor traps (foot-noose traps baited with a mouse), a home-made trap baited with a mouse, and with mist-nets set up near nests (Vehrencamp and Halpenny 1982). The raptor traps caught many of the non-breeding males. Capture of birds at the nest frequently caused the nest to be abandoned. The treadle trap, placed along known foraging routes, more successfully captured breeders without causing nest abandonment. Most birds were sexed by laparotomy. Nests were found by searching systematically among the larger clumps of prickly pear cactus (*Opuntia*), the preferred nesting site in this area.

Temperature-sensitive, miniature radio transmitters were constructed by inserting a 100 Kohm Yellow Springs Instrument Co. thermistor in series with the 82 Kohm resistor of the standard "Cochran" transmitter described in Bradbury et al. (1979). All radios operated in the 148 MHz range and were monitored with an AVM receiver and a hand-held Yagi antenna. Two pulse-interval timers were used, a home-made device which provided for continuous recording on a Rustrak strip chart recorder, and an AVM pulse timer that had no provision for automatic recording. Ambient temperatures were variously recorded at 1 m above the ground using a Schulteis thermometer, a thermistor-diode attachment to the home-made pulse timer, records from the San Onofre power plant, and a Tempscribe temperature recorder.

Two implantation methods were employed: (1) The transmitter was harnessed externally on the back of the Roadrunner, and the thermistor was mounted at the end of long leads, sealed in silastic tubing and silastic medical cement, and implanted in the body cavity of the bird. The entire package weighed between 10 and 15 g, representing about 5% of the bird's weight. This method had the advantages of (a) allowing a large battery to be used, which gave a radio life of three to six months, and (b) allowing a whip antenna to be used, which gave a transmitting range of 1 to 2 km. This method had the disadvantages of difficult surgery in the field and the need for a correction factor in the calibration curve following implantation, i.e., there was a significant difference between cloacal and radio-derived temperatures. (2) The transmitter was further miniaturized by substituting a smaller crystal, transistor, and battery, sealed in wax, and entirely implanted in the abdominal cavity. This package weighed 1–2 g and had the advantages of greater accuracy and easier surgery, but radio life was short (one to two weeks) and transmitting range poor (due to removal of the antenna). The poor transmitting range (10–20 m) made diurnal temperatures very difficult to obtain. Radio attachment and surgery techniques are described in Vehrencamp and Halpenny (1982).

Each radio was calibrated between 30 and 45°C in a slowly cooling water bath using a fast-reading Schulteis thermometer. After implanting the radio in the bird, the bird's cloacal temperature was recorded and checked against the temperature computed from transmitter calibrations. For the implanted radios, core body temperature as measured by the radio averaged 1.0°C less than a simultaneous measurement of cloacal temperature with a Schulteis thermometer; cloacal temperature was typically 41.0° while core temperature was usually 40.0°. Similar discrepancies between cloacal and intraperitoneal temperatures have been recorded in sparrows (Southwick 1973) and Burrowing Owls (*Athene cunicularia*; Coulombe 1970). Slightly higher temperatures were recorded from birds captured on hot afternoons (e.g., 42.4° cloacal), and slightly lower temperatures were recorded from birds captured early on cool mornings or during rainstorms (e.g., 38.5° core). Unless otherwise noted, all temperatures given are core temperatures (T_b). For the externally mounted units, core body temperature was 3 to 6° higher than cloacal temperatures (T_b). This obvious error was apparently due to a faulty design in the radio circuit that manifested itself when the thermistor element was extended from the rest of the circuitry on long leads. These calibration curves were therefore linearly corrected using the measured cloacal temperature and the known 1° difference between cloaca and core. The use of a linear correction term is of course an approximation, but external corrected readings gave results identical to internal radio data.

RESULTS

ACTIVITIES OF BREEDING PAIRS

I found eight nests during the two-year study period. Extensive behavioral observations were made at two nests where one or both parents were banded and abandonment did not occur. My observations agreed well with other published accounts (Bryant 1916, Bent 1940, Woods 1960, Calder 1967, Ohmart 1973, Whitson 1976, Folse and Arnold 1978). Clutch size of nests found prior to hatching
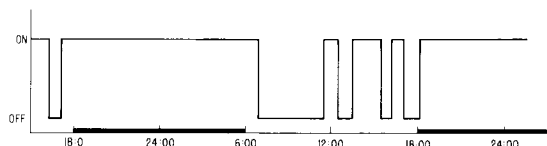
FIGURE 1. Continuous Rustrak recording of a breeding male Roadrunner carrying a miniature radio transmitter (Bird 1), showing time spent on and off the nest. The receiving antenna was permanently aimed at the nest, so that a positive voltage was recorded only when the bird was on or very near it. This observation took place during the early hatching period, when both young nestlings and eggs were present.

ranged from four to six (mean = 5.0, $n = 4$). Incubation commenced with the laying of the first egg. The eggs and chicks were covered almost continuously, except for occasional absences of up to an hour around noon. Both the male and the female incubated during the day. Figure 1 shows a continuous Rustrak recording of a male's presence at one nest during the early hatching period (eggs and nestlings were present). Simultaneous observations indicated that the male did not leave the nest until the female came on the nest. Female activity at the nest is therefore the converse of the male's activity. Because nestlings were present, both sexes usually brought food when they came to the nest, and incubation bouts were somewhat shorter than in nests with only eggs. Observations at a second nest in the early stages of incubation indicated that the female usually took two long bouts, one in the morning and one in the afternoon, with the male sitting most of the rest of the time. Males sat on nests on 12 of 13 nights of observation (five nests). The one exception occurred when I removed the male, forcing the female to sit that night; she subsequently abandoned the nest. My observations suggest that male and female Roadrunners share diurnal incubation equally, and that nocturnal incubation is entirely performed by the male.

BODY TEMPERATURES OF INCUBATING AND NON-INCUBATING BIRDS

Nine birds were outfitted with temperature-sensitive radios. Body temperatures were successfully recorded from one to three days and nights in six of these birds. The sexes and breeding stages of these six birds were as follows: 1) a normal breeding male that incubated each night (external radio); 2) a breeding male that abandoned his nest and roosted in a distant tree during the night of recording (internal radio); 3) a non-breeding male (external radio); 4) a normal breeding female that did not incubate at night (internal radio); 5) a breeding female that was forced to incubate at night by
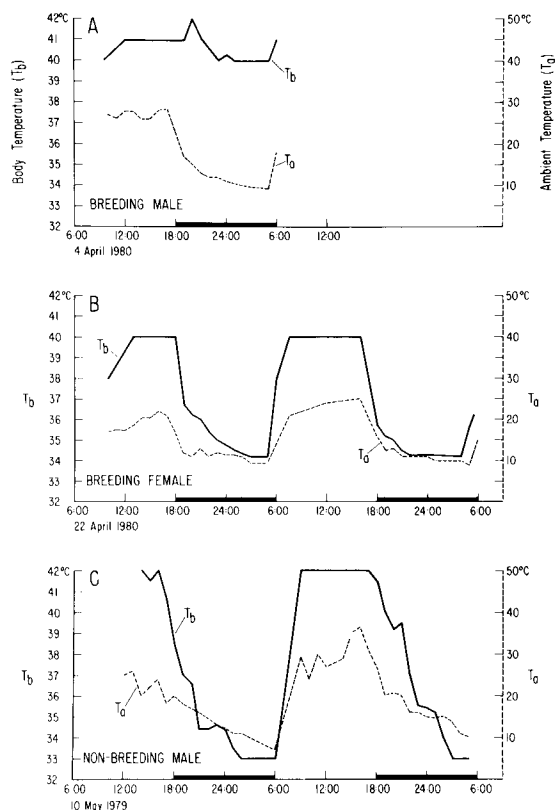

FIGURE 2. Hourly readings (where possible) of core body temperature (T_b) and ambient temperature (T_a) for three Roadrunners: A, breeding male (Bird 1); B, breeding female (Bird 4); and C, non-breeding male (Bird 3).

removal of the male (internal radio); and 6) a non-breeding female (external radio).

Examples of daily variations in T_b are illustrated (Fig. 2) for a breeding male (Bird 2), a breeding female (Bird 4), and a non-breeding male (Bird 3). Core body temperatures of the two breeding males remained nearly at daytime levels throughout the night. Bird 1's temperature dropped from 41.7 to 39.9°C at night and Bird 2's temperature dropped from 41.5 to 39.0°C at night. Temperatures of females and non-breeding males, on the other hand, were frequently much lower at night than during the day. All female breeders that were recorded either immediately post-laying, during incubation, or during early nestling feeding, dropped their body temperatures at night well below daytime levels. The lowest temperature recorded was 34°C. A non-breeding male also dropped his body temperature at night to 33°C. When ambient temperature fell rapidly at dusk, body temperature also fell rapidly; in one case T_b fell about 4°C in one hour (Fig. 2B). Body temperatures rose quickly at dawn. Temperatures began to rise slightly just at dawn but before the bird became visibly active. As soon as sunlight touched the ground,
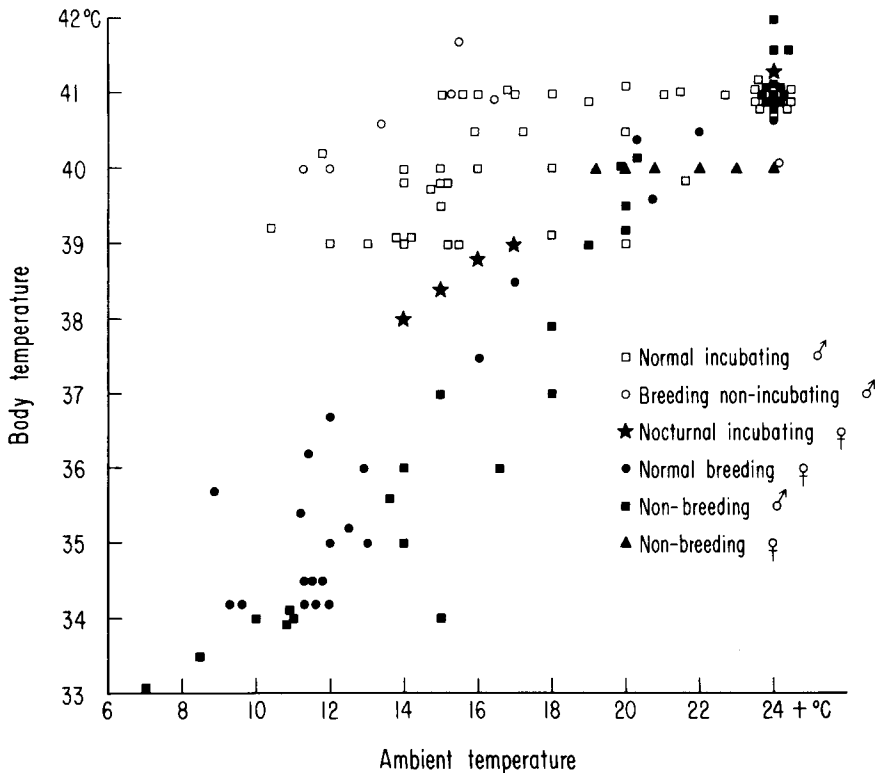
FIGURE 3. Combined plot of hourly readings of core body temperature (T_b) versus ambient temperature (T_a) for breeding and non-breeding male and female Roadrunners.

the birds became active and could often be seen sunning.

One non-breeding female was monitored late in the season and was found not to lower her T_b. However, ambient temperatures were high at this time and her failure to reduce T_b suggested that the degree of hypothermia was related to ambient temperature. A plot of body temperature versus ambient temperature (Fig. 3) for all birds indicates that T_b for all females and non-breeding males varied directly as a function of T_a ($r = .89$, $n = 45$, $P < 0.001$ for all closed-symbol nocturnal points in Fig. 3), while T_b for breeding males remained constant ($r = .32$, $n = 27$, $P > 0.05$ for all open-symbol nocturnal points in Fig. 3).

Several lines of evidence suggest that the elevated nocturnal body temperature of incubating males was not merely a consequence of the insulative properties of the nest (Walsberg and King 1978). Firstly, a female whom I forced to incubate one night by removing the male lowered her body temperature in a manner similar to that of a non-incubating female (closed stars in Fig. 3). Secondly, a breeding male that abandoned his nest and roosted in a distant tree maintained a high body temperature (open circles in Fig. 3). Breeding males therefore appeared to employ a different ther-

moregulatory pattern from females during the incubation period.

DISCUSSION

Nocturnally incubating male Roadrunners maintained distinctly higher body temperatures than roosting non-incubating females under the same ambient conditions. The difference appeared to be a sexual one and not merely a function of the insulation provided by the nest. These findings suggest that incubation is fairly expensive metabolically. This cost can be estimated using published data on oxygen consumption for normothermic and hypothermic Roadrunners (Ohmart and Lasiewski 1971). At an ambient temperature of 10°C, a normothermic bird expends about 1.5 cm¹ g⁻¹ hour⁻¹ of oxygen, while a hypothermic bird expends about 1.1 cm¹ g⁻¹ hour⁻¹. The normothermic bird is therefore metabolizing about 36% more energy than the hypothermic bird. This represents a minimum estimate of the cost of incubation. This calculation may underestimate the actual cost of incubation for several reasons. Ohmart and Lasiewski's normothermic birds were "post-absorptive and resting in the dark," and may have maintained slightly lower body temperatures than incubating birds under the same conditions. Fur-

ther, a large clutch of eggs may act as a heat sink, requiring the incubator to expend slightly more energy than a non-incubator. On the other hand, the nest itself may provide insulcation for the incubator that could reduce its warming costs relative to a non-incubator (Walsberg and King 1978). Direct measurements of oxygen consumption for incubators and non-incubators must be made in order to precisely quantify the caloric cost of incubation (Biebach 1979, Gessaman and Findell 1979, Mertens 1980, Vleck 1981).

The sexual difference in thermoregulation may be a correlate of the different physiological conditions of the two sexes at onset of incubation. Breeding males have conspicuous fat deposits, and are significantly heavier than non-breeding males (354 ± 18 g vs. 314 ± 20 g, $P < 0.001$), although breeding and non-breeding males do not differ statistically in other body measurements (bill, wing, tarsus). None of the females captured showed conspicuous fat deposits. Laying females were significantly heavier than non-breeding females (318 ± 2 g vs. 283 ± 10 g, $P < 0.01$), but they reach pre-breeding weights during early incubation (290 g) and gain even more by the nestling period (325 g). Thus, males are in very good condition at the onset of incubation, whereas post-laying females have depleted their energy reserve and must regain it rapidly in anticipation of the nestling feeding period. Females therefore stand to gain more from an energy-saving thermoregulatory habit such as nocturnal hypothermia, and males are in a better position to perform the apparently expensive nocturnal incubation.

ACKNOWLEDGMENTS

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