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Fasting triggers hypothermia, and ambient temperature modulates its depth in Japanese quail *Coturnix japonica*

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ABSTRACT

We tested three hypotheses regarding the cues that elicit facultative hypothermia in Japanese quail (*Coturnix japonica*): H_1) Ambient temperature (T_a), alone, influences the onset and depth of hypothermia; H_2) Fasting, alone, influences the onset and depth of hypothermia; H_3) T_a acts synergistically with fasting to shape the use of hypothermia. Eight quail were maintained within their thermoneutral zone (TNZ) at 32.6 ± 0.2 °C, and eight below their lower critical temperature (T_{lc}) at 12.7 ± 3.0 °C. All quail entered hypothermia upon food deprivation, even quail kept within their TNZ. Body temperature (T_b) decreased more (38.36 ± 0.53 °C *vs.* 39.57 ± 0.57 °C), body mass (m_b) loss was greater (21.0 ± 7.20 g *vs.*12.8 ± 2.62 g), and the energy saved by using hypothermia was greater (25.18–45.01% *vs.* 7.98–28.06%) in low the T_a treatment than in TNZ treatment. Interestingly, the depth of hypothermia was positively correlated with m_b loss in the low T_a treatment, but not in TNZ treatment. Our data support H_3, that both thermoregulatory costs and body energy reserves are proximate cues for entry into hypothermia in quail. This outcome is not surprising below the T_{lc}. However, the quail kept at their TNZ also responded to food deprivation by entering hypothermia with no apparent dependence on m_b loss. Therefore inputs, other than thermoregulatory costs and body condition, must serve as cues to enter hypothermia. Consequently, we address the role that tissue sparing may play in the physiological 'decision' to employ hypothermia.

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1. Introduction

Facultative hypothermia, the down regulation of metabolic rates and body temperature (T_b) below normorthermic levels, is a widespread physiological mechanism used by birds to save energy (McKechnie and Lovegrove, 2002; Schleucher, 2004). Some birds use hypothermia on a regular basis, even daily, to reduce energy expenditure required for thermoregulation despite their nutritional status, while other species enter hypothermia only in response to food deprivation (Graf et al., 1989; Hohtola et al., 1991; Schleucher, 2001; McKechnie and Lovegrove, 2002). Although hypothermia has been shown to occur in many avian species (McKechnie and Lovegrove, 2002), the cues eliciting this phenomenon are not yet well understood.

Numerous researchers found that the decrease in T_b during hypothermia is dependent on ambient temperature (T_a) and therefore concluded that hypothermia is a mechanism for reducing energy expenditure necessary for thermoregulating in the cold (Haftorn, 1972; Chaplin, 1976; Reinertsen and Haftorn, 1983; Reinertsen and Haftorn, 1986; Merola-Zwartjes, 1998; Brigham et al., 2000; Merola-Zwartjes and Ligon, 2000; Dolby et al., 2004; Fletcher et al., 2004; Cooper and Gessaman, 2005). Their assumption was that at low T_a, a decrease in T_b will lower the T_b–T_a difference and decrease the rate of heat loss, thereby reducing the demand for metabolic heat production (Kleiber, 1975; McNab, 2002; Welton et al., 2002). However, in eight passerine species, no relationship between T_a and the depth of hypothermia (*i.e.*, the decrease in T_b during the rest-phase compared to nighttime normothermia) was found within a range of temperatures below their lower critical temperatures (T_{lc}) (Steen, 1958; Cooper and Gessaman, 2005). Furthermore, in 17 species of hummingbirds, in Japanese quail (*Coturnix japonica*) and in red-headed finches (*Amadina erythrocephala*), T_a was not found to trigger hypothermia (Kruger et al., 1982; Hohtola et al., 1991; McKechnie and Lovegrove, 2003). Thus, T_a alone may not fully explain the use of hypothermia.

Some cases of decreased T_b in birds have been linked to reduced food availability or depletion of body energy reserves. With respect to the latter, food-restricted rock pigeons (*Columba livia*) and Japanese quail used shallow nocturnal hypothermia (Graf et al., 1989; Hohtola et al., 1991), and it has been found that the depth of hypothermia is proportional to changes in body energy reserves (Reinertsen and Haftorn, 1983; Reinertsen and Haftorn, 1986; Cooper and Gessaman, 2005). For example, in Japanese quail, continuous fasting induced progressively deeper nocturnal hypothermia (Laurila and Hohtola, 2005). A decline in energy reserves is thus followed by enhanced

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energy conservation that presumably enables the birds to withstand periods of fasting (Castellini and Rea, 1992).

Given that the use of hypothermia in birds seems to be influenced by T_a as well as by nutritional status, it is likely that the 'trigger' to entering hypothermia is under the control of multiple physiological inputs (Schleucher, 2004) and may even differ among species. Consequently, we examined whether the use of hypothermia by Japanese quail is associated with thermoregulatory requirements, fasting-induced decreases in energy reserves, or a combination of both.

We manipulated T_a, thus changing the quails' thermoregulatory demands, and evaluated their energy reserves by monitoring body mass loss (Δm_b). We hypothesized (H_1) that T_a alone, triggers hypothermia and that quail acclimated to thermal conditions within their thermal neutral zone (TNZ) avoid facultative hypothermia even when they are deprived of food. An alternative hypothesis (H_2) is that fasting alone, triggers hypothermia and that Δm_b is correlated with depth of hypothermia independent of T_a. Lastly, we hypothesized (H_3) that T_a acts synergistically with fasting-induced decreases in body energy reserves to trigger the use of hypothermia. Consequently, we tested the following corresponding predictions: (1) When deprived of food, quail kept within their TNZ do not use hypothermia, while birds kept below their T_{lc} respond by decreasing T_b during their rest-phase. Substantiation of this prediction implies that thermoregulatory costs are the main trigger of hypothermia since quail kept within their TNZ do not use hypothermia. (2) When deprived of food, quail kept within their TNZ and birds kept below their T_{lc} all respond with similar reductions of T_b. Support for this prediction implies that endogenous energy reserves are the main cue for use of hypothermia because of the similar depth of hypothermia observed in birds kept at different T_as. (3) When deprived of food, quail kept within their TNZ and those kept below the T_{lc} decrease their T_bs to different extents, with the latter entering deeper hypothermia. Finally, if this prediction holds, we will conclude that both energy reserves and T_a influence the hypothermic response.

2. Materials and methods

2.1. Animals

Sixteen Japanese quail chicks, eight of each sex and of similar age were purchased from a commercial breeder (Joseph Yanai, Mata, Israel) and were maintained in outdoor aviaries (2.5 × 2.5 × 3 m) on the Sede Boqer Campus of Ben-Gurion University (30° 52′ N, 34° 46′ E) until the experiments began. Fully-grown quail (6 weeks old) were assigned to one of two experimental groups of about the same m_b (173.7 ± 12.44 g and 171.4 ± 7.14 g), each of four males and four females. During experiments the quail were housed individually in cages (40 × 30 × 30 cm), where tap water and feed consisting of grained corn, wheat, soy, plus a mixture of vitamins and minerals (Hemed Lachay, Hemed, Israel) were available *ad libitum*; during periods of food deprivation only tap water was supplied.

2.2. Experimental design

First, we measured the metabolic rates (MR) of nine birds using indirect calorimetry to quantify rates of oxygen consumption (VO_2) and rates of carbon dioxide production (VCO_2) over a range of T_as wide enough to allow determination of their TNZ. Next, two groups of eight quail each were acclimated for seven days to two T_as until they reached stable m_b. One group was kept in a temperature-controlled room, at a constant T_a of 32.6 ± 0.2 °C, within the birds' TNZ; the second group was kept in an air-conditioned animal room, where the T_a was always below the quails' T_{lc} (12.7 ± 3.0 °C). Photoperiods were identical in both treatment groups (following natural cycle). After seven days, four quail from each group were deprived of food for four days to induce hypothermia. Food was removed from the cages at sunset, and the following photophase and the subsequent scotophase were considered as the first day of food deprivation. We measured MR of four quail from each treatment group on the first and fourth days of food deprivation, and of two individuals that were fed *ad libitum* for comparison. Measurement of VO_2 and VCO_2 were made during their rest-phase (ρ-phase) to determine resting metabolic rate (RMR) and MR during hypothermia (HMR), while we took the minimum value overnight for each bird measured. We then repeated the procedure in the reverse order, *i.e.* the four birds in each group that were deprived of food were allowed to feed and those that were fed *ad libitum* were deprived of food. Quail were weighed to ±0.1 g at sunrise each morning. Ambient temperature was continually monitored using temperature-sensitive data loggers (iButton, Maxim Integrated Products, Dallas Semiconductor), that were placed in shaded, well-ventilated areas adjacent to each quail cage.

2.3. Body temperature measurements

We implanted miniature data loggers (iBBat modified by Alpha Mach Inc., Mont-Saint-Hilaire, Canada) weighing 1.1 ± 0.1 g in the peritoneal cavities of the quail to record T_b. Birds were anesthetized with Isoflurane®, and the loggers, potted in paraffin wax, were inserted into the peritoneal cavity through a small incision in the abdominal wall. The incision was sutured, and four days were allowed for recovery in outside aviaries before experiments. We used the temperature correction factors supplied for each logger by the manufacturer to adjust the measured values. Although we began with eight birds in each treatment group, logger malfunctions occurred in six birds so we report results for five birds per treatment group.

2.4. Respirometry

We measured MR by indirect calorimetry with an eight-channel open-flow gas analysis system. VO_2 was calculated from measurements made while six quail rested in individual 1.9 L plastic chambers (Lock and Lock, Korea) with walls covered with black tape to insure that chamber temperature and T_a were equal (Porter, 1969). Each chamber was equipped with a hardware-cloth floor above a paraffin oil trap for excreta. Chamber temperatures were maintained by placing them together in a controlled temperature cabinet (Refritherm-5, Struers, Denmark). Each group of birds was measured at its maintenance T_a, namely 12 °C and 32 °C for quail kept below their T_{lc} and within their TNZ, respectively.

Air from outside the building was pumped through a purge gas generator (Pure Gas, Broomfield, CO, USA, model #PCDA-1-12-m-32-C) that removed CO_2 and water vapor to less than 1 ppm. The fractional concentrations of oxygen in the incurrent and excurrent gas streams (F_IO_2; F_EO_2) were monitored by a dual cell oxygen analyzer (AEI Technologies, Inc. Naperville, IL, USA, model S-3A) and the concentration of carbon dioxide (F_ECO_2) was measured with a CO_2 analyzer (AEI Technologies, Inc. Naperville, IL, USA, model CD-3A). The CO_2 analyzer was zeroed using CO_2-free air and spanned using a 10% CO_2 mixture (Scott Specialty Gases, Plumsteadville, PA, USA), and the differential O_2 analyzer was calibrated by flushing dry air through both cells at the same flow rates.

$\dot{V}O_2$ and $\dot{V}CO_2$ were calculated using well-known respirometry equations (Hill, 1972; Depocas and Hart, 1975; Withers, 1977), andVO_2 (mL O_2 h^{-1}) was converted to units of power (watts), taking the respiratory quotient (RQ) into account (Kleiber, 1975; Schmidt-Nielsen, 1997) and was expressed in mass-specific units (W/g).

2.5. Energetic benefit of hypothermia

We used McKechnie and Wolf's (A. E. McKechnie, personal communication) bioenergetic model to estimate the energetic benefits of hypothermia. This approach allowed us to quantitatively

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