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The effect of ambient temperature and simulated predation risk on fasting-induced nocturnal hypothermia of pigeons in outdoor conditions

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Abstract

Body temperature (T_b) of semi-free pigeons maintained in outdoor conditions was measured for 12 weeks during two winters using intra-abdominal data loggers. In fed birds, the amplitude of the T_b cycle was about 2.5 °C and diurnal T_b increased with decreasing ambient temperature (T_a), but nocturnal T_b did not correlate with T_a . In fasted birds, a well-defined nocturnal hypothermia was seen with minimal T_b 's reaching 36 °C. The depth of fasting-induced nocturnal hypothermia increased with decreasing temperature, and at the lowest T_a 's (−25 °C) a slight diurnal hypothermia was also seen. The presence of a perched avian predator (a stuffed goshawk) had no effect on the fasting-induced hypothermia, but a “flying” goshawk attenuated the hypothermic response.

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1. Introduction

Almost all avian species respond to food restriction or starvation with regulated hypometabolism and hypothermia (reviews: Reinertsen, 1996; McKechnie and Lovegrove, 2002). This is generally seen as an amplification in the rest-phase (nocturnal) decrease in body temperature (T_b), although in some special cases also diurnal hypothermia is seen (Butler and Woakes, 2001; Laurila et al., 2005). Only a few avian taxa can enter deep torpor, but even small decreases of nocturnal T_b permit significant reductions in metabolic rate and thus

confer energetic savings (e.g. Phillips and Berger, 1991; Laurila et al., 2005).

The fact that most birds use hypothermia only when food availability is reduced, suggests that the costs of hypothermia prevent its use in fed birds. The other alternative that hypothermia during food deprivation is a passive result of a failure in thermoregulation can be rejected, because hypothermia is restricted to only a certain phase of the day and because birds actively defend their hypothermic T_b (e.g. Graf et al., 1989). Ecological models that analyze hypothermia on a cost–benefit basis suggest that the hypothermic reaction is influenced by body size, daylength, ambient temperature (T_a) and predation risk (Pravosudov and Lucas, 2000; Welton et al., 2002). While analyses based on re-warming costs indicate that small birds benefit more of hypothermia, the relative savings per degree of decrease

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in T_b during hypothermia are greater for larger birds (Chaplin et al., 1984). Assuming a constant (maximal) insulation in sleeping birds (Phillips and Berger, 1991), the savings are directly related to the depth of hypothermia. Consequently, the absolute savings are independent of T_a , but the relative savings decrease with decreasing T_a (e.g. Reinertsen, 1996). On the other hand, the absolute amount of energy saved may be more critical to survival in cold.

The postulated increase in predation risk due to hypothermia has two consequences: (1) Assuming that the risk is higher during the active phase of the day, hypothermia should be restricted to the resting (dark) phase and (2) Assuming that hypothermia decreases rest-time vigilance, actual presence of a predator should result in a less-deep hypothermia. Whether shallow torpor really has an effect on vigilance is not well known (see however, Haftorn, 1972; Rashotte et al., 1998; Merola-Zwartjes and Ligon, 2000).

In captive pigeons and quails, ambient temperature or photoperiod exert only a slight modulatory effect on the otherwise well-defined hypothermic reaction induced by fasting (Laurila et al., 2005). In addition, the effect of body mass is in contrast with predictions. The 350 g pigeon shows a much deeper hypothermia than the 120 g quail. Phylogenetic history probably explains this difference between the two species, as columbiform birds seem to have a very pronounced hypothermic reaction to starvation (Schleucher, 2001). Several studies suggest that food restriction in captive and free-living birds may induce different responses (Lovegrove and Smith, 2003). Thus, experimental conditions may have an influence on the depth and pattern of hypothermia. Although the hypothermic reaction is “ballistic” on the one hand (Laurila et al., 2005), the propensity to starvation-induced shallow torpor seems quite labile on the other. Even different strains of the same species may respond differently to starvation (Hohtola et al., 1991; Laurila et al., 2005; Rikke et al., 2003).

In this work, we study the effect of photoperiod, ambient temperature and simulated predation on T_b of birds in winter. The experiments were carried out in semi-natural conditions using pigeons that have hatched and lived all their life in an open-air aviary.

2. Materials and methods

2.1. Animals

Altogether nine adult (>1 yr) male and female domestic pigeons (*Columba livia*), bred and housed in large outdoor aviaries at the Zoological Garden of the University of Oulu, Finland, were used in the experiments. Water and commercial pelleted food (Huippu-Punahelhta, Rehuraisio, Finland) with oat grains (1:1)

were given ad libitum, but only water was available during fasting. The experiments were approved by the Animal Care and Use Committee of the University of Oulu.

2.2. Body and ambient temperatures

For measuring body temperature (T_b), a temperature data logger (iButton Thermochron DS 1921H, Dallas Instrument, USA; resolution 0.125 °C; diameter 17 mm, weight 3.13 g) was implanted into the abdominal cavity. The logger registered and recorded data at 1 h intervals allowing a record length of 85 d. After the experiment, the data were downloaded from the loggers by iButton Viewer (Dallas Instrument, USA). Calibration tests showed that, in the temperature range used, the loggers were accurate to 1 or 2 resolution units (see also Davidson et al., 2003).

The operations were performed under isoflurane (Forene[®], Abbott, Sweden) anesthesia, 5% for induction and 1.5–2.5% for maintenance. A small incision was made in the abdominal skin and underlying connective tissue, and the logger was implanted into the abdominal cavity. The incision was closed with sutures. For analgesia, buprenorphine (Temgesic, Reckitt & Colman, UK, 0.1 mg/kg, i.m.) was given post-operatively. The birds were allowed one week for recovery.

Ambient temperature (T_a) was obtained from a weather station located less than 1 km from the experimental site (see <http://weather.willab.fi/weather.html>).

3. Experimental protocol

The experiments were done during two winters in the large outdoor aviary at the Zoological Garden of the University of Oulu (65°3'N 25°27'E). The birds were housed as a group in both experiments. The aviaries had a base area of ca. 25 m² and a height of 5 m. The first experiment (three pigeons) was done during the winter 2003 (from January to April) and the second experiment (six pigeons) in the same months of the winter 2004. In the first experiment (Fig. 1), the birds were maintained normally and food was given ad libitum.

The time scale and the protocol of the second experiment are shown in Fig. 2. The maintenance of the birds was done at 09:00 a.m. and food was available ad libitum in the interval days between fasts. The birds were subjected to 1-, 2- or 3-d fasts were repeated 12 times with or without a predator. Ambient temperature (T_a) during the fasts ranged from very cold to mild cold (see Fig. 2). To simulate predator presence, stuffed goshawks (*Accipiter gentilis*) were introduced to the aviary (P = a perched hawk, F = a “flying” hawk). The

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