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Estimating resting metabolic rate by biologging core and subcutaneous temperature in a mammal

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ABSTRACT

Tri-axial accelerometry has been used to continuously and remotely assess field metabolic rates in free-living endotherms. However, in cold environments, the use of accelerometry may underestimate resting metabolic rate because cold-induced stimulation of metabolic rate causes no measurable acceleration. To overcome this problem, we investigated if logging the difference between core and subcutaneous temperatures (ΔT_{c-s}) could reveal the metabolic costs associated with cold exposure. Using implanted temperature data loggers, we recorded core and subcutaneous temperatures continuously in eight captive rabbits (*Oryctolagus cuniculus*) and concurrently measured their resting metabolic rate by indirect calorimetry, at ambient temperatures ranging from −7 to +25 °C. ΔT_{c-s} showed no circadian fluctuations in warm (+23 °C) or cold (+5 °C) environments implying that the ΔT_{c-s} was not affected by an endogenous circadian rhythm in our laboratory conditions. ΔT_{c-s} correlated well with resting metabolic rate ($R^2 = 0.77$) across all ambient temperatures except above the upper limit of the thermoneutral zone (+25 °C). Determining ΔT_{c-s} could therefore provide a complementary approach for better estimating resting metabolic rate of animals within and below their thermoneutral zone. Combining data from accelerometers with such measures of body temperature could improve estimates of the overall field metabolic rate of free-living endotherms.

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1. Introduction

Fundamental and applied sciences, such as wildlife physiology, ecology and conservation benefit from knowledge of the energy expenditures of free-living animals to aid in determining their fitness and overall population viability (Cooke et al., 2004; Halsey, 2011a). The standard method for measuring aerobic metabolic rate is respirometry, first employed by Lavoisier at the end of the eighteenth century (Lavoisier and Seguin, 1789). However, respirometry is a laboratory procedure and cannot easily be implemented to measure field metabolic rates of free-living animals (Halsey et al., 2011b). While isotope turnover determined by the doubly-labeled water technique is one of the most popular methods for measuring the aerobic metabolism of free-living animals, it returns only average metabolic rate over the period between isotope administration and subsequent sampling (Butler et al., 2004). Thus the technique does not provide the minute-by-minute, or even the day-by-day, measurements necessary to establish an animal's precise time-energy budget. For such estimates one has to resort to proxies for field metabolic rate that can be measured continuously. Among these proxy-based methods is the acceleration-technique. Acceleration data loggers record acceleration, and derivations of the raw data, which separate dynamic acceleration from static acceleration (Qasem et al., 2012), relate well to magnitude of total body motion in a range of species in the laboratory (Wilson et al., 2006; Green et al., 2009; Halsey et al., 2009) and in the field (Elliott et al., 2013).

However, a potential drawback of the accelerometry technique is that it cannot detect increases in metabolic rate that are not associated with movements, such as thermogenic processes. Indeed, thermogenesis derived from shivering was not detected by bi-axial accelerometers in cold-exposed chickens (Green et al., 2009). Stimulation of aerobic metabolism through non-shivering mechanisms, by definition, does not involve movements (Silva, 2006) and thus is unlikely to be detected with accelerometers. Measurements based on accelerometry alone may thus substantially underestimate resting metabolic rate in cold environments (Halsey et al., 2011b).

In the present study we have tested a proxy for metabolic rate not subject to the same limitations as measures of activity, and is theoretically valid in endotherms resting in ambient temperatures below the thermoneutral zone. Our approach relies on the observation that below the thermoneutral zone, peripheral vasoconstriction is maximal, so that the thermal conductance between body core and periphery

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remains constantly at its minimal value (Scholander et al., 1950). With conductance constant, the temperature difference between core and periphery is directly proportional to the rate of heat transfer between them. If the animal is in thermal equilibrium, that rate of heat transfer must equal metabolic heat production. Therefore, for an animal in thermal equilibrium below the thermoneutral zone, the difference between core and peripheral temperature should be proportional to metabolic rate. These physical and physiological considerations inspired previous laboratory work on humans to determine metabolic heat loss by measuring the gradient between skin and rectal temperatures (Hardy and Soderstrom, 1938). The availability of data loggers capable of measuring core (abdominal) and peripheral (subcutaneous) temperatures continuously creates the opportunity to apply this method to free-living animals. In the present study, we tested the principle in controlled conditions. We used implanted temperature loggers and assessed the difference between core and subcutaneous temperature (ΔT_{c-s}) over a range of ambient temperatures in rabbits (*Oryctolagus cuniculus*) extending beyond both the lower and upper limits of their thermal neutral zone, and correlated those differences with metabolic rate measured concurrently by respirometry. To ascertain whether ΔT_{c-s} reflects physiological changes associated with ambient temperature and is not confounded by endogenous circadian rhythms, we also investigated how ΔT_{c-s} varies over 24 h periods in warm (+23 °C) and cold (+5 °C) environments.

2. Materials and methods

This study was performed in accordance with the recommendations provided by the European Convention for the protection of Vertebrate Animal use for Experimental and Scientific purposes (Council of Europe no. 123, Strasbourg, 1985) and in accordance with the French Department of Animal and Environment Protection for the care and use of laboratory animals (accreditation number no. 692260602).

2.1. Animals and procedure

Eight female rabbits (*O. cuniculus*; New Zealand white breed) were purchased from a commercial animal breeder (CEGAV SSC animal breeding, EARL, Saint Mars d'Egrenne, France). This animal model was preferred because rabbits present no marked circadian pattern of activity and very narrow daily maximum-to-minimum heart rate variation when kept in controlled laboratory conditions of constant temperature and non-limited access to food and water (Luo et al., 1997; Akita et al., 2002). In our laboratory conditions, we thus assumed the rabbit exhibited low daily changes in energy expenditure. We used females because males exhibit aggressive behaviors and territorial marking in captivity which are likely to affect activity budget and stress level with uncontrolled effects on core and subcutaneous temperatures.

Rabbits were caged in groups of two or three in an animal housing facility under constant 12:12 hour light–dark cycles (light from 7:00 to 19:00) with air temperature at 23 ± 1 °C. Rabbits were fed a standard rabbit diet (Huttepain-Bouix SA, Piacé, France) ad libitum and had free access to water. After one week, rabbits underwent surgery for implantation of two temperature loggers (see below). The temperature loggers were programmed to start recording one week after surgery. Rabbits were subjected to two consecutive experiments. The first experiment consisted of keeping the rabbits in their home cage at two ambient temperatures (23 ± 1 °C and 5 ± 1 °C) for a minimum of one week each, to quantify how core and subcutaneous temperatures fluctuate over a 24 h period when rabbits are exposed to temperatures within and below their thermoneutral zone. In the second experiment, the rabbits were exposed to 7 ambient temperatures ranging from −7 °C to 25 °C, each for 1–2 hour duration, during which time we measured metabolic rate by respirometry, along with core and subcutaneous body temperatures. At the end of the study, animals were euthanized by overdose of sodium pentobarbitone administered intravenously.

2.2. Measurement of core and subcutaneous temperature

Temperature loggers (DS1922L Thermochron iButtons, Dallas Semiconductor, USA; resolution 0.0625 °C), were coated with inert wax (Sasol, South Africa), clock synchronized, and calibrated in a water bath against a high-accuracy thermometer (Quat 100, Heraeus, Germany). Core (abdominal) and subcutaneous temperatures were recorded simultaneously at ten-minute intervals. Before implantation, the loggers were sterilized in formaldehyde vapor.

For logger implantation, the rabbits were anesthetized with 48 $mg \cdot kg^{-1}$ sodium pentobarbitone (Sanofi, France) injected into the marginal vein of the ear. Rabbits received retro-tracing injections of local anesthetic (1 ml Xylocaine 2%, AstraZeneca, France) at the implantation sites, and were washed twice with antiseptic scrub (povidone-iodine, Betadine, Purdue Products). One logger was inserted into the abdominal cavity through a midline laparotomy incision (~25 mm), and tethered to the linea alba. A second incision was made on the right flank and the second logger was inserted under the skin and tethered to the dermis. After the loggers were implanted, the incisions were sutured closed and treated with an antiseptic wound-healing agent (Aluminium stearate, Alumisol, CEVA, France). The rabbits received a subcutaneous injection of anti-inflammatory medication (0.3 $mg \cdot kg^{-1}$ meloxicam, Vetoquinol, France) and an antibiotic (1 $mg \cdot kg^{-1}$ oxytetracycline 5%, Vetoquinol, France). The rabbits were monitored by animal care technicians on a daily basis. In particular, recovery was assessed by checking for incision healing; no post-surgical adverse events were observed.

2.3. Measurements of resting metabolic rate

Body mass of the rabbits at the time of the metabolic measurements was 2150 ± 78 g (mean ± SD; range of 1814 g–2319 g). Implanted rabbits were placed in a cylindrical metabolic chamber offering limited movement (internal diameter 240 mm, height 200 mm) and metabolic rate was continuously measured during 12 h (between 07:00 and 19:00) using an open-circuit respirometer (Teulier et al., 2014). During this period, ambient temperature was stabilized for a minimum of 1 h (range 62 to 112 min) at each of the following temperatures: 25, 20, 15, 10, 5, 0 and −7 °C. At each ambient temperature resting metabolic rate was averaged over a minimum period of 15 min during which the rabbit showed no visible signs of movement (e.g., exploring, grooming), based on recorded observations from a webcam (Logitech, Switzerland). We measured ambient temperature in the respirometer using copper-constantan thermocouples, barometric pressure using a digital barometer (GE Druck, United States), and relative humidity with a wet-and-dry bulb psychrometer (Prolabo, France). Air flow was obtained using a pull-system and rates were measured with a Platon volumeter (Domont, France) and corrected to temperature of the flowing air and barometric pressure, dry. The air sample was dried by passage through a cold trap and a drying agent (silica gel) before oxygen (O_2) and carbon dioxide (CO_2) concentrations were measured. The fractional concentration of O_2 was measured with a Servomex 1100 paramagnetic gas analyzer (Taylor Instrument Analytics Ltd, Sussex, UK) calibrated with pure nitrogen gas and atmospheric air assuming oxygen content of 20.93%. CO_2 concentration was measured with a Servomex 1400 infrared gas analyzer (Taylor Instrument Analytics Ltd, Sussex, UK) calibrated with pure nitrogen gas and a known mixture containing 0.502% CO_2. The rates of O_2 consumption and CO_2 production were calculated according to the equations of Depocas and Hart (1957):

$$\dot{V}_{O_2} = \left[\dot{V}_E F_{IO_2}\left(1 - F_{ECO_2}\right) - \dot{V}_E F_{EO_2}\left(1 - F_{ICO_2}\right)\right] / \left(1 - F_{IO_2} - F_{ICO_2}\right)$$

$$\dot{V}_{CO_2} = \left[\dot{V}_E\left(F_{IO_2} - F_{EO_2}\right) - \dot{V}_{O_2}\left(1 - F_{IO_2}\right)\right] / F_{IO_2}$$

where $\dot{V}_{O_2} = {}_{O_2}$ consumption rate ($L \cdot h^{-1}$), $\dot{V}_{CO_2} = {}_{CO_2}$ generation rate

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