

REVIEW

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Challenges of measuring body temperatures of free-ranging birds and mammals

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Abstract

The thermal physiology of most birds and mammals is characterised by considerable spatial and temporal variation in body temperature. Body temperature is, therefore, a key parameter in physiological, behavioural and ecological research. Temperature measurements on freely moving or free-ranging animals in the wild are challenging but can be undertaken using a range of techniques. Internal temperature may be sampled using thermometry, surgically implanted loggers or transmitters, gastrointestinal or non-surgically placed devices. Less invasive approaches measure peripheral temperature with subcutaneous passive integrated transponder tags or skin surface-mounted radio transmitters and data loggers, or use infrared thermography to record surface temperature. Choice of technique is determined by focal research question and region of interest that reflects appropriate physiological or behavioural causal mechanisms of temperature change, as well as welfare and logistical considerations. Particularly required are further studies that provide opportunities of continuously sampling from multiple sites from within the body. This will increase our understanding of thermoregulation and temperature variation in different parts of the body and how these temperatures may change in response to physiological, behavioural and environmental parameters. Technological advances that continue to reduce the size and remote sensing capability of temperature recorders will greatly benefit field research.

Keywords: Thermometry, Radio-telemetry, Temperature data logger, Passive integrated transponder, Infrared thermography, Thermocouple, Thermoregulation, Heterothermy

Background

The thermal physiology of vertebrates can be broadly classified by their stability in body temperature and source of body heat [1]. Ectotherms are most commonly poikilothermic where body temperature tracks environmental temperature, allowing thermal tolerances across a wide range of temperatures [2, 3]. Endothermy is the maintenance of a high and relatively constant homeothermic body temperature through high metabolic heat production that appears to have evolved separately in avian and mammalian lineages [4]. Core temperature in birds ranges between 34 and 44 °C, scaling with body

size in some groups. Mammalian core temperature varies between 30 °C in the monotremes and as high as 40 °C in other groups [5]. However, many species of both mammals and birds are regionally or temporally heterothermic, with variable endothermic heat production and a body temperature that is not regulated within a narrow range [1, 6].

Common to all these groups, body temperature is a key physiological parameter that provides important insights into the study of thermoregulation, physiology and behaviour or responses to environmental change [7, 8]. However, while the ectotherm to endotherm continuum is useful for broadly describing the mean physiological state of an organism, this may mask our understanding of the dynamic nature of thermoregulation. The complex control of body temperature in endotherms occurs through autonomic regulation of blood flow in combination with

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a number of processes including shivering and non-shivering thermogenesis, panting or sweating and by a range of thermoregulatory behaviours [1, 9]. It is a common misassumption that there exists a standard reference core or deep body temperature for each species and each individual [10]. The temperature of any anatomical region is a product of metabolic heat production and blood flow within that region, including the rate of heat lost from physical processes [10]. Confusingly rectal or cloacal temperature is often used synonymously with the terms core or deep body temperature and not surprisingly considerable research effort has been invested in cross-validation of techniques to measure these respective temperatures [11–14]. Therefore, for any study involving body temperature measurement it is important to understand the spatial variation and differential regulation in temperature within the body and how the temperature of different body regions may change with time and environmental context. Here, the term core temperature is used throughout to describe the homeostatic temperature within the centre of the body.

Accordingly, the first step in deciding which technique to use when sampling temperature from an animal is to determine which body region is suited to answer the research question and on what timescale measurements are required. Precision and response time of the sensor should be chosen to reflect the rate of change of temperature at that site. However, choice of measurement sites may be constrained by the extent to which invasive methods are appropriate for the study species.

This review is aimed at researchers wishing to undertake body temperature measurements on freely moving or free-ranging birds and mammals. In particular, the merits of a range of techniques that are suited to studies of animals in the wild are considered (Table 1). This is intended to help researchers choose the most appropriate technologies and complements previous reviews that have focused either on single techniques [15–17] or have examined body temperature measurement in particular taxonomic groups [10, 18, 19]. The current review compares techniques that measure core and peripheral temperature and discusses calibration, analytical approaches and future instrument design.

Internal temperature

Thermometry

Rectal or cloacal temperature is commonly measured using thermometry. This fast, affordable, and minimally invasive method relies on inserting a thin temperature-sensitive probe into the rectum via the anus or cloaca [20–22]. It is commonly undertaken using thermocouples or thermistors either custom adapted for use or using standard medical or veterinary thermometers.

Oesophageal temperature may also be taken in this way [23]. Thermometry has wide applicability in ecology, and has been used for example to record functional thermoregulation in relation to climatic variables, immune function, natural occurrence of pathogen infection and when studying the ontogeny of thermoregulation [20, 24–27]. While highly accurate and repeatable [20], thermometry generally only provides a cross-sectional temperature sample, because subjects must be captured and handled during sampling. The stress of capture and indeed the temperature measurement itself can bring about stress-induced hyperthermia (SIH) mediated by the sympathetic adrenal and the hypothalamic–pituitary–adrenal (HPA) axes, as well as through increased metabolic heat production associated with the escape response [28, 29]. Therefore, the time from capture to measurement should be as rapid as possible, particularly for small animals. For example, measurement of rectal temperature in mice typically results in an increase of 0.5–1.5 °C in 10–15 min [23] and is associated with peripheral cooling at the surface through vasoconstriction [30]. Thermometry is, therefore, inappropriate for studying functional body temperature responses or longitudinal patterns in body temperature regulation in free-ranging or free-moving animals. This problem can be partly remedied by physically attaching one or several thermocouples by leads to different body regions to allow for continuous body temperature recordings (Nord and Folkow, unpublished data) or by connecting temperature sensors to an externally mounted radio transmitter [31]. However, physical attachment is a viable option only for inactive, or relatively inactive animals or when contained in a confined space (such as a metabolic chamber or a roosting cavity) where thermocouple wiring can be adjusted to confinement size and animal movement is relatively small. Stress from having the thermocouple attached may also bias the temperature reading (Esa Hohtola, pers. comm., see also [32]). Regardless of such shortcomings, thermometry remains an inexpensive, fast, and attractive method for body temperature recording, especially when cross-sectional data are desirable and subjects can be caught and measured with relative ease. With larger animals, measurements of blood and muscle temperature may be made by percutaneous insertion of a thermistor via a catheter and temperature logged with a surface-mounted recorder [33–35]. This allows for continuous monitoring of body temperature while animals are exhibiting natural behaviours but requires recapture of the animal for removal of instrument.

One indirect thermometry method of estimating rectal temperature is to measure the temperature of newly defecated faeces [36]. This technique has recently been applied to body temperature measurement by careful

Table 1 Advantages and disadvantages of different methods used to measure body temperature of birds and mammals

Method	Capture	Surgery	Continuous	Advantages	Disadvantages
Thermometry, e.g. rectal, oesophageal	✓	×	×	Quick, low-cost, core temperature measurement	Single point measurement, difficult to make on freely moving animals. Stress responses may influence body temperature
Implanted data loggers	✓	✓	✓	Measurement of internal temperature(s) over many months/years. Can be combined with other sensors, e.g. heart rate	Surgical constraints, most cases require recapture for data recovery. Data logger size limitations
Radio transmitters: Implanted	✓	✓	✓	Measurement of internal temperature(s) that can be remotely recorded	Measurement duration limited by battery power. External receiver or manual data logging system required for continuous recording
Radio transmitters: Skin surface	✓	×	✓	Remote measurement of skin temperature. Easily attached by glue	As above. Skin temperature is influenced by environmental conditions as well as physiological parameters. Signal noise increased by movement. External devices increase drag
Gastrointestinal devices	✓	×	✓	Deployment by feed tube/ingested. Continuous recording of internal temperature. Detection of prey/food intake	May require anaesthesia or sedation. Temperature influenced by ingestion/digestion. Measurement period may be limited by gut passage time. Device size limitations
Non-surgical implants, e.g. rectal, aural, vaginal	✓	×	✓	Internal temperature measurement avoiding surgery	Temporary measurement of body region may constrain biological function and limits measurement duration
Faecal temperature	×	×	×	Non-invasive proxy of rectal temperature	Calibration of rectal temperature with faecal temperature required. Temperature prone to vary with environmental conditions
PIT tags	✓	×	×	Low-cost, minimally invasive, multiple discrete measurements avoiding recapture. Temperature measurement possible throughout life of organism	Non-continuous measurement limited by RFID receiver placement. Reading range restricts measurement to close proximity. Migration of tag in some cases
IR thermography	×	×	✓	Remote, non-invasive, sampling with high spatial and temporal resolution. Thermal video allows temperature measurement of discrete behaviours	Influenced by environmental conditions and may not clearly reflect internal temperature. Continuous recording of thermal video over several hours may be limited by memory. Animal must be within field of view of researcher/camera
IR thermometry	×	×	×	Remote, non-invasive recording of surface temperature. Low cost (cf. IRT)	Spatial resolution limited by increasing measurement area with distance. Typical distances of 1–5 m
Temperature-sensitive paint	✓	×	×	Rapid assessment of temperature range of surface by colour change	Low accuracy and resolution. Toxicity and visual marking may affect health/behaviour/predation risk

Capture, surgery or continuous recording is noted: yes (✓), no (×)

calibration of the rate of temperature change following defecation [37]. However, it is likely to have limited applicability by the fact that it only provides single time point measurement and will be strongly influenced by changes in environmental conditions.

Surgical implants

Intra-peritoneal (and sometimes also intra-abdominal) implants are commonly used when continuous long-term body temperature profiles are desirable, such as when studying the functional characteristics of thermoregulation. Implantable temperature-sensitive devices have been used for this purpose in a wide range of species (see references in [17]), and have provided considerable insights into the thermal biology of a large number of free-ranging animals. The devices basically come in two forms; data loggers and radio transmitters. Common to all implants is the need for surgery, which requires anaesthesia. Sedation itself is often unproblematic, but mortality may occur despite proper dosage [38] so care must be taken to monitor vital signs and provide post-surgical recovery. Although surgical implantation is logistically demanding, it has been successfully used on wild animals by either transporting animals to temporary surgical facility [39] or directly undertaking surgery in the field [40]. Implantation of devices may actually be preferable to externally attached loggers in long-term studies [41].

Data loggers

Most data loggers integrate a thermistor, a real-time clock, and an internal memory for storing temperature, time and date at a user-defined interval. Temperature sensors may be held within the body of the logger but where more rapid response rates are required these can be mounted on external leads or on the surface of the instrument [42]. Data loggers are invaluable when recording long-term body temperature profiles and are often combined with heart rate loggers [43–45]. Logger weight considerations can constrain use of many commercially available data loggers on small species. For example, Thermocron iButtons (Dallas Semiconductor, Sunnyvale, CA, USA), which are amongst the smallest available data loggers, weigh approximately 3 g in their standard format. However, iButtons can be remodelled for a 50 % weight reduction [17] and water proofing [19], which allows for measurements on considerably smaller subjects (≥ 30 g).

Implanted data loggers are, therefore, particularly suited to long-term deployments. Examples of these include studies on thermoregulation [42, 43], circadian rhythms [39, 46–48], hibernation and torpor [40, 49, 50], temperature change during diving and foraging [43, 51, 52], incubation [53], egg laying in monotremes [54] and

comparison between wild and captive species [47, 55]. One disadvantage with data loggers is that animals must normally be recaptured for data retrieval, which can be difficult or even impossible for some species. Technological solutions have been developed to remedy this, for example using UHF transmission of temperature data to a telemetry collar that can then transmit data by VHF [56] or implanted archive tags on pinnipeds that float to the sea surface and transmit data by satellite when the animal dies [57].

Radio transmitters

Animals implanted with radio temperature transmitters do not require recapture as data are transmitted continuously, and in general the small size does not impose weight constraints. However, the applicability of radio transmitters can be constrained by battery life and signal strength is sometimes compromised in structurally complex habitats. In addition, transmitters do not have internal storage capacity, which requires manual recording of signal pulse rate or the purchase of automated recording equipment [58]. Care must, therefore, be taken when tracking animals to ensure that disturbance does not disrupt natural behaviours. Automated recording systems provide a solution to this problem, allowing recording of multiple individuals where good signal transmission is possible but will obviously be constrained by range size and habitat complexity for some species. Regardless of such potential shortcomings, radio transmitters continue to provide an effective option for remote recording of body temperature in free-ranging animals over relatively long time periods [50, 59–62].

Gastrointestinal devices

Ingestion of radio-telemetry pills or miniaturised data loggers allows a relatively non-invasive method of measuring internal temperature. These devices record temperature during passage through the gastrointestinal tract and have been used widely on relatively large species and in humans [10, 63, 64]. Recording duration is determined by gut passage rate, which may vary from hours to weeks but in large ruminants devices have been retained for up to 4 years (retention time was actually improved by increasing the size of the device) [56]. The extent to which gastrointestinal temperature reflects core temperature is dependent on food ingestion and subsequent digestion (and fermentation in the case of ruminants). The temperature recorded may be filtered to account for these processes and thereby provide informative longer term recording of core temperature [56]. Radio-telemetry pills have the advantage that temperature can be recorded externally and do not require recovery of the pill. Systems that provide a combination of radio-telemetry and data

logger output have been custom built for this purpose [56, 64]. By far the greatest application of gastrointestinal sensors in wild species has been to detect feeding events in marine endotherms, to which these devices are especially appropriate as the stomach temperature of these animals drops temporarily during the ingestion of cooler ectothermic prey [65–67]. The location of the temperature sensor in the stomach will affect the likelihood that ingested prey comes into contact with the sensor [65, 68]. Thermistor pills can either be gently pushed through the oesophagus via a flexible silicone intubation tube under anaesthesia or fed to the studied animal inside a refrigerated prey during captive experiments. Recorded temperature measurements are stored in the device and retrieved through stomach flushing at the end of experimentation, e.g. after about 10 days for captive seabirds [69]. Measured stomach temperatures of free-ranging species are transmitted to an external logger placed on the back of the animals that is subsequently retrieved. More recently signals from temperature sensors are monitored by satellite transmitters and data are directly relayed through the Argos Data Collection and Location System [70]. Stomach temperature sensors have also been used in conjunction with other temperature loggers to examine physiological processes such as hypothermia [71] and the heat increment of feeding [72]. More recently, stomach temperature sensors have been identified as a promising method to study the suckling behaviour and the transition to nutritional independence of pinnipeds [73, 74].

Non-surgical methods for measurement of internal temperature

In cases where surgical implantation of temperature sensors may not be possible some novel methods of have been used to obtain internal body temperatures. For example, these include temporarily inserted rectal [75], vaginal [76] or aural temperature [77] data loggers. These techniques may be suited to relatively short time periods (days–weeks) and are especially useful for large species where subjects can be recaptured.

Peripheral temperature

Temperature at the periphery, either below (subcutaneous) or at the skin surface is controlled by peripheral blood circulation and body insulation, and is also affected by environmental factors such as ambient temperature and wind speed. For small animals (where body size typically is not sufficiently large to maintain a regulated core-to-shell temperature gradient), changes in skin surface temperature may be closely correlated with internal temperature [18, 58, 78, 79] but with increasing body size peripheral temperature is generally not a reliable predictor of core temperature [80, 81]. These factors will be

important to consider when evaluating the suitability of peripheral temperature measurement for any given project/research question.

Passive integrated transponder (PIT) tags

In situations where surgery is not practical, it is possible to implant subjects subcutaneously with small temperature-sensitive transponders. These self-contained devices provide both a unique identification number and temperature data [82]. Devices were developed for veterinary applications but have since been used to study body temperature profiles in wild birds [79] and mammals [18]. At least in birds, implantation is minimally disturbing and does not cause bleeding or subsequent inflammation. Thus, it is not necessary to apply anaesthesia and analgesia and recovery time can be kept short. In addition, because these devices are both small (approximately 12×2 mm) and lightweight (<0.1 g) they can be implanted into small animals (body mass ≥ 2 g). Being contained within a glass container they are also biologically inert, and will remain active throughout the life of the animal. Migration of the tag may be reduced by choosing PIT tags that have an anti-migration cap. However, unlike transmitters or data loggers, the implantable transponders do not transmit or store data, but must be within the electromagnetic field of a receiving unit for data to be collected. This poses two problems: firstly, the need for sufficient field strength constrains the maximum distance between the subject and the receiving unit to about 0.3 m. Secondly, because of interference, data collection will become arbitrary if more than one transponder is contained within the same electromagnetic field at any given time. For these reasons, the use of implantable transponders may be more appropriate in captive settings or in field situations where subjects could be contained within the field of the receiving unit (e.g. roosting animals) or can be attracted to the receiver by other means (e.g. receiving unit set up at nests or feeding stations [19]), and in those cases where only one animal's temperature is of interest. Although PIT tags are generally inserted subcutaneously to record temperature it would be possible to implant them deeper within the body, but of course detection distance would limit the implant location and so may not be suitable for larger species. Care must also be taken to interpret temperature data from PIT tags implanted into different body regions. For example, PIT tags inserted subcutaneously or in semi-membranous muscle in goats differed by up to 3.5 °C, while a PIT tag inserted into the retroperitoneum was only 0.2 °C less than temperature recorded by a digital rectal thermometer and an intra-abdominal data logger [14].

Skin temperature measurement

A commonly used and moderately non-invasive method for temperature sampling involves fitting subjects with an externally attached radio transmitter [83]. Having captured the animal, it is often necessary to trim or remove part of the plumage or fur (normally on the lower back) for the transmitter to be attached in close proximity to the skin. Because only a relatively small area of integument is removed, remaining feathers or fur can effectively cover the attachment site. Thermal images of birds instrumented in this way reveal no obvious differences in surface temperature and, therefore, attachment seems to have little (if any) influence on insulation (McCafferty & Nord, unpublished data; see also [84]). Other methods of measuring skin temperature include using data loggers mounted to radio collars [49, 85] or glued securely with epoxy to the integument to track temperature over several days [86].

Provided that transmitters are in proper contact with the skin, they will provide reliable, high-resolution data on skin temperature fluctuations [58, 87]. Data can also be received over long distances (1000+ m). Variation in the proximity of attachment to the skin, which is likely when the pelage or plumage is trimmed rather than removed, will introduce between-subject variation in transmitted temperature and skin temperature will always be influenced to some extent by environmental conditions (Lehmann *et al.* in review). One additional constraint of externally mounted instruments is the effect of the device on the animal. The recommended size of instruments is 1–5 % of body mass for birds or bats, and 10 % for non-flying animals [88, 89], although it is advisable to assess the full impact of device on drag and energy expenditure [90].

Infrared thermography

When subjects cannot or need not be captured, there are possibilities to study body temperature patterns using infrared thermography (IRT). IRT involves the detection of infrared radiation, which is emitted from all surfaces with a temperature above 0 K [16]. An obvious strength of IRT as compared to other means of temperature sampling is that it allows for an integrated measure of the thermal properties of different surfaces of the body in freely moving animals and functional variation in heat loss from the surface of different body regions [91, 92]. In endotherms with a relatively thin pelage or plumage, thermal imaging could also be optimised to investigate regional heterothermy. This would allow assessment of the extent to which animals strategically alter blood flow to the body periphery to control heat loss. However, IRT only determines surface temperature and, therefore, changes in internal temperature must be measured using

other techniques (e.g. [93]). Attempts have been made to correlate IRT surface temperature measurements with core body temperature. For example, by removing a small area of plumage from the head of ducklings, scalp temperature was shown to be within 1 °C of cloacal measurements over a range of ambient temperatures [94]. Similarly, facial skin temperature measured via thermal imaging explained more than 80 % of the variation in core body temperature in domestic fowl [95]. Due to the lack of insulation around the eye, the temperature of this region is often closest to core temperature compared to other peripheral regions. The surface temperature of the eye region is not a reliable predictor of core temperature [96]. However, measurement of temperature of the eye region or other bare skin areas may be useful for detecting stress responses [97, 98].

Alternatives to infrared thermography for remote, non-contact sampling

Although recent technological advancements have made thermal imaging cameras more affordable, infrared thermometers provide the opportunity to obtain non-invasive measurements of surface temperature at a fraction of the cost. These devices are most accurate when animals can be approached within a few metres and mean (min and max) temperature can be recorded from a given area highlighted by a laser guide [99]. With increasing distance the measurement 'spot' becomes too large for measuring the temperature of specific regions. Nevertheless, these devices gave equally good measurements of skin temperature in ectotherms as did thermistors placed on the skin [100], but of course peripheral temperature recorded with this technique will differ from cloacal temperature [101]. Infrared sensors can provide continuous monitoring of surface body temperature with an automated data collection system or can also be used remotely in nest boxes to study thermoregulation and torpor [102]. Surface temperature has been recorded using temperature-sensitive paint but accuracy is relatively poor (ca. 1 °C) and requires careful colour calibration [94]. Toxicity and influence of colour marking on behaviour or predation risk also need to be considered.

Calibration and data analysis

An essential requirement of all body temperature measurement is to calibrate instruments against known standards (i.e. mercury thermometer or platinum resistance thermometer). This can be undertaken in water baths (in the laboratory) or thermos flasks (in the field) or in air in temperature chambers, and is a crucial step to improve the accuracy of temperature data [103]. It is also essential to account for inter-instrument variation whenever multiple instruments are used on a single animal, single

instruments are used on many individuals or where many identical temperature-sensing setups are deployed in the same experiment [104]. The importance of calibration drift over time is an important consideration for implanted logging systems and externally mounted radio transmitters [105]. Where possible, it is, therefore, prudent to check calibration before and after deployment to account for this. For infrared thermography, calibration can be checked against a blackbody of known emissivity that is monitored by a thermocouple/data logger before and after the measurement session or continuously in the field of view [77].

An essential consideration when interpreting peripheral temperature data relates to the temporal and functional variation in internal–external temperature covariance, especially in large animals [81, 106]. The relationship between internal and peripheral temperature is not always the same in active and inactive animals. For example, when studying the body temperature response to a simulated pathogen infection in birds, there was a strong linear relationship between implanted and externally attached transmitters during the night (when birds were roosting), whereas skin temperature varied independently of core temperature during the day (when active and subjected to variation in ambient temperature and exposure to shade/sun) [58]. However, skin temperature was a good predictor of cloacal temperature throughout the daily cycle in a different bird species [107]. Care must be taken to investigate the nature of the relationship between core and peripheral temperatures and understand how temperature of different body regions varies with both temporal (day/night, active/passive) and state-dependent (age, sex, size, etc.) factors. Studies relying on remote sensing techniques should, therefore, take proper care to carefully calibrate sampling methods against other regions of the body to assess the extent to which peripheral temperature reflects internal and external temperature. One useful approach that may aid choice of the most reliable/consistent indicator of internal temperature has been to apply multivariate statistical techniques such as principle component analysis to multiple peripheral measurements [108].

Continuous sampling of body temperature is often considered advantageous as it avoids errors associated with non-random point sampling of temperature [109]. As a consequence researchers are faced with the analysis of high-resolution data over long time periods. Certain data (e.g. those collected by externally mounted radio-telemetry system) may also require filtering due to sampling artefacts associated with movement of animals and/or signal noise [58]. Customised filtering programs are, therefore, supplied as part of proprietary software or require development of appropriate algorithms. Similarly

thermal imaging requires considerable post-collection extraction of temperature from still or thermal video using image analysis software. One of the greatest difficulties involved is tracking regions of interest as animals move. Researchers should thus not underestimate the time taken for image processing to extract temperature data from complex shapes of animals. Some attempts have been made to use pattern detection algorithms in humans [110] but as yet, automated systems for complex shape recognition are not widely used in animal studies, with the exception of counting animals from heat signatures [111].

For all methods that generate continuous data, it is advised that researchers consider sampling interval prior to the start of data collection, to set the interval between successive data points such that it corresponds to the rate of change expected in any parameter that is investigated (e.g. short sampling interval in studies of thermoregulatory mechanisms; longer sampling interval for core temperature in hibernating animals). Prudence with regard to sampling interval will also maximise logger performance, such that internal memory (where applicable) is not exhausted after an insufficiently long measurement period.

Conclusions and future directions

Measuring internal body temperature in freely moving animals is especially challenging due to the need to implant data loggers or radio transmitters. Where this is not possible for logistical or welfare concerns, less invasive techniques involving measurement of subcutaneous or peripheral temperature, or thermal imaging are widely available (Table 1). Researchers should, therefore, consider carefully if it is the all important ‘core’ temperature that is needed to answer research questions or if peripheral temperature may be either a suitable proxy or even a more informative measure for the particular questions of interest. For example, in many physiological studies multiple measurements from different regions are likely to be necessary to obtain a sufficiently detailed view of thermoregulatory processes, while in ecological/behavioural studies one appropriately chosen single temperature measurement may suffice. To this end, sampling interval should also be adjusted such that it provides the necessary temporal resolution in situation where study design may risk exhausting device memory. Particularly required are the development of appropriate methods for sampling from multiple sites from within the body, which will increase our understanding of how temperature varies in different regions/organs and how these change in response to physiological, behavioural and environmental parameters. Acoustic temperature telemetry that is currently used to measure temperature in fish and aquatic

reptiles [112] could also be useful for remote temperature sensing of diving birds and mammals. Future applications will be aided by technological advances that continue to reduce the size and data gathering capabilities of temperature-sensing methods. In particular, the development of medical sensing systems linked to mobile phone and wifi communication [113] provides considerable potential for remote sensing of body temperature in wild animals.

Authors' contributions

DM, SG and AN jointly organised workshop that provided conceptual basis for review and all undertook writing and editing of the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

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