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The value of infrared thermography for research on mammals: previous applications and future directions

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ABSTRACT

1. Infrared thermography (IRT) involves the precise measurement of infrared radiation which allows surface temperature to be determined according to simple physical laws. This review describes previous applications of IRT in studies of thermal physiology, veterinary diagnosis of disease or injury and population surveys on domestic and wild mammals.
2. IRT is a useful technique because it is non-invasive and measurements can be made at distances of <1 m to examine specific sites of heat loss to >1000 m to count large mammals. Detailed measurements of surface temperature variation can be made where large numbers of temperature sensors would otherwise be required and where conventional solid sensors can give false readings on mammal coats. Studies need to take into account sources of error due to variation in emissivity, evaporative cooling and radiative heating of the coat.
3. Recent advances in thermal imaging technology have produced lightweight, portable systems that store digital images with high temperature and spatial resolution. For these reasons, there are many further opportunities for IRT in studies of captive and wild mammals.

Keywords: disease, infrared thermography, injury, population surveys, temperature measurement, thermal physiology

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INTRODUCTION

Infrared thermography (IRT) involves the precise measurement of infrared radiation emitted by an object, which allows the surface temperature to be determined according to relatively simple physical laws and known properties of the surface (see Speakman & Ward, 1998). Specialized thermographic cameras produce images that show the variation in temperature of a surface by representing different temperatures with a grey or coloured shaded scale (Fig. 1). Although thermal imaging was developed principally for industrial, medical and military applications (Burnay, Williams & Jones, 1988), it has been used to study many animal groups including insects, reptiles, birds and mammals (see McCafferty *et al*., 1998).

Infrared thermography can examine many different aspects of thermal physiology, diagnose injury and disease and is a useful technique for counting animal populations. The great advantage of IRT in animal research is that measurements can be made without touching or disturbing the animal and depending on the instrument type and application, measurements can be made either at close range (<1 m) or at large distances (>1000 m). Detailed measurements of the temperature variation of mammals can be made where large numbers of temperature sensors would otherwise be required. Conventional solid probes can also give

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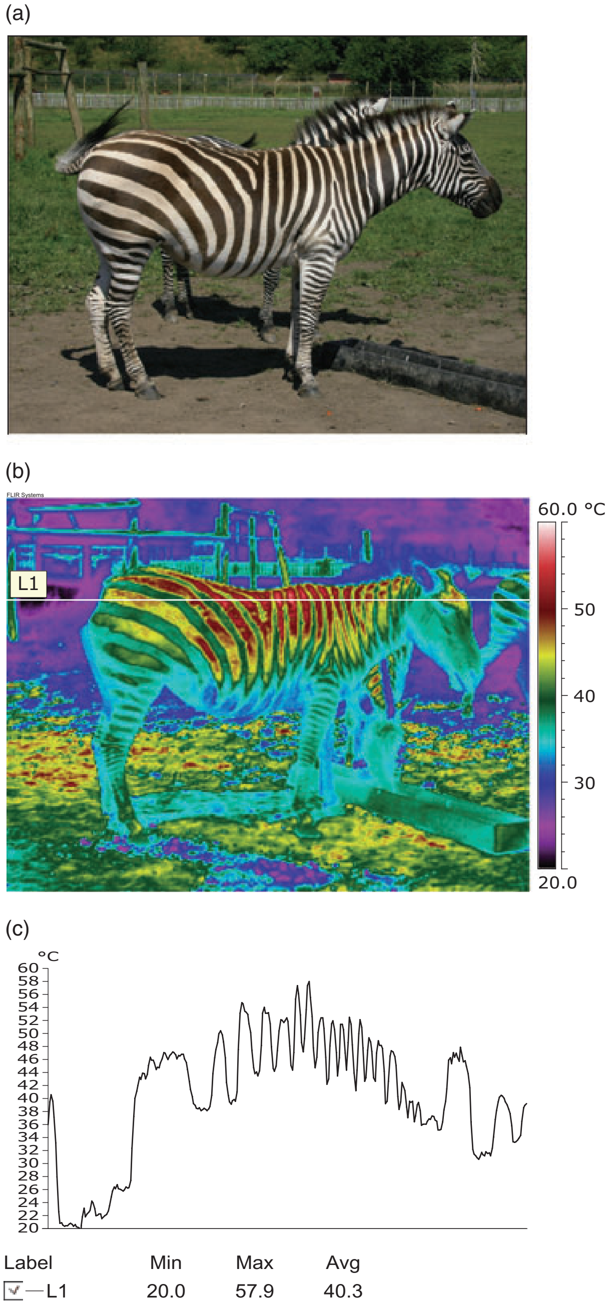

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Fig. 1. Photograph (a) of Grant's zebra *Equus burchelli boehmi* with corresponding infrared image (b) in full sun. The temperature profile L1 displayed in the graph below (c) shows the variation in temperature across the body, with black stripes more than 10 °C warmer than white striped areas of the coat. Mean air temperature = 28.3 °C, relative humidity = 44%, solar radiation = 860 Wm^{-2} and wind speed = 0.3 ms^{-1}.

false readings due to the difference in heat capacity between sensor and coat or through disruption of the hair fibres by sensors (Cena, 1974; Mohler & Heath, 1988). Previously, Cena & Clark (1973) outlined important theoretical aspects of this technique for research on domestic and zoo animals, Yang & Yang (1992) reviewed biomedical and veterinary applications and Speakman & Ward (1998) gave an account of the principles of IRT and demonstrated its usefulness for studying thermoregulation. More recently, Kastberger & Stachl (2003) highlighted several interesting veterinary and physiological applications.

The aim of this review was to examine the value of thermal imaging for research on non-human mammals. In particular, this paper brings together findings from physiological, ecological and veterinary investigations to generate new ideas on how to use IRT to investigate wild mammal populations. This review is timely given recent advances in thermal imaging technology and a reduction in the cost of these devices, both of which will provide future research opportunities.

APPLICATIONS

For this review, a literature search was undertaken using ISI Web of Knowledge^{SM} (http://wok.mimas.ac.uk/). This was followed by compiling a reference list from each of these papers to include older studies that may not have been listed in current electronic databases and supplementing these with other known studies. This is therefore not an exhaustive list as this is a widely used technique, but it is likely to cover a large proportion of the main empirical studies to date. For the purposes of this review, studies on humans and closely related clinical applications were not considered.

Seventy-one empirical studies using IRT on mammals since 1968 (Tables 1–3) were examined. These studies involved domestic and wild mammals from 11 mammalian orders. Two-thirds of the studies involved terrestrial species and a third were on aquatic mammals, mostly marine species. These included 34 studies on thermal physiology (48%), 19 involving veterinary diagnosis of disease and injury (27%) and 18 population surveys (25%). Seventy per cent of studies were on captive mammals.

Thermal physiology

Infrared thermography has been used to examine many different aspects of thermoregulation (Table 1) and much of this work has focused on identifying parts of the body with relatively high temperature which can be related to an animal's anatomy and physiology. This has signaled that the head is a major source of heat loss for most species of mammals and also identified the importance of appendages in controlling heat loss. These studies demonstrate the clear link between surface temperature and underlying blood circulation and brown adipose tissue, as well as the role of fur in reducing heat loss from the skin surface. Many studies have examined the relationship between body surface temperature and air temperature. However, a novel approach with IRT has been to examine the relationship between environmental temperature and the sensitivity of vibrissal follicles in seals and dolphins (Dehnhardt, Mauck & Hyvärinen, 1998; Mauck, Eysel & Dehnhardt, 2000). These studies demonstrated that even in the cold, blood is circulated to these areas to maintain the function of these essential sensory organs.

A major strength of IRT is its ability to relate changes in surface temperature to particular physiological states or associated with certain behaviours such as huddling or vocalization. Recent studies have also shown that IRT is capable of detecting surface temperature changes in response not only to physical activity but also to fear. Particularly significant were the findings of Nakayama *et al.* (2005) which showed that changes in facial surface temperature patterns of Rhesus monkeys *Macaca mulatta* occurred in response to the threat of capture. IRT is particularly suited to examining changes in surface temperature during activities such as running, flying and even swimming. The latter application on marine mammals was an interesting applied study to examine the significance of changes in circulation associated with exercise in dolphins when chased and captured in the Pacific tuna fishery (Pabst *et al.*, 2002). This study found that dolphins increased their rate of heat dissipation from dorsal fins to the environment from the start of the chase. During prolonged chases, animals had higher skin surface temperatures, presumably as a result of greater blood flow to these areas.

Table 1. Thermo-physiology studies using IRT on captive (c) and wild (w) mammals showing measurements taken, distance (m) and imaging system used

Species			Measurement	Distance	Camera type	Author
Harp seal	*P. groenlandicus*	c	Exercise and heat loss	–	–	Ørtisland (1968)
Elephant and zebra	*L. africana, E. chapmani*	c	Colouration	5–15	Agavision 680	Cena & Clark (1973)
Polar bear	*U. maritimus*	c	Sites of heat loss	–	AGA Thermovision 720	Ørtisland *et al.* (1974)
Jackrabbit	*L. californicus*	c	Exercise and heat loss	–	AGA Thermovision 680-120B	Hill *et al.* (1976)
Harp seal	*P. groenlandicus*	w	Vasoconstriction/dilation	–	AGA 750 Thermovision	Blix *et al.* (1979)
Jackrabbit	*L. californicus*	c	Vascular patterns	–	AGA Thermovision 680-120B	Hill *et al.* (1980)
Raccoon dogs and blue foxes	*N. procyonoides, A. lagopus*	c	Thermoregulation and heat loss	–	AGA Thermovision 720	Korhonen & Harri (1986)
Rabbit	*O. cuniculus*	c	Thermoregulation of ear	–	Inframetrics 525	Mohler & Heath (1988)
Coypu	*M. coypus*	c	Insulation	–	Philips Medical	Doncaster *et al.* (1990)
Mongolian gerbil	*M. unguiculatus*	c	Responses to air temperature	0.5–1	Inframetrics 525	Klir *et al.* (1990)
Elephants	*L. africana, E. maximas*	c	Avenues of heat loss	–	AGEMA 728	Williams (1990)
Laboratory rat	*R. norvegicus*	c	BAT tissue and vocalization	–	Thermovision 870	Blumberg *et al.* (1992)
3 species foxes	*V. vulpes, A. lagopus, V. macrotis*	c	Sites of heat loss	0.5–15	Inframetrics 525	Klir & Heath (1992)
Long eared bats	*P. auritus*	c	Body temperature and energy savings	–	EEV P7000	Webb *et al.* (1993)
29 different species		c	Control of heat loss	–	Inframetrics	Phillips & Heath (1995)
Egyptian fruit bats	*R. aegyptiaeus*	c	Temperature changes during flight	<2	AGEMA Thermovision 880	Lancaster *et al.* (1997)
Harbour seal	*P. vitulina*	c	Vibrissae sensitivity	0.8	AGEMA Thermovision THV450D	Dehnhardt *et al.* (1998)
Bottlenose dolphin	*T. truncatus*	?	Circulation system in fluke	–	–	Williams *et al.* (1999)
Harbour seal & River dolphin	*P. vitulina, S. fluviatilis*	c	Sensory physiology	0.07–0.8	AGEMA 870	Mauck *et al.* (2000)
Field vole	*M. agrestis*	c	Non-shivering thermogenesis	0.5	AGEMA Thermovision 880	Jackson *et al.* (2001)
Woodchuck	*M. monax*	c	Temperature responses	–	Inframetrics 525	Phillips & Heath (2001)
Laboratory rats	*R. norvegicus*	c	Huddling	–	FLIR	Sokoloff & Blumberg (2001)
Bottlenose dolphin	*T. truncatus*	?	Superficial veins	–	AGEMA 570	Meagher *et al.* (2002)
Spinner and spotted dolphins	*S. attenuata, S. longirostrus orientalis*	w	Temperature effects of capture	–	AGEMA 570	Pabst *et al.* (2002)
3 seal species	*H. grypus, P. vitulina, P. groenlandicus*	c	Evaporation	0.5–2.5	AGEMA 870	Mauck *et al.* (2003)
Golden mantled ground squirrel	*S. lateralis*	c	Hypoxic metabolic response	–	Inframetrics 522	Tattersall & Milsom (2003)
Zebra	*E. quagga, E. zebra, E. grevyi*	c	Effect of solar radiation	–	Thermovision 695	Benesch & Hilsberg (2003)
Ground squirrel & marmot	*S. tridecimlineatus, M. flaviventris*	c	Hibernation	–	Inframetrics 525	Phillips & Heath (2004)
Greater mouse eared bat	*M. myotis*	w	Roosting behaviour and microclimate	2.5	Thermacam PM595	Sandel *et al.* (2004)
Dairy cattle	*B. taurus*	c	Climate effects on housing conditions	–	Thermotracer 6T62 NEC	Zähner *et al.* (2004)
Steller sea lion	*E. jubatus*	c	Sensor placement	–	Thermacam PM695	Willis *et al.* (2005)
Laboratory rat	*R. norvegicus*	c	Response to fear	0.7	TVS-100, Avio	Vianna & Carrive (2005)
Rhesus monkeys	*M. mulatta*	c	Assessment of emotional state	0.23	TH5100 NEC	Nakayama *et al.* (2005)
Laboratory rat	*R. norvegicus*	c	Inflammation and thermoregulation	–	Thermovision A20M	Almeida *et al.* (2006)
Grey seal	*H. grypus*	c	Effect of instrument attachment	1–3	Thermacam PM595	McCafferty *et al.* (2007)

IRT, infrared thermography.

Table 2. Veterinary studies using IRT on captive (c) and wild (w) mammals showing measurements taken, distance (m) and imaging system used

Species			Measurement	Distance	Camera type	Author
Horse	*E. caballus*	c	Clinical disorders	–	AGA Thermovision 680	Purohit & McCoy (1980)
Horse	*E. caballus*	c	Posture and anaesthesia	0.01	Mikron 25	Palmar (1981)
Horses	*E. caballus*	c	Podotrochlosis	–	Dynarad 209a	Turner *et al*. (1983)
Dairy cattle	*B. taurus*	c	Estrus detection	2.5	AGA Thermovision 750	Hurnik *et al*. (1985)
Bull	*B. taurus*	c	Scrotal disease	–	AGA IR system	Purohit *et al*. (1985)
Cattle	*B. taurus*	c	Effects of transportation	–	AGEMA 782	Schaefer *et al*. (1988)
Horse	*E. caballus*	c	Back pain	–	Insight Visions Systems	Colles *et al*. (1995)
Horse	*E. caballus*	c	Rug and whip damage	–	AGEMA 450	Holah (1995)
Cattle	*B. taurus*	c	Scrotal temperature	1	AGA Thermovision 782	Kastelic *et al*. (1996)
Cattle	*B. taurus*	c	Inflammation and branding	–	Thermovision 470	Schwartzkopf-Genswein & Stookey (1997)
Spanish Ibex	*C. pyrenaica*	w	Sarcoptic mange disease	39–221	Milcam	Arenas *et al*. (2002)
Wapiti	*C. elaphus canadensis*	c	Antler removal	–	Inframetrics 760	Cook & Schaefer (2002)
Horse	*E. caballus*	c	Injections and digital neurectomy	1.2	DTIS-500 Emerge Vision	Van Hoogmoed & Snyder (2002)
Dairy cattle	*B. taurus*	c	Barn management	3	AGA 570 DEMO	Knizkova *et al*. (2002)
Dairy cattle	*B. taurus*	c	Variation in udder temperature	2–2.5	Inframetrics 760	Berry *et al*. (2003)
Cattle	*B. taurus*	c	Infection detection	1.3	FLIR Inframetrics 760	Schaefer *et al*. (2004)
Dairy cattle	*B. taurus*	c	Climate and housing conditions	–	Thermotracer 6T62 NEC	Zahner *et al*. (2004)
Dairy cattle	*B. taurus*	c	Health and condition of hooves	1.5–2.0	FLIR Inframetrerics 760	Nikkhah *et al*. (2005)
Holstein heifers	*B. taurus*	c	Tail docking and pain	–	eMerge, Sebastian FL	Eicher *et al*. (2006)

IRT, infrared thermography.

Table 3. Mammal surveys using IRT on captive (c) and wild (w) mammals showing measurements taken, distance (m) and imaging system used

Species			Measurement	Distance	Camera type	Author
White-tailed deer	*O. virginianus*	w	Population counts	300	Classified	Croon *et al*. (1968)
White-tailed deer	*O. virginianus*	w	Population counts	300	Classified	McCullough *et al*. (1969)
Polar bear	*U. maritimus*	w	Detection & counts	150	Test	Brooks (1972)
White-tailed deer	*O. virginianus*	w	Population census	300	Test equipment	Graves *et al*. (1972)
Ringed seal	*P. hispida*	w	Snow lairs	180	FLIR 1000 A	Kingsley *et al*. (1990)
Walrus	*O. rosmarus divergens*	w	Numbers & group size	400–2400	DFORS	Barber *et al*. (1991)
Whales	5 species	w	Counts and temperature	10–70	AGEMA Thermovision 880	Cuyler *et al*. (1992)
Ringed seal	*P. hispida*	w	Snow lairs	30	Inframetric 600	Sipilä & Kurlin (1992)
White-tailed deer	*O. virginianus*	w, c	Population census	170–450	FLIR 2000G	Wiggers & Beckerman (1993)
Squirrels, hares & mice	4 species	w	Detection of animals, nests and burrows	2–40	Thermovision 210, Inframetrics 5226	Boonstra *et al*. (1994)
Gray bats	*M. grisescens*	w	Population estimates	–	AGEMA 782	Sabol & Hudson (1995)
Grey whale	*E. robustus*	w	Migration counts	2000	AN/KAS-1 A (US Navy)	Perryman *et al*. (1999)
Manatee	*T. manatus latirostris*	c	Detection	–	PalmIR Pro Raytheon	Keith (2002)
Harbour seal	*P. vitulina*	w	Population counts	3000	–	Duck & Thompson (2003)
Polar bear	*U. maritimus*	w	Den Surveys	61–244	FLIR Safire AN/AAQ-22	York *et al*. (2004)
Deer	*O. virginianus*	w	Detection to aid capture	max 72	PalmIR 250 Raytheon	Ditchkoff *et al*. (2005)
Walrus	*O. rosmarus divergens*	w	Group size and counts	800–3200	Airborne Multispectral Scanner	Burn *et al*. (2006)
Deer	*O. virginianus* *O. hemionus*	w	Detection to aid capture	15–50	PalmIR 250 Raytheon	Butler *et al*. (2006)

IRT, infrared thermography.

Thermal imaging is also a useful tool for refining research methods, for example as a guide for the placement of heat flux sensors to study metabolic heat production of Steller sea lions *Eumetopias jubatus* (Willis *et al*., 2005) and to determine the effects of attaching bio-logging devices to the pelage of grey seals *Halichoerus grypus* (McCafferty, Currie & Sparling, 2007).

Veterinary diagnosis of disease and injury

Infrared thermography has largely been a diagnostic tool in veterinary science in combination with other indicators of disease. A major application of this technique has been to diagnose injury and disease in horses and there have been several useful studies detailing factors influencing normal temperature distributions and outlining appropriate measurement protocols (see review by Eddy *et al*., 2001). Abnormal or asymmetrical temperature distributions have been used as indicators of underlying problems with blood circulation or inflammatory responses (Table 2).

The non-invasive nature of IRT makes it particularly suited for studying farm animal welfare (see review by Stewart *et al*., 2005). Studies have examined the extent and duration of inflammation observed on branding sites, effects of antler removal, changes in the thermal status of cattle during transportation, detecting hoof disorders and rises in body temperatures due to infection. An interesting veterinary application has been to detect estrus in cows by examining temperature distribution of the gluteal region. In this case, IRT was more effective than experienced dairy staff in detecting estrus in early stages but was less accurate in later postpartum due to a greater number of false positives (Hurnik, Webster & DeBoer, 1985).

Thermal imaging on captive species other than horses and cattle is less common, although Kouba & Willard (2005) reported anecdotally how IRT was being used to monitor a range of illnesses in zoo species. One of the first attempts to use IRT to detect disease in a wild mammal population was undertaken to diagnose sarcoptic mange in wild Spanish ibex *Capra pyrenaica*. Unfortunately, this was found to be not as affective as visual observation due to the limitations of the thermal imaging system used for distances greater than 100 m (Arenas *et al*., 2002).

Population surveys

A variety of thermal imaging devices have been used from aircraft or road vehicles to detect and/or count large mammals (Table 3). This application does not require precise temperature measurements but simply detects individuals or dens by a warm signal against a cool background. IRT has been used in this way for counts of deer and pinnipeds. Thermal imaging has also been able to detect the blows of large whales. For example, a remotely operated thermal imaging system from a shore based station was used to count Pacific grey whales *Eschrichtius robustus* over a period of a month and across three years. Numbers of whales were detected from their blows and showed that migration rates were greater during the night than throughout the day (Perryman *et al*., 1999). Although IRT was also found to be effective in detecting relatively small mammals, transect surveys on foot with handheld infrared cameras have been less commonly used in the past, most probably limited by the relatively large size of imaging systems. More recently, counts of grey bats *Myotis grisescens* using IRT have produced colony estimates similar to those counted visually and have opened up possibilities of using automated systems for monitoring purposes (Sabol & Hudson, 1995).

These studies demonstrate the usefulness of using thermal imaging to survey remote geographical areas. Similar to conventional aerial photography, thermal imaging from aircraft can be hindered by cloud cover since infrared radiation is absorbed by water vapour. The success of the technique relies on a relatively large temperature difference between the study animal and the ground surface. This is dependent on the temperature of the ground surface and the insulation properties of the animal. Surveys using IRT are therefore often undertaken at night when the thermal contrast between animal and background is greatest. Animals living in open habitats such as coastal areas or areas with sparse vegetation are suited to aerial survey methods compared to forest dwelling species. The usefulness for population monitoring relies on being able to ground-truth thermal imaging counts with visual counts and to choose periods of the day or season of the year when animals can be most easily detected.

INTERPRETATION OF THERMAL IMAGES

For some applications, such as population counts, accurate temperature measurements of detected animals are not required. However, for the study of thermal physiology and energetics, the infrared radiation detected by the equipment must be converted to an accurate estimate of surface temperature. Infrared radiation emitted by bare-skinned animals is governed by the skin surface temperature but the radiation emitted from most mammals may originate either from the skin, if this is incompletely obscured by hairs, or from the hairs themselves. The radiating surfaces of the hairs are at a range of temperatures determined by the temperature gradient between the skin and the coat surface. The exchange of radiation may be further complicated by external fluxes that contribute to the heat balance of the hairs. For an animal with thick fur, the surface temperature measured by IRT is typically several millimeters beneath the physical surface of the coat. The equilibrium temperature of this surface is determined by the loss of heat from radiation and convection to the surroundings, the conduction of heat through the coat and the exchange of thermal and short wave radiation (Cena, 1974). The radiative environment in which measurements are carried out is therefore important because of its influence on coat temperature. It has been clearly shown that different coloured coats influence solar heating at the surface, with black areas of a coat having greater surface temperatures than white areas in strong sunshine (Cena & Clark, 1973; Benesch & Hilsberg, 2003). This is clearly seen in infrared images of zebras that show black stripes to be more than 10 °C warmer than white strips in full sun (Fig. 1). The temperature pattern does not reflect underlying circulation or large differences in emissivity as the temperature pattern almost disappears after a few minutes in the shade (Fig. 2). Even where solar radiation is excluded care should be taken to use enclosures that have wall temperatures close to air temperature to avoid additional radiative heating and avoid small enclosures that reflect significant amounts of thermal radiation from the animal.

Surprisingly, there have been relatively few comparisons between IRT and solid temperature probes. In a study of a rabbit pinna, Mohler & Heath (1988) showed that although thermocouple measurements gave the same trends in surface temperature, thermocouples consistently recorded higher temperatures when the pinna was vasodilated and recorded lower temperatures when vasoconstricted. The added value of IRT is its ability to measure easily the spatial variation in surface temperature and therefore produce more accurate temperature records of whole body regions.

The surface temperature of a mammal will not only be influenced by its skin temperature but by the thickness, density and quality of hair covering different parts of the body and this may differ between individuals and vary due to seasonal moult. Some veterinary studies on horses have controlled for this by shaving small sections of hair from limbs in order to determine the temperature of the underlying skin surface (Holah, 1995). This is not feasible or indeed desirable for most investigations. Studies should therefore take into account these sources of variation most easily by following the same individual throughout experiments or by sampling a large group of individuals to account for this variation.

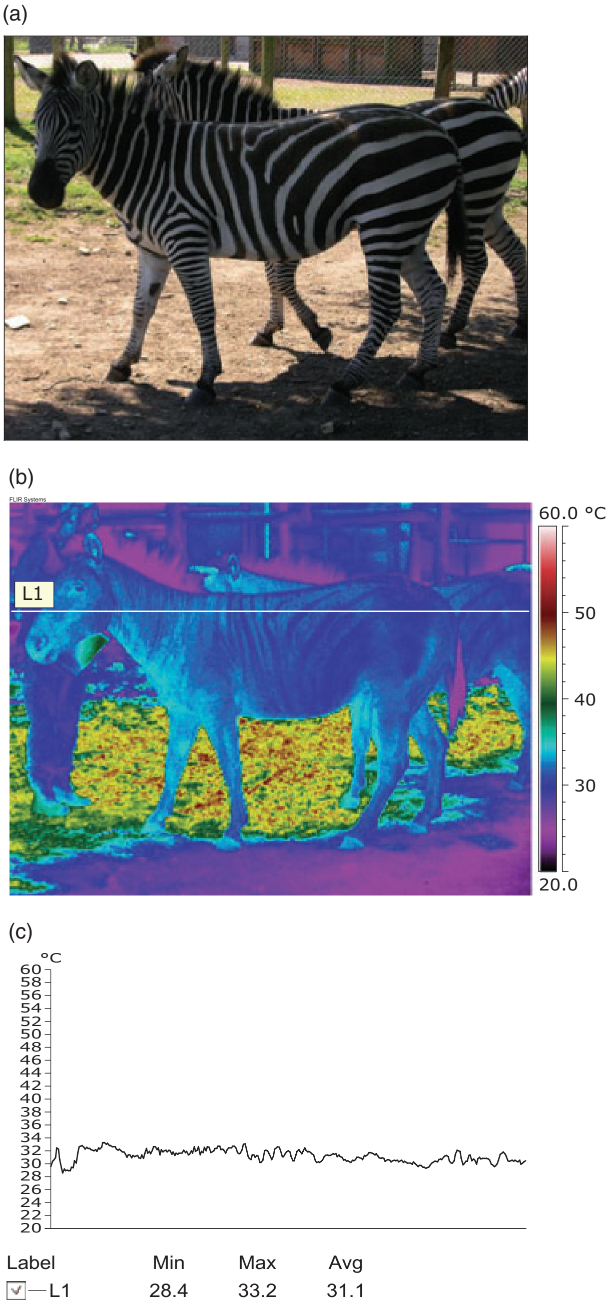

Fig. 2. Photograph (a) of Grant's zebra with corresponding infrared image (b) after 5–10 min in the shade of a tree. The temperature profile L1 displayed in the graph below (c) shows the variation in temperature across the body, with black stripes on average less than 2 °C warmer than white striped areas of the coat. Mean air temperature = 27.4 °C, relative humidity = 45%, wind speed = 0.6 ms^{-1} and solar radiation was not recorded.

In order to obtain accurate surface temperature measurements a surface emissivity value is a required parameter for infrared imaging systems. Bare skin has an emissivity of 0.98 and the emissivity of dry fur is relatively uniform in mammals, in the range 0.98–1.0 (Monteith & Unsworth, 1990). The emissivity of the coat can also be changed by dirt or other materials (e.g. soil = 0.93–0.96 or water = 0.96, Campbell & Norman, 1998). This can be easily addressed with captive animals by brushing or cleaning coats prior to measurement. Since radiative heat transfer scales linearly with emissivity and as surface temperature scales to the

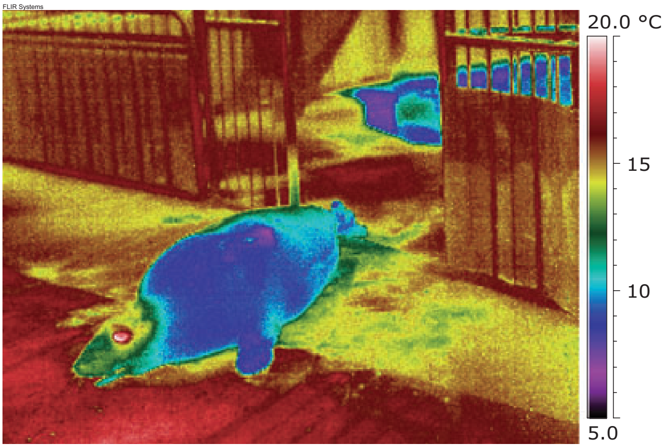

Fig. 3. Infrared image of female adult grey seal recently hauled out from a seawater pool (background) in captivity. Note that most of body is at uniform surface temperature corresponding to the temperature of seawater. The head is warmer than the body trunk as the seal held its head above water prior to leaving the pool. A small temperature logger for recording stomach temperature is also visible on the centre of the back. Air temperature = 16.2 °C.

power of four, these small differences in emissivity can be shown by calculation to account for less than 0.5 °C difference at typical mammalian coat temperatures. In this case, computer software for image analysis can be useful in providing error analysis by simply changing the emissivity of different regions. Alternatively, the temperature of fur with and without dirt/water can be measured to exclude this source of variation.

Temperature errors associated with alterations in the emissivity of a wet coat are small in comparison to changes in coat temperature due to evaporative cooling. This is pertinent for studies on aquatic mammals or animals wet by precipitation in natural conditions. Wetting leads to an apparent uniformity in surface temperature due to the retention of water in the coat. In addition, the greater thermal conductivity of water means that heat may be rapidly conducted from warm parts of the body, particularly as aquatic mammals are seen to leave the water. Both these factors may obscure the variation in underlying skin temperature. This can be seen in an image of an adult grey seal recently hauled out from a seawater pool in captivity, where the temperature of the body corresponds to the temperature of seawater trapped in the fur (Fig. 3). Care should be taken therefore to ensure that animals are kept dry or in the case of aquatic mammals, the period of time out of water is standardized. The influence of wetting may therefore be problematic for studies in the field when accurate temperature measurements are required. One way to correct for this would be to first determine rates of drying from animals in captivity (Mauck *et al.*, 2003) or to use heat transfer models in the laboratory to determine the relationship between surface temperature and wetting (e.g. McArthur & Ousey, 1994).

Wet environments are not usually a problem for most IR imaging systems because of the environmental protection/waterproofing of these devices to high industrial standards. However, water on the lens due to rain or spray is a potential difficulty for accurate temperature measurements in the field. Pabst *et al.* (2002) took images from a boat and therefore covered the lens with polyethylene film and recalibrated the temperature measurements. Similarly, Tattersall & Milsom (2003) took images through a polyethylene 'window' to take images of animals in a metabolic chamber. This is possible over a limited range of temperatures, typical in animal studies but it should be remembered that this additional coating will alter the spectral sensitivity of the device.

The detection of radiation by infrared cameras means that curved surfaces are subject to detection errors compared to flat surfaces. This gives rise to a cool edge effect seen on many images of animals. For a surface with emissivity of 0.98, the associated temperature error has been shown to be independent of viewing angle up to about 30° but increased from 0.5 to 3 °C at 30–70° and was greater than 4 °C at angles above 70° (Watmough, Fowler & Oliver, 1970; Clark, 1976). If necessary, this can be overcome using a composite image produced from several images taken from different positions.

FUTURE DIRECTIONS

Developments in technology have meant that infrared imaging devices are now the size of conventional video cameras or smaller and it is relatively easy to capture and store high-resolution thermal images in single image or video format. In the past, IR imaging systems relied on liquid nitrogen cooled detectors that made field studies difficult. Imaging systems nowadays have electronically cooled detectors allowing them to be easily used in remote areas. Custom written software is also available that allows rapid image analysis and summary statistics. Lower cost devices <£10k compared with more advanced systems costing £30–40k with similar temperature resolution (±0.1 °C) are now becoming available and therefore there are future opportunities for using IRT in mammal research.

The non-invasive nature of this technique will continue to provide the basis of future applications and previous studies show that IRT can be used to answer many interesting research questions. Unique opportunities now exist to examine thermoregulation of wild mammals in natural conditions. By combining measurements of surface body temperature with measurements of internal body temperature using implanted temperature loggers or other physiological parameters such as heart rate (e.g. Butler *et al.*, 1995), we will more fully understand thermal responses of animals to a range of environmental conditions. Bakken *et al.* (2005) have shown in birds that by removing a very small section of plumage to reveal the skin temperature, cloacal temperature could be estimated to within 1 °C. Although this is subject to some error, it does provide a method of estimating internal body temperature without the need for internal temperature loggers that has not often been considered in IRT applications with mammals. Preliminary reports also suggest that eye temperature recorded by IRT can be used to determine rectal and vaginal measurements in domestic animals (Sykes *et al.*, 2006; Willard, Vinson & Godfrey, 2006). If this method can be substantiated further, then it may provide opportunities of monitoring internal temperature non-invasively in captive experiments and field studies.

Previous studies have used surface temperature measurements to determine rates of heat loss and thereby estimate metabolic heat production (e.g. Williams, 1990). As yet, there has been no evaluation of how accurate these estimates are likely to be for domestic or free ranging mammals. IRT together with indirect calorimetry could validate heat transfer models that estimate metabolic costs of mammals. This has indeed been successfully carried out on captive birds where the metabolic power of flight determined by heat transfer modelling agreed with measurements using doubly labelled water and mask respirometry (Ward *et al.*, 1999, 2004). Surprisingly, there have been relatively few IRT studies examining changes in surface temperature during exercise in mammals. Surface temperatures could parameterise biophysical models of heat loss that investigate how exercise metabolism compensates for thermoregulatory costs and determine energy costs associated with locomotion or foraging behaviour. However, it should be remembered that although IRT can be used to derive reasonable estimates of heat loss by convection and radiation from the surface of animals, heat losses through respired gases (particularly by latent heat loss) must also be considered in order to estimate total heat loss from the organism.

The absolute accuracy of metabolic rate derived from IRT measurements may be relatively uncertain unless cross-calibration is made with existing metabolic methods as described above for birds. However, IRT is of great value in determining relative estimates of metabolic rate, particularly where natural behaviour does not occur in small metabolic chambers. Ward & Slater (2005) used this approach to estimate the increased metabolic cost of bird song by comparing heat loss between singing and non-singing birds in captivity. This approach could also be used to derive relative energy costs of a wide range of behaviours in the wild.

It is likely that IRT will continue to be a useful tool for the diagnosis of disease and injury in domestic and zoo animals, used in conjunction with existing veterinary procedures (Head & Dyson, 2001; Webbon, 2002). The development of small handheld instruments might soon allow these to be standard pieces of equipment for vets. Given concerns about infectious diseases among farm animals or within wild animal populations, IRT will be useful for early detection of disease, if further clinical trials can be undertaken. This may be achieved by remote monitoring systems such as those outlined by Stewart *et al.* (2005) that are recording the eye temperature of cattle with an automated system. The requirement of studies such as these will be to demonstrate convincingly that surface temperatures strongly correlate with the occurrence of infection. One of the most exciting opportunities in this area will be to extend veterinary applications of thermal imaging to study the health of wild mammal populations. Although an earlier attempt to diagnose disease in wild mammals with IRT was unsuccessful because of the distances involved (Arenas *et al.*, 2002), this may not apply in all cases and more appropriate choice of camera lenses may make distance work feasible.

The use of IRT for population monitoring is likely to be limited as much by the cost of aircraft or ship time as it is by the cost of imaging systems. However, surveys on foot or by vehicle will be easier with the highly portable imaging systems. IR imaging systems are likely to be particularly useful for monitoring nocturnal species. There is already considerable interest in using IRT to monitor large colonies of bats (Sabol & Hudson, 1995; Hristov, Betke & Kunz, 2005; Reichard, Frank & Kunz, 2005). For this purpose, automated image recognition systems provide the opportunity to monitor large colonies, not easily undertaken using traditional methods.

CONCLUSION

Infrared thermography has been successfully used in studies of thermal physiology, disease and population monitoring of captive and wild mammals since the 1960s. Its main advantage is that it is a non-invasive technique for measuring radiative surface temperature and therefore it can be either used to infer underlying circulation that is related to physiology, behaviour and disease or simply to detect a warm body against a cool background. The major limitation of this technique is that radiative surface temperature is also influenced by solar radiation, wetting and evaporation. For accurate temperature measurements in the field, it is therefore best suited for studies at night or in situations where animals experience low solar irradiances. Where environmental conditions prevent accurate temperature measurement comparative studies can still be undertaken provided conditions are equivalent between groups. For studies in captivity, experimental design should also consider the radiative environment of housing where measurements are made and also how underlying physiological responses and disease may influence surface temperature patterns. Nevertheless, if these factors are taken into account, the increased portability and reduced cost of IR imaging systems provide further opportunities for a range of studies that wish to measure surface temperature or detect animals non-invasively.

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