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Title: Metabolic heat loss in southern elephant seals (*Mirounga leonina*) differs with stage of moult and between habitats

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Highlights

- Metabolic heat loss in moulting southern elephant seals differed between terrestrial habitats.
- Greatest heat loss was in beach habitat during the late moult.
- Heat loss was lower in wallow and lower still in vegetation habitats.
- Body condition and skin temperature both decreased at the end of the moult.

Abstract

The moult in southern elephant seals (*Mirounga leonina*) represents an especially energetically demanding period during which seals must maintain high skin temperature to facilitate complete replacement of body fur and upper dermis. In this study, heat flux from the body surface was measured on 18 moulting southern elephant seals to estimate metabolic heat loss in three different habitats (beach, wallow and vegetation). Temperature data loggers were also deployed on 10 southern elephant seals to monitor skin surface temperature. On average, heat loss of animals on the beach was greater than in wallows or vegetation, and greater in wallows than in vegetation. Heat loss across all habitats during the moult equated to 1.8 x resting metabolic rate (RMR). The greatest heat loss of animals was recorded in the beach habitat during the late moult, that represented 2.3 x RMR. Mass loss was 3.6 ± 0.3 kg day^{-1}, resulting in changes in body condition as the moult progressed. As body condition declined, skin surface temperature also decreased, suggesting that as animals approached the end of the moult blood flow to the skin surface was no longer required for hair growth.

Keywords

Mirounga leonina, marine mammals, pinnipeds, heat loss, skin temperature, moult, thermoregulation

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1. Introduction

The annual moult in phocid seals represents a distinct, energetically demanding period during which animals spend an increased amount of time on land as they shed and renew their entire coat (Hindell and Burton 1988; Thompson et al. 1989; Boyd et al. 1993). Conditions for the proliferation of hair follicles and skin cells during this time are optimised by increasing skin surface temperature closer to core body temperature (Feltz and Fay 1966; Paterson et al. 2012). This is achieved by increasing perfusion of blood at the skin surface (Khamas et al. 2012). Thermal conduction in water is 25 times that in air (Nadel 1984) meaning that increasing skin surface temperature while at sea would result in a physiologically unsustainable heat loss (Boily 1995; Watts 1996). High skin temperature with minimal heat loss is therefore most efficiently achieved while animals are on land. For some seal species, moulting involves a diffuse process lasting several weeks with intermittent trips to sea, such as for the grey seal (*Halichoerus grypus*) (Boily, 1996) and the harbour seal (*Phoca vitulina*) (Ashwell-Erickson et al., 1986). In these species, moulting is visually apparent during a four-week period (Thompson and Rothery 1987). However, the underlying process of hair follicle regrowth, which is much less conspicuous, may be evident for a period of up to 12 weeks (Ashwell-Erickson et al. 1986). This is also the case for moulting southern elephant seals (*Mirounga leonina*) that have active hair follicles for approximately 12 weeks (Ling, 2012). For species such as the northern elephant seal (*Mirounga angustirostris*) and the southern elephant seal that undergo a catastrophic moult, hair and the upper dermis are shed together over a period of 25-32 days with the most shedding of skin and hair taking place on land (Worthy et al. 1992; Boyd et al. 1993).

The behavioural adaptation of spending more time on land during the moult allows phocid seals to overcome the thermoregulatory constraints of moulting in an aquatic environment (Boily 1996; Watts 1996). However, for species found in more extreme climatic conditions at higher latitudes, further behavioural adaptations may be necessary to minimise heat loss. In Antarctic and sub-Antarctic regions southern elephant seals that come ashore to moult initially search for muddy pools or wallows (Boyd et al. 1993; Chaise et al. 2017) where they often aggregate in tight groups (Riedman 1990; Cruwys and Davis 1995). This behaviour may serve to minimise the amount of skin surface area exposed to the air by either being in contact with other animals or being partially covered in mud warmed by body heat from large groups of seals. Huddling is an adaptive response seen in many species of birds and mammals (Canals et al. 1997; Ostner 2002; Gilbert et al., 2010) that minimises metabolic costs of thermoregulation (Gilbert et al. 2010). If moulting southern elephant seals elevate skin temperature as is seen in other phocid species (Paterson et al. 2012) then huddling in wallows may help to conserve heat when actively perfusing the skin with blood. The final stage of the moult process in southern elephant seals is characterised by animals remaining on land but moving out of wallows and closer to shore (Boyd et al. 1993; Chaise et al. 2017). Choice of habitat and stage of moult are therefore important factors when considering the environmental conditions affecting the moult in southern elephant seals.

Several studies have relied on theoretical heat flux models to estimate heat loss from phocid seals while hauled out (Boily 1995; Harding et al. 2005). However, these models can significantly overestimate or underestimate heat transfer rates (Kvadsheim et al. 1997; Boily et al. 2000, respectively). More accurate estimates are achieved when theoretical models are validated with concurrent recordings of metabolic rate (Kvadsheim and Folkow 1997; Kvadsheim et al. 1997) or by measuring heat flux directly (Kvadsheim and Folkow 1997; Hindle et al. 2015). Direct measurements of heat flux in phocid seals have quantified how heat is differentially lost from parts of the body in contact with the ground (Mellish et al. 2015) and in air (Hindle et al. 2015). Meteorological conditions and substrate temperature can then be used to explain changes in heat transfer of animals.

Direct measurement of heat loss in moulting seals in the wild has rarely been successful (though see Walcott et al. 2020) due to the difficulties of gluing devices to hair that is being shed or that is newly grown and too weak to support device attachment. New research is required to determine heat loss of moulting phocid seals to be able to estimate the energetic cost of the moult associated with thermoregulation and choice of habitat when hauling out. An increased metabolic rate during the moult has been demonstrated in previous studies on pinnipeds (Slip et al. 1992; Boyd et al. 1993; Paterson et al. 2012; Paterson et al. 2021). This increased energetic demand is compounded by the fact that animals fast on land (Slip et al. 1992; Hindell et al. 1994). As a result, body condition decreases as blubber reserves become depleted during the moult (Hindell et al. 1994; Carlini et al. 2005; Postma et al. 2013). Meteorological conditions and choice of habitat that increase heat loss from animals to the ground and air will increase energy costs as a greater metabolic rate will be required to maintain high skin temperatures necessary for hair and skin growth.

The aim of this study was to determine the energetic cost of a catastrophic moult in southern elephant seals and how this may be influenced by terrestrial habitat and climate. Measurements of heat flux and body surface temperature were used to determine the extent to which environmental drivers such as habitat and meteorological conditions influenced the energetic cost of moult in this species. Furthermore, because the moult fast decreases body condition which may compromise their ability to thermoregulate, we investigated how body surface temperature varied with body condition.

2. Materials and methods

2.1. Study animals

Southern elephant seals were captured during the early part of the moult, shortly after they arrived onshore and as they moved away from the beach passing through vegetation en route to wallows. Where recaptures were possible in the latter part of the moult, animals were captured either while still in wallows or when they had moved back to the beach before departure to sea. A total of 18 adult females, 4 sub-adult females and 1 sub-adult male southern elephant seals were sampled between 14/01/2014 and 26/02/2016 at Point Suzanne, Kerguelen Islands (49°26'S, 70°26'E) during this study. Animals were anaesthetised with a 1:1 combination of Tiletamine and Zolazepam (Zoletil® 100), either administered intramuscularly with a blow dart at a dose rate of 1ml/100kg or intravenously at a dose rate of 0.5ml/100kg (Baker et al. 1990). Moult stage of each individual was estimated at capture and recapture based on the percentage area of the body over which old skin and hair had been shed and new hair was growing through (Chaise et al. 2019). Upon capture at early moult when 20-60% of old skin and hair had been shed, and recapture at late moult when 90-100% of shedding was complete, individuals were weighed (± 0.5kg) using a tripod and scales (HST Mini-Weigher, HST Scales, Milton Keynes, UK). Linear measurements of body length (± 1.0cm) from nose to tail were also taken while animals were in ventral recumbency (Table 1).

Southern elephant seal work (Program IPEV 1037 HENERGES) was approved by The Antarctic Committee for Environmental Protection and the Ethics Committee (Cometh ANSES/ENVA/UPEC n°16: n°14-055 and n°15-061). The program was also authorised by the French Southern and Antarctic Lands

(Decree 2014-131, 15th October 2014; Decree 2015-110, 4th September 2015). All applicable international, national and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

2.2. Heat flux measurements

Heat flux (Wm^{-2}) from the body of animals to the surrounding environment was measured while animals were under anaesthesia, using heat flux discs (HFP01, Huxseflux Thermal Sensors B. V., Delft, Netherlands) with data recorded to a logger (SQ2010, Omni Instruments Ltd., Dundee, UK). Heat flux measurements were taken while animals were in a ventral recumbency position. To measure heat flux from the body surface to air, a heat flux disc was placed on the dorsal midline posterior to the axial line between the fore flippers. A second heat flux disc was also placed posterior to the axial line but on the ventral surface measuring heat flux to the ground (Fig. 1). Data were recorded at a sampling interval of once every minute.

Animals were captured in three different types of habitat to determine differences in heat flux dependent on substrate. The three main substrate types found at the Point Suzanne study site are; "vegetation" composed of plant species *Azorella selago*, *Acaena magellanica* and *Taraxacum officinale* (Chapuis et al. 2004), "beach" composed of basalt pebbles (Nicolaysen et al. 2000) and "wallows" that are normally characterised as depressions in the land in which aggregations of seals create wet, muddy conditions. It should be noted that animals captured in the present study had to be isolated from groups in order to be able to take measurements safely. This included those in wallows which resulted in heat flux measurements being taken of isolated animals, usually at the edge of wallows, rather than in the centre. Effects of heat flux to other animals while huddling and heat flux affected by large areas of the body covered in mud were therefore not possible. However, the substrate type and ground temperature differences at the edge of wallows was sufficiently different from vegetation and beach habitats to make valid comparisons (Chaise et al. 2019).

2.3. Conversion of heat flux measurements to whole body heat loss

To extrapolate measurements of heat flux taken on the dorsal and ventral surfaces to the whole body required a measure of the total body surface area of animals. Previously, this has been done by predicting maximal surface area based on mass, according to the allometric equation developed for phocid seals by Innes et al. (1990): $\log A = \log 0.14 + 0.51 * \log m$ where A is body surface area (m^2) and m is the mass (kg) of the animal. This allometric relationship was based on post-mortem measures of surface area of 56 skins removed from individuals of five different seal species including harbour seals, harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), ringed seals (*Pusa hispida*) and grey seals.

A photogrammetry method was developed to test whether the previous equation held true for southern elephant seals by creating fully scaled 3D models using the software package AutoDesk® Photo Recap™. 3D photogrammetric generation of volumetric estimates for southern elephant seals has been previously used and validated by de Bruyn et al. (2009) and in a variety of large mammal species by Bester and de Bruyn (2015). More recently, McKnight et al. (2017) conducted a calibration study to quantify the volumetric estimate error of 3D photogrammetry models of grey seals, showing high levels of accuracy of within 4% of actual volume. To create 3D models, the photo-capture technique used and validated by McKnight et al. (2017) was used. A series of approximately 40 photographs were taken at different angles around the circumference of animals while they were anaesthetised. Accurate 3D models of animals were then generated and scaled using nose to tail length measurements taken during captures. Fig. 2 shows examples of 3D models generated for animals in each of the three habitats; vegetation, beach and wallow.

Previous theoretical heat flux studies have assumed that 20% of the body surface of pinnipeds was in contact with the substrate (Luecke et al. 1975; Paterson et al. 2012) and the remaining 80% exposed to the surrounding environment. The 3D models were used to calculate the amount of model mesh, and therefore area of the body, that was in contact with the air and with the ground. Heat flux (Wm^{-2}) measurements taken on the ventral and dorsal side of animals were extrapolated over the area of skin in contact with the air and the ground and weighted accordingly to give an overall estimate of whole-body heat loss (W). For animals that had no photogrammetry taken, 3D models could not be created. In these cases, the proportion of surface area in contact with the ground was assumed to be the mean of the proportions calculated for all animals with photogrammetry measurements.

2.4. Body surface temperature measurements

Body surface temperature between the time of capture and recapture were recorded (± 0.5°C) using miniaturised temperature loggers (iButton® DS1922L-F5, Maxim Integrated, San Jose, USA). In 2014 and 2015, average temperature was sampled at an interval of 10 minutes. However, in 2016 this was increased to a one minute interval. This type of logger was chosen due to its small size (diameter = 17.4mm, thickness = 5.9mm, weight = 3g) and its reliable use in a range of other studies (McCafferty et al. 2015). Each logger was located over newly grown hair on either flank, dorsal to the fore flipper and held in place by covering with a fine nylon mesh and a layer of two-part epoxy (Araldite® AW 2101, Huntsman International LLC, Texas, USA) (Fig. 3).

2.5. Environmental measurements

Environmental conditions were recorded within one metre of animals during captures. Air temperature (± 0.1°C), ground temperature (± 0.1°C), relative humidity (± 1%), wind speed (± 0.1ms-$^{-1}$) and solar radiation (Wm^{-2} error ± 5%) were all measured using handheld instruments (Kestrel 3000 Pocket Weather Meter, Kestrel Instruments, Pennsylvania, USA; Pyranometer SKS111, Skye Instruments Ltd., Llandrindon Wells, UK). Measurements were taken at the beginning and end of captures with the average of those two values being used.

Additionally, a weather station recorded environmental conditions (air temperature (± 0.1°C), relative humidity (± 1%), wind speed (± 0.1ms^{-1}) and solar radiation (Wm^{-2} error ± 5%)) every 30 minutes. Rainfall (mm error <6%) was recorded as the total every 30 minutes. These environmental conditions were logged using an automatic weather station (Minimet, Skye Instruments Ltd., Powys, UK) in a fixed location with study animals being captured within a 350m radius around this location.

All means reported in the results below are given as ± SE.

2.6. Statistical analyses

2.6.1. 3D models and predictions of surface area

The 3D models generated for animals caught in 2016 were used to estimate total body surface area. A multiple linear regression model was then used to predict total body surface area (m^2) as a function of mass (kg), length (cm) and girth (cm). Predictions allowed for estimation of total body surface area for all animal captures in each year and not just those for which photogrammetry data were collected. Results were compared to predictions of surface area derived from Equation 1 developed by Innes et al. (1990) which relied solely on mass as the predictor. All dependent and explanatory variables were log-transformed for multiple regression analyses. The full model used for selection was therefore log (surface area) ~ log (mass) + log (length) + log (girth) with all variables being treated as continuous. Model selection was performed in a step-wise backwards selection process dropping non-significant explanatory variables as appropriate. The final model could then be used to predict total surface area while accounting for variation in morphometrics. Table 1 summarises captures during which photogrammetry images were taken that were then developed into 3D models.

2.6.2. Heat loss

Whole body heat loss (W) was converted to kcal/day. This allowed for comparisons with estimations of resting metabolic rate based on mass according to Kleiber (1932): $RMR = 70 * M^{0.75}$ where RMR is resting metabolic rate in kcal day^{-1} and M is mass (kg). Estimations of metabolic rate were expressed as a multiple of resting metabolic rate (RMR multiplier), defined as dividing whole body heat loss (kcal day^{-1}) based on measurements by predictions of RMR (kcal day^{-1}) from Kleiber's equation. In this definition, Kleiber's prediction is referred to as 1 x Kleiber.

Analysis of co-variance (ANCOVA) was used to determine differences in the continuous response variable, RMR multiplier, dependent on habitat consisting of three levels; vegetation, wallow and beach. A post-hoc Tukey's test was used to make pairwise comparisons of RMR multiplier across the three habitats. To reduce the number of explanatory variables used, air temperature and wind speed were combined to create the variable windchill, defined by the equation: windchill = 13.12+(0.6215*Ta)-11.37*($v^{0.16}$)+(0.3965*Ta*$v^{0.16}$) where Ta is air temperature (°C) and v is wind speed (km h^{-1}) (Environment and Climate Change Canada, Government of Canada; NOAA's National Weather Service, USA). The environmental variables included as covariates were therefore windchill, ground temperature, relative humidity and solar radiation. Time since initiation of general anaesthesia (minutes) was also included as a continuous covariate to determine how changes in body temperature associated with anaesthesia may have influenced recorded heat flux. Moult stage at capture during early moult (20-60% of old skin and hair shed) and recapture at late moult (90-100% of old skin and hair shed) was treated as a two-level factor. The full model before selection was RMR multiplier ~ habitat type + windchill + ground temperature + relative humidity + solar radiation + time since anaesthesia + moult stage. ANCOVA model selection was performed in a step-wise backwards selection process dropping non-significant explanatory variables as appropriate.

2.6.3. Body surface temperature

Changes in body surface temperature (response variable) dependent on body condition were modelled using a Generalised Additive Model (GAM) approach from the mgcv library (Wood 2004). In this case, a proxy for body condition was used which was body mass index (BMI = mass (kg)/length^2 (m)). This index was chosen for consistency with a previous study of habitat use and movements of the same study animals (Chaise et al. 2018). Calculations of BMI between captures assumed that mass changed linearly between measurements at capture and recapture. In the full GAM model, body surface temperature was fitted as a smooth (thin plate regression spline) over values of BMI. Pre-screening of the measured environmental variables showed that air temperature and solar radiation were correlated (Pearson, $r=0.55$, $p<0.001$). Air temperature was therefore used and solar radiation was excluded from the analysis. To further reduce the number of explanatory variables, air temperature and wind speed were combined to create the smoothed variable windchill (as above). Rainfall was included as a continuous explanatory variable and relative humidity as a smoothed explanatory variable. Moult stage was included as a continuous explanatory variable which was estimated at capture and recapture as the percentage of body surface where old skin and hair had been shed and new hair growth was evident. Animals were assumed to shed and renew skin and hair linearly between those observations allowing moult stage to be treated as a continuous variable rather than a categorical variable. Similarly, rate of change of moult was also included as a continuous explanatory variable calculated as the change in percentage moult per day between capture and recapture. The full GAM model before selection was body surface temperature ~ smooth(BMI) + moult stage + rate of moult + s (windchill) + rainfall + smooth(relative humidity). Model selection during GAM analyses were performed by step-wise backwards selection of candidate models i.e. starting with the full model and sequentially dropping variables to make model comparisons. Models with the lowest Akaike's Information Criterion (AIC) scores were considered the most parsimonious with variables either being dropped or retained based on those AIC scores.

All statistical analyses were carried out using the statistical package R (R Development Core Team 2017).

3. Results

3.1. Environmental measurements

Environmental measurements taken with handheld instruments during captures were: air temperature 9.7 ± 0.4 °C, ground temperature 8.9 ± 0.2 °C, wind speed 6.9 ± 0.7 ms^{-1}, relative humidity 78.5 ± 0.9 % and solar radiation 320.8 ± 33.5 Wm^{-2} respectively (Table 2). Weather station measurements throughout the study period were: air temperature 7.3 ± 0.1 °C, wind speed 6.0 ± 0.1 ms^{-1} and relative humidity 76.2 ± 0.2 %. Solar radiation during daylight hours averaged 313.6 ± 6.9 Wm^{-2} and there were 34 days of rain (>0.2mm) with a total rainfall of 122.0 mm.

3.2. 3D models and predictions of surface area

A total of 18 scaled 3D models involving 12 individuals were created for animals captured in 2016 (Table 1). The mean surface area measured using photogrammetry and 3D modelling software (3.20 ± 0.08m^2)

was higher than that predicted using equation by Innes et al. (1990) (2.54 ± 0.04m^2). Similarly, mean surface area in contact with the ground measured using 3D modelling software was 1.27 ± 0.04m^2, equivalent to 39.7% of total surface area and greater than an assumed 20% of total surface area used previously (0.64 ± 0.02m^2) (Luecke et al. 1975, Paterson et al. 2012).

Model selection during multiple linear regression analyses showed that girth measurements did not explain a significant amount of the observed variation in surface area. After omission of girth measurements during the selection process, the final model was log (surface area) ~ log (mass) + log (length). The explanatory variable log (mass) was also not significant during model selection (t(15) = 0.85, p=0.41) but was retained due to it being the primary explanatory variable of interest. The final model showed that surface area had a positive relationship with mass, increasing by 0.16 (SE = 0.19) units of log (surface area) for every unit of log (mass) when controlling for length (Fig. 4). Surface area was related to length, increasing by 1.34 (SE = 0.40) units of log (surface area) for every unit of log (length) when controlling for mass (Fig. 5). The final model explained 59% of the variation in log (surface area) overall (F = 10.93, df = 2,15, p=0.001). This final model was then used to predict surface area using mass and length measurements for the animals captured in all years and not just those for which photogrammetry data were collected. Surface area predictions from this model were subsequently used for all animals throughout the study period for heat flux analyses.

3.3. Heat loss

Of the 23 southern elephant seals in this study, a total of 18 individuals (13 adult females, 4 juvenile females and 1 juvenile male) were used for measuring heat flux to the environment (Table 1). During model selection, time since start of anaesthesia until the end of heat flux measurements was not a significant explanatory variable and was subsequently excluded. The final model after selection was therefore RMR multiplier ~ habitat type + windchill + ground temperature + relative humidity + solar radiation + moult stage. ANCOVA results showed that RMR multiplier was different between the three habitats sampled (F = 21.86, df = 2,77, p<0.001). Post-hoc Tukey comparisons indicated that the RMR multiplier was greater for animals on the beach (2.3 ± 0.1) than in both vegetation (1.3 ± 0.1) (p<0.001) and wallow (1.8 ± 0.1)

($p<0.001$) habitats and greater in wallows compared with vegetation ($p=0.001$). Across all habitats, the mean predicted RMR multiplier was 1.8. There was a decrease in RMR multiplier with increasing windchill ($F = 20.53$, $df = 1,77$, $p<0.001$), ground temperature ($F = 19.19$, $df = 1,77$, $p<0.001$), relative humidity ($F = 6.40$, $df = 1,77$, $p=0.013$) and solar radiation ($F = 4.40$, $df = 1,77$, $p=0.039$). The RMR multiplier increased ($F = 4.89$, $df = 1,77$, $p=0.030$) as animals progressed in their moult stage. Mean RMR multiplier with 95% confidence intervals adjusted for the effects of covariates are presented for each habitat in Fig. 6. The final model explained 51.4% of the variation in RMR multiplier across the three habitats. The final ANCOVA model was checked and met assumptions of homogeneity and normal distribution of residual errors.

3.4. Body surface temperature

A total of 10 adult females were instrumented with temperature loggers with a mean deployment duration of 5.1 ± 0.7 days (Table 1). A further 14 deployments were attempted but instruments were either quickly lost due to hair not being strong enough to support device attachment or water damage causing instruments to fail. During model selection, all explanatory variables were retained, meaning the final GAM model selected was body surface temperature ~ smooth(BMI) + moult stage + rate of moult + s (windchill) + rainfall + s (relative humidity). GAM model predictions showed there to be an overall non-linear decrease in body surface temperature with decreasing BMI ($p<0.001$). Animals with a BMI of between 55 and 66 kg m^{-2} maintained a surface temperature of between 26.7°C and 28.8°C which then rapidly declined to 9.0°C when animals had a BMI of between 47 and 54 kg m^{-2} (Fig. 7). Body surface temperature decreased linearly with increasing moult stage ($p<0.001$) and rainfall ($p<0.001$) and increased linearly with increasing rate of moult ($p<0.001$). BMI, windchill and relative humidity were all significant smooth terms (all $p<0.001$) included in the final model. The amount of variability in body surface temperature explained by the final GAM model was 19.5% indicating that the extent to which external conditions affect surface temperature is relatively small and that other behavioural/physiological factors may be more important.

4. Discussion

Southern elephant seals that come ashore to moult initially reside in vegetation before seeking out muddy wallows (Boyd et al. 1993; Chaise et al. 2017) where they aggregate in tight groups (Riedman 1990; Cruwys and Davis 1995). When the moult is nearing completion, they move towards the beach before eventually going to sea (Boyd et al. 1993; Chaise et al. 2017). In this study, animals showed a similar temporal and spatial pattern of behaviour while moulting in that the initial part of the moult was characterised by movements across vegetation towards wallows when initial captures were made. Having completed the moult, animals then left the wallows and moved back through vegetation towards the beach where they would reside for several days before leaving the study site (Chaise et al. 2017). All second captures of animals took place either as animals were in wallows or on the beach as they were getting ready to leave. This study sought to determine possible drivers of these behaviours by examining heat loss in each of the three different habitats and by assessing temperature profiles of animals as body condition decreased during the moult fast.

Heat loss from animals to their surrounding environment resulted in predictions of RMR multiplier that were 38% higher in individuals that had already moved to wallow habitat (1.8 x Kleiber) compared with those that were moving towards wallows through vegetation (1.3 x Kleiber). This may be partly explained by the fact that the largest visual changes in terms of renewing skin and hair occurred while animals were in wallows and so could be considered to be at the peak of moulting. At this time, phocid seals are expected to be maximally perfusing blood to the skin surface which facilitates the renewal of skin and hair (Paterson et al. 2012). Animals captured around wallows may therefore simply have had a higher skin temperature gradient with the surrounding environment because they were at the peak of the moult, resulting in higher heat flux measurements. Conversely, animals moving towards wallow habitat through vegetation had lower heat fluxes. This could have been due to the fact that animals were at an earlier stage in the moult process and so elevation of skin temperature was less evident. Additionally, the thermal properties of vegetation may mean that conduction of heat from the animals to the ground was reduced. Whether heat loss differences were due to substrate type or stage of moult, these findings contradict those of Guerrero et al. (2021) that suggested substrate and moult stage had no effect on surface temperature in southern elephant seals.

Heat loss from animals to the surrounding environment resulted in predictions of RMR multiplier that were 77% higher when animals had appeared visually to have completed the moult and moved to beach habitat (2.3 x Kleiber) compared with vegetation habitat (1.3 x Kleiber), and 28% higher compared with wallow habitat (1.8 x Kleiber). Visually, study animals appeared to have completed the moult process when they left wallow and vegetation habitats and arrived at the beach. However, previous studies on other phocid species have shown that the period during which hair follicles are active extends beyond the point when visual signs of moulting are apparent (Ashwell-Erickson et al. 1986; Ling 2012). It is therefore likely that animals captured in the beach habitat were still actively moulting. RMR on the beach, measured at 2.3 x Kleiber, approached the 2.8 x Kleiber reported by Boyd et al. in 1993 for animals captured at a lower latitude in South Georgia. The two studies are comparable given that data collected by Boyd et al. (1993) were also for adult females. However, the average RMR across the three habitats in the present study was lower overall at 1.8 x Kleiber, which may be partly due to study animals moulting in a less extreme environment at a higher latitude. It could also be that the higher RMR in the study by Boyd et al. (1993) was influenced by factors such as a different habitat use or differences in the stage of moult stage. A limitation of the current study is that moult stage was either categorized as early moult (20-60% skin and hair shed) during capture or late moult (90-100% skin and hair shed) during recapture. More data with detailed longitudinal estimates of moult stage, as outlined by de Kock et al. (2021), are required to better understand the effects of moult stage on metabolic heat loss.

Predictions of heat loss expressed as RMR multiplier in different habitats were performed using a modelling approach that accounted for the effects of environmental variables. Choice of habitat would therefore appear to influence how heat is lost to the environment in moulting southern elephant seals. Behavioural adaptations to reduce heat loss are rarely assessed in hauled out phocids, though lair use in ringed seals (*Phoca hispida*) (Kelly and Quakenbush 1990) represents a rare example. A lack of research in this area may be due to the thick insulating blubber layer in phocid seals being considered to provide sufficient insulation in cold environments (Hart and Irving 1959; Hansen et al. 1995). However, the results of this study suggest that differences in heat loss between habitats was enough to influence where animals chose to reside at certain stages of the moulting process. Mellish et al. (2015) predicted that in Weddell seals (*Leptonychotes weddellii*), conduction of heat to the substrate accounted for 28% of total heat loss while hauled out on ice. In the present study, average conduction of heat to the substrate averaged 37% after accounting for the increased surface area in contact with the ground shown by 3D models. It may therefore be the case that differential conduction of heat away from animals dependent on substrate type and localised environmental conditions was a significant driver of habitat choice while animals were moulting. The data also suggest that the relatively high energetic cost of moulting in southern elephant seals described by Boyd et al. (1993) may be more evident when animals have established themselves in wallows and when they are on the beach before heading out to sea.

Surface temperature decreased with decreasing BMI between capture and recapture. The body condition and thickness of blubber of animals that come ashore to begin moulting is expected to be relatively high and decrease thereafter as the moult proceeds (Slip et al. 1992; Hindell et al. 1994). This is physiologically important as the blubber layer is the primary means of insulation due to its low thermal conductivity and high insulative properties when not perfused (Ling 1968; Kvadsheim and Aarseth, 2002). However, the insulative properties of blubber may be bypassed to some extent through venous return from the skin surface when animals must lose excess heat (Kvadsheim and Folkow 1997; Mauck et al. 2003). Heat may also be lost by perfusion of blood through anastomoses at the skin surface to facilitate hair renewal during the moult (Paterson et al. 2012). Mean mass loss in the present study was 3.6 ± 0.3 kg day^{-1} which was similar to that found for moulting southern elephant seals in other studies (Carlini et al. 1999; Postma et al. 2013; Chaise et al. 2019). The fact that body surface temperature decreased at BMI values of less than 54 kg m^{-2} suggests that perfusion of blood to the skin surface was reduced beyond this point. However, it is unlikely that a lowered BMI and a resultant reduction in blubber layer thickness would occur to the extent that animals were forced to reduce perfusion of blood to the skin surface as a thermoregulatory response. Lower body surface temperature at the end of the moult was likely the result of a reduced need to elevate skin temperature for hair and skin growth. Beyond this point, hair follicles would be expected to remain active for a further two to three months while at sea (Ling 2012), albeit at a lower level compared to when on land during peak moulting.

Higher body surface temperatures at the beginning and middle of deployments were likely a reflection of increased perfusion of blood to the skin surface as part of the moult process. This was also hypothesised in a similar study by Guerrero et al. (2021). Additionally, behavioural changes associated with moulting in southern elephant seals could have contributed to elevated body surface temperatures. Southern elephant seals huddle during the moult (Riedman 1990; Cruwys and Davis 1995; Chaise et al. 2019) which results in a large proportion of the body being in contact with other individuals and not the ground or air. The behavioural adaptation of aggregating (huddling) may be influenced by a number of social factors (Gilbert et al. 2010) but the main function for southern elephant seals appears to be for behavioural thermoregulation through sharing body heat with other individuals (Riedman 1990). However, Chaise et al. (2019) found that stomach and skin temperature were in fact lower in aggregated seals compared with solitary ones. Huddling animals may be able to reduce core and skin temperature as a means of saving energy while also benefitting from heat shared between individuals in contact with each other. Animals in the present study were likely to have been huddling some of the time in wallow habitats and vegetation but unfortunately no behavioural observations between capture and recapture were undertaken.

5. Conclusions

This study showed that heat transfer between skin surface and the surrounding environment in southern elephant seals was dependent on habitat selection. Moving from the haulout beach to aggregate in wallows or in vegetation may have allowed animals to increase skin surface temperature while minimising heat loss. The relatively high body condition of animals during the initial stages of moult would have afforded animals higher energy stores to cope better with the thermoregulatory costs at this time. As the moult proceeded, body condition declined which was concomitant with a lowering of skin surface temperature. In late moult, this may have been due to vasoconstriction of anastomoses in the skin to minimise heat loss when moving back to the beach before heading out to sea. However, the main reason for reduced skin temperatures was likely a reduced need to perfuse blood to the skin surface as peak moulting had passed. This study provides valuable insights into the ecophysiology of the catastrophic moult in southern elephant seals, showing that the behaviour of animals coming onto land and moving from the beach across vegetation and into wallows influences meatabolic heat loss. Longitudinal observations concurrent with sequential heat flux and surface temperature measurements are recommended as the next step to examine more fully the relationship between behavioural and physiological adaptations that facilitate the moult process. Further research is also required to determine differences in the energy cost of the moult with age and sex, particularly to address the lack of data available for adult males. This research may be particularly relevant for southern elephant seals faced with environmental change in polar regions.

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References

Ashwell-Erickson, S., F. H. Fay and R. Elsner. 1986. Metabolic and hormonal correlates of molting and regeneration of pelage in Alaskan harbor and spotted seals (*Phoca vitulina* and *Phoca larga*). Canadian Journal of Zoology 64:1086-1094.

Baker, J. R., M. A. Fedak, S. S. Anderson, T. Arnbom and R. Baker. 1990. Use of a tiletamine-zolazepam mixture to immobilize wild gray seals and southern elephant seals. Veterinary Record 126:75-77.

Bester, L. C. and P. J. N. de Bruyn. 2015. Simplifying photogrammetric analysis for assessment of large mammal mass: Automated targeting and 3D model building. The Photogrammetric Record 30:227-241.

Boily, P. 1995. Theoretical heat-flux in water and habitat selection of phocid seals and beluga whales during the annual molt. Journal of Theoretical Biology 172:235-244.

Boily, P. 1996. Metabolic and hormonal changes during the molt of captive gray seals (*Halichoerus grypus*). American Journal of Physiology-Regulatory Integrative and Comparative Physiology 270:1051-1058.

Boily, P., P. H. Kvadsheim and L. P. Folkow. 2000. Cutaneous heat flux models do not reliably predict metabolic rates of marine mammals. Journal of Theoretical Biology 207:317-323.

Boyd, I., T. Arnbom and M. Fedak. 1993. Water flux, body composition and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). Physiological Zoology 66:43-60.

Canals, M., M. Rosenmann and F. Bozinovic. 1997. Geometrical aspects of the energetic effectiveness of huddling in small mammals. Acta Theriologica 42:321-328.

Carlini, A. R., G. A. Daneri, M. E. I. Marquez, H. Bornemann, H. Panarello, R. Casaux, S. Ramdohr and J. Plotz. 2005. Food consumption estimates of southern elephant seal females during their post-breeding aquatic phase at King George Island. Polar Biology 28:769-775.

Carlini, A. R., M. E. I. Marquez, G. A. Daneri and S. Poljak. 1999. Mass changes during their annual cycle in females of southern elephant seals at King George Island. Polar Biology 21:234-239.

Chaise, L. L., W. D. Paterson, T. G. Laske, S. L. Gallon, D. J. McCafferty, M. Thery, A. Ancel and C. Gilbert. 2017. Implantation of subcutaneous heart rate data loggers in southern elephant seals (*Mirounga leonina*). Polar Biology:1-6.

Chaise, L. L., D. J. McCafferty, , S. L. Gallon, W. D. Paterson, M. Thery, A. Ancel and C. Gilbert. 2018. Local weather and body condition influence habitat use and movements on land of molting female southern elephant seals -(*Mirounga leonina*). Ecology and Evolution 8:6081-6090.

Chaise, L. L., D. J. McCafferty, A. Krellenstein, S. L. Gallon, W. D. Paterson, M. Thery, A. Ancel and C. Gilbert. 2019. Environmental and physiological determinants of huddling behavior of molting female southern elephant seals (*Mirounga leonina*). Physiology and Behavior 199:182-190.

Chapuis, J. L., Y. Frenot and M. Lebouvier. 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. Biological Conservation 117:167-179.

Cruwys, E. and P. Davis. 1995. The effect of local weather conditions on the behaviour of moulting southern elephant seals, *Mirounga leonina* (L). Polar Record 31:427-430.

de Bruyn, P. J. N., M. N. Bester, A. R. Carlini and W. C. Oosthuizen. 2009. How to weigh an elephant seal with one finger: a simple three-dimensional photogrammetric application. Aquatic Biology 5:31-39.

de Kock, L., W. C. Oosthuizen, R. S. Beltran, M. N. Bester and P. J. N. de Bruyn. 2021. Determinants of molt haulout phenology and duration in southern elephant seals. Scientific Reports 11:13331 (2021).

Erdsack, N., F. D. Hanke, G. Dehnhardt and W. Hanke. 2012. Control and amount of heat dissipation through thermal windows in harbor seals (*Phoca vitulina*). Journal of Thermal Biology 37:537-544.

Feltz, E. T. and F. H. Fay. 1966. Thermal requirements in vitro of epidermal cells from seals. Cryobiology 3:261-264.

Guerrero, A. I., T. L. Rogers and M. Sepulveda. 2021. Conditions influencing the appearance of thermal windows and the distribution of surface temperature in hauled-out southern elephant seals. Conservation Physiology 9: DOI 10.1093/conphys/coaa141.

Gilbert, C., D. McCafferty, Y. Le Maho, J.-M. Martrette, S. Giroud, S. Blanc and A. Ancel. 2010. One for all and all for one: the energetic benefits of huddling in endotherms. Biological Reviews 85:545-569.

Hansen, S., D. M. Lavigne and S. Innes. 1995. Energy metabolism and thermoregulation in juvenile harbor seals (*Phoca vitulina*) in air. Physiological Zoology 68:290-315.

Harding, K. C., M. Fujiwara, Y. Axberg and T. Harkonen. 2005. Mass-dependent energetics and survival in Harbour Seal pups. Functional Ecology 19:129-135.

Hart, J. S. and L. Irving. 1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. Canadian Journal of Zoology 37:447-457.

Hindell, M. A. and H. R. Burton. 1988. Seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. Journal of Mammalogy 69:81-88.

Hindell, M. A., D. J. Slip and H. R. Burton. 1994. Body mass loss of molting female southern elephant seals, *Mirounga leonina*, at Macquarie Island. Polar Biology 14:275-278.

Hindle, A. G., M. Horning and J. Mellish. 2015. Estimating total body heat dissipation in air and water from skin surface heat flux telemetry in Weddell Seals. Animal Biotelemetry 3:50.

Innes, S., G. A. J. Worthy, D. M. Lavigne and K. Ronald. 1990. Surface areas of phocid seals. Canadian Journal of Zoology 68:2531-2538.

Kelly, B. P. and L. T. Quakenbush. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). Canadian Journal of Zoology 68:2503-2512.

Khamas, W. A., H. Smodlaka, J. Leach-Robinson and L. Palmer. 2012. Skin histology and its role in heat dissipation in three pinniped species. Acta Veterinaria Scandinavica 54:46 (2012).

Kleiber, M. A. X. 1932. Body size and metabolism. Hilgardia 6:315-353.

Kvadsheim, P. H. and L. P. Folkow. 1997. Blubber and flipper heat transfer in harp seals. Acta Physiologica Scandinavica 161:385-395.

Kvadsheim, P. H., A. R. L. Gotaas, L. P. Folkow and A. S. Blix. 1997. An experimental validation of heat loss models for marine mammals. Journal of Theoretical Biology 184:15-23.

Ling, J. K. 1968. The skin and hair of the southern elephant seal *Mirounga leonina*. III Morphology of the adult integument. Australian Journal of Zoology 16:629-645.

Ling, J. K. 2012. The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.). IV. Annual cycle of pelage follicle activity and moult. Australian Journal of Zoology 60:259-271.

Luecke, R. H., V. Natarajan and F. E. South. 1975. Mathematical model of California sea lion. Journal of Thermal Biology 1:35-45.

Mauck, B., K. Bilgmann, D. D. Jones, U. Eysel and G. Dehnhardt. 2003. Thermal windows on the trunk of hauled-out seals: hot spots for thermoregulatory evaporation? Journal of Experimental Biology 206:1727-1738.

McCafferty, D. J., S. Gallon and A. Nord. 2015. Challenges of measuring body temperatures of free-ranging birds and mammals. Animal Biotemelemetry:DOI 10.1186/s40317-40015-40075-40312.

McKnight, J. C. 2017. Counting the Cost of Tagging: Quantifying and Reducing the Behavioural and Energetic Impacts of Tags in a Large Marine Vertebrate.PhD Thesis. University of St. Andrews, Scotland, UK.

Mellish, J. A., A. Hindle, J. Skinner and M. Horning. 2015. Heat loss in air of an Antarctic marine mammal, the Weddell seal. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 185:143-152.

Nadel, E. R. 1984. Energy exchanges in water. Undersea Biomedical Research 11:149-158.

Nicolaysen, K., F. A. Frey, K. V. Hodges, D. Weis and A. Giret. 2000. Ar-40/Ar-39 geochronology of flood basalts from the Kerguelen Archipelago, southern Indian Ocean: implications for Cenozoic eruption rates of the Kerguelen plume. Earth and Planetary Science Letters 174:313-328.

Ostner, J. 2002. Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). Folia Primatologica 73:175-180.

Paterson, W., C. E. Sparling, D. Thompson, P. P. Pomeroy, J. I. Currie and D. J. McCafferty. 2012. Seals like it hot: Changes in surface temperature of harbour seals (*Phoca vitulina*) from late pregnancy to moult. Journal of Thermal Biology. 37:454-461.

Paterson, W., S. E. Moss, R. Milne, J. I. Currie, D. J. McCafferty and D. Thompson. 2021. Increased metabolic rate of hauled out harbour seals (*Phoca vitulina*) during the molt. Physiological and Biochemical Zoology 94. https://doi.org/10.1086/713958.

Postma, M., M. N. Bester and N. de Bruyn. 2013. Spatial variation in female southern elephant seal mass change assessed by an accurate non-invasive photogrammetry method. Antarctic Science. 25:731-740.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riedman, M. 1990. The Pinnipeds, Seals, Sea Lions and Walruses. University of California Press.

Slip, D. J., N. J. Gales and H. R. Burton. 1992. Body mass loss, utilization of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the molting fast. Australian Journal of Zoology 40:235-243.

Thompson, P. and P. Rothery. 1987. Age and sex differences in the timing of molt in the common seal, *Phoca vitulina*. Journal of Zoology 212:597-603.

Thompson, P. M., M. A. Fedak, B. J. McConnell and K. S. Nicholas. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). Journal of Applied Ecology 26:521-535.

Walcott, S. M., Kirkham, A. L. and Burns, J. M. 2020. Thermoregulatory costs in molting Antarctic Weddell seals: impacts of physiological and environmental conditions. Conservation Physiology 8: coaa022; doi:10.1093/conphys/coaa02.

Watts, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: Correlates and constraints. Journal of Zoology 240:175-200.

White, F. N. and D. K. Odell. 1971. Thermoregulatory behavior of northern elephant seal, *Mirounga angustirostris*. Journal of Mammalogy 52:758-774.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99:673-686.

Worthy, G. A. J., P. A. Morris, D. P. Costa and B. J. Leboeuf. 1992. Molt energetics of the northern elephant seal (*Mirounga angustirostris*). Journal of Zoology 227:257-265.

Tables

	Date		Mass (kg)			Girth (cm)			Heat flux (Wm^{-2})	
Animal sex	Capture	Recapture	Capture	Recapture	Length (cm)	Capture	Recapture	iButton® (°C)	Capture	Recapture
9 A ♀	14/01/2014	23/01/2014	313.0	279.6	228	171	164	21.1 ± 0.4	NA	NA
10 A ♀	15/01/2014	22/01/2014	289.4	259.4	230	170	158	19.7 ± 0.3	NA	NA
30 J ♂	24/12/2014	NA	279.0	NA	217	165	NA	NA	78.05 ± 3.86 (V)	NA
31 J ♀	24/12/2014	NA	222.0	NA	212	150	NA	NA	115.67 ± 8.63 (W)	NA
32 J ♀	24/12/2014	NA	268.0	NA	207	170	NA	NA	185.62 ± 4.46 (W)	NA
33 J ♀	24/12/2014	NA	183.0	NA	192	144	NA	NA	167.10 ± 6.67 (B)	NA
34 J ♀	25/12/2014	NA	185.0	NA	166	153	NA	NA	175.15 ± 4.04 (B)	NA
38 A ♀	09/01/2015	12/01/2015	323.0	313.0	222	172	175	26.4 ± 0.1	NA	NA
39 A ♀	09/01/2015	13/01/2015	297.0	284.0	221	165	163	26.8 ± 0.1	NA	NA
40 A ♀	09/01/2014	13/01/2014	259.0	249.0	211	161	160	21.4 ± 0.1	NA	NA
43 A ♀	25/01/2016 (P)	01/02/2016 (P)	298.0	275.0	236	166	152	NA	97.54 ± 1.96 (V)	NA
44 A ♀	25/01/2016 (P)	NA	326.5	NA	247	177	NA	NA	96.00 ± 2.15 (V)	NA
45 A ♀	27/01/2016 (P)	02/02/2016 (P)	319.0	300.5	218	177	169	23.9 ± 0.1	126.66 ± 3.48 (V)	NA
47 A ♀	27/01/2016 (P)	02/02/2016 (P)	298.5	288.5	231	158	168	26.2 ± 0.1	NA	161.94 ± 1.66 (B)
50 A ♀	27/01/2016 (P)	01/02/2016 (P)	286.0	273.0	237	136	155	25.8 ± 0.1	93.51 ± 2.38 (V)	NA
51 A ♀	27/01/2016	31/01/2016 (P)	313.5	299.0	226	163	174	23.3 ± 0.1	200.38 ± 2.06 (V)	NA
52 A ♀	28/01/2016 (P)	02/02/2016 (P)	265.5	250.5	230	154	167	NA	103.54 ± 4.72 (W)	NA
53 A ♀	28/01/2016 (P)	NA	284.0	NA	227	170	NA	NA	134.07 ± 6.50 (V)	NA
54 A ♀	28/01/2016 (P)	01/02/2016	322.5	311.0	236	176	172	27.4 ± 0.1	165.23 ± 1.36 (V)	NA
56 A ♀	16/02/2016	22/02/2016 (P)	308.5	290	228	170	171	NA	NA	277.22 ± 4.18 (B)
57 A ♀	17/02/2016 (P)	NA	420.0	NA	250	193	NA	NA	NA	145.18 ± 2.93 (W)
58 A ♀	17/02/2016 (P)	25/02/2016 (P)	265.5	248.0	203	210	165	NA	132.82 ± 1.81 (W)	128.86 ± 3.11 (B)
59 A ♀	21/02/2016	26/02/2016	NA	383.5	253	NA	187	NA	146.39 ± 1.75 (B)	NA

Table 1. Sex and age class are indicated in individual codes (A = adult, J= juvenile). Mass, length and girth measurements as well as mean ± SE heat flux (Wm^{-2}) are shown for each individual on the date of capture and recapture. Also given are mean ± SE iButton® (°C) measurements over the course of deployment. Habitats in which captures took place are indicated next to heat flux values as B=beach, W=wallow and V=vegetation. P next to dates indicates 3D photogrammetry. NA values indicate no data were collected.

	Habitat		
Environmental measure	**Vegetation**	**Beach**	**Wallow**
Air temperature (°C)	8.8 (0.3)	9.2 (0.3)	11.7 (1.1)
Ground temperature (°C)	7.4 (0.1)	10.5 (0.3)	9.5 (0.2)
Relative humidity (%)	76.5 (1.8)	81.5 (1.5)	77.2 (1.0)
Wind speed (ms^{-1})	5.5 (0.7)	5.7 (1.0)	10.6 (1.9)
Solar radiation (Wm^{-2})	211.2 (42.5)	260.6 (43.1)	568.1 (76.9)

Table 2. Mean ± SE of environmental conditions recorded using handheld instruments during captures in each of the three habitats: vegetation, beach and wallow.

Figure Captions

Fig. 1. Placement of heat flux disc on the dorsal midline posterior to the axial line between the fore flippers to measure heat flux from the animal to the air. Heat flux to the ground was measured with a heat flux disc placed on the ventral midline (not shown) directly opposite to the dorsal surface.

Fig. 2. 3D models using the software package AutoDesk® Photo Recap™ to measure surface area of animals in contact with the air and with the ground. From top to bottom models shown are for each of the three habitats: vegetation (Individual 45 at recapture), beach (Individual 56 at recapture) and wallow (Individual 58 at capture).

Fig. 3. Location of iButtons® placed on the flank of animals, posterior to the fore flipper. iButtons® were covered with a combination of fine nylon mesh and a layer of two-part epoxy. Also attached on the dorsal surface were a GPS transmitter and a VHF transmitter for locating animals.

Fig. 4. Partial residual plot of log (area) against log (mass). The black solid line is the predicted linear relationship between log (area) and log (mass) with 95% confidence intervals shaded grey. Points represent the prediction of log (area) dependent on log (mass) for each capture. The predicted linear relationship is given after accounting for the other explanatory variable used, which in this plot was log (length).

Fig. 5. Partial residual plot of log (area) over log(length). The black solid line is the predicted linear relationship between log (area) and log(length) with 95% confidence intervals shaded grey. Points represent the prediction of log (area) dependent on log (length) for each capture. The predicted linear relationship is given after accounting for the other explanatory variable used, which in this plot was log (mass).

Fig. 6. ANCOVA predictions of corrected mean multiple of resting metabolic rate (RMR multiplier) according to allometric equations by Kleiber (1932) (left y-axis) in three different habitats; vegetation, wallow and beach (x-axis) based on heat flux calculations. Also shown are predicted values for RMR multiplier converted to kcal day^{-1} (right y-axis). 95% confidence intervals of corrected means are also shown.

Fig. 7. Predictions (solid black line) of body surface temperature (°C) (y-axis) dependent on body mass index (BMI (kgm^{-2})) (x-axis). 95% confidence intervals of predictions (grey) are also shown. Black circles indicate mean body surface temperature for each value of BMI.