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2 **Title:** How catastrophic is it? Increased heat loss during the moult in southern elephant seals

3

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25 **Highlights**

- 26 • Heat loss in moulting southern elephant seals (SES) differed between habitat types.
- 27 • Greatest heat loss was in beach habitat during the late moult.
- 28 • Heat loss was lower in wallow and lower still in vegetation habitats.
- 29 • Body condition and skin temperature both reduced at the end of the moult.

30

31 **Abstract**

32 The moult in southern elephant seals (SES, *Mirounga leonina*) represents an especially energetically
33 demanding period during which seals must maintain high skin temperature to facilitate complete
34 replacement of body fur and upper dermis. In this study, heat loss was measured on the body surface of
35 18 moulting SES in three different habitats (beach, wallow or vegetation) to estimate heat loss.
36 Temperature data loggers were also deployed on 10 SES to monitor skin surface temperature. On average,
37 heat loss of animals on the beach was greater than in wallows or vegetation, and greater in wallows than
38 in vegetation. Average heat loss across all habitats during the moult equated to 1.8 x resting metabolic
39 rate. The greatest heat loss of animals was recorded in the beach habitat during the late moult, that was
40 estimated to represent 2.3 x RMR. Mean mass loss was 3.6 ± 0.3 kg per day, resulting in changes in body
41 condition as the moult proceeded. As body condition decreased, skin surface temperature also decreased,
42 suggesting that as animals approached the end of the moult blood flow to the skin surface was no longer
43 required for growth of hair follicles.

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47 **Keywords**

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

49

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72 **1. Introduction**

73 The annual moult in phocid seals represents a distinct, energetically demanding period during which
74 animals spend an increased amount of time on land as they shed and renew their entire coat (Hindell and
75 Burton 1988; Thompson et al. 1989; Boyd et al. 1993). Conditions for the proliferation of hair follicles
76 and skin cells during this time are optimised by increasing skin surface temperature closer to core body
77 temperature (Feltz and Fay 1966; Paterson et al. 2012). This is achieved by increasing perfusion of blood
78 at the skin surface (Khamas et al. 2012). Thermal conduction in water is 25 times that in air (Nadel 1984)
79 meaning that increasing skin surface temperature while at sea would result in a physiologically
80 unsustainable heat loss (Boily 1995; Watts 1996). High skin temperature with minimal heat loss is
81 therefore most efficiently achieved while animals are on land. For some seal species, moulting involves a
82 diffuse process lasting several weeks with intermittent trips to sea, such as for the grey seal (*Halichoerus*
83 *grypus*) (Boily, 1996) and the harbour seal (*Phoca vitulina*) (Ashwell-Erickson et al., 1986). In these
84 species, moulting is visually apparent during a four-week period (Thompson and Rothery 1987).
85 However, the underlying process of hair follicle regrowth, which is much less conspicuous, may be
86 evident for a period of up to 12 weeks (Ashwell-Erickson et al. 1986). For species such as the northern
87 elephant seal (*Mirounga angustirostris*) and the southern elephant seal (*Mirounga leonina*) (hereafter
88 referred to as SES) that undergo a catastrophic moult, hair and the upper dermis are shed together over a
89 period of 25-32 days with the majority if not the entire moult process being completed on land (Worthy et
90 al. 1992; Boyd et al. 1993).

91 The behavioural adaptation of spending more time on land during the moult allows phocid seals to
92 overcome the thermoregulatory constraints of moulting in an aquatic environment (Boily 1996; Watts
93 1996). However, for species found in more extreme climatic conditions at higher latitudes, further
94 behavioural adaptations may be necessary to minimise heat loss. In Antarctic and sub-Antarctic regions
95 SES that come ashore to moult initially search for muddy pools or wallows (Boyd et al. 1993; Chaise et
96 al. 2017) where they often aggregate in tight groups (Riedman 1990; Cruwys and Davis 1995). This
97 behaviour may serve to minimise the amount of skin surface area exposed to the air by either being in
98 contact with other animals or being partially covered in mud warmed by body heat from large groups of

99 seals. Huddling is an adaptive response seen in many species of birds and mammals (Canals et al. 1997;
100 Ostner 2002; Gilbert et al., 2010) that minimises the metabolic input required for thermoregulation
101 (Gilbert et al. 2010). If moulting SES elevate skin temperature as is seen in other phocid species (Paterson
102 et al. 2012) then huddling in wallows may help to conserve heat when actively perfusing the skin with
103 blood. The final stage of the moult process in SES is characterised by animals remaining on land but
104 moving out of wallows and closer to shore (Boyd et al. 1993; Chaise et al. 2017). Choice of habitat type
105 and stage of moult are therefore important factors when considering the environmental conditions
106 affecting the moult in SES.

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

116 Direct measurement of heat loss in moulting seals in the wild has rarely been successful (though see
117 Walcott et al. 2020) due to the difficulties of gluing devices to hair that is being shed or that is newly
118 grown and too weak to support device attachment. New research is required to determine heat loss of
119 moulting phocid seals to the surrounding environment to be able to estimate the energetic cost of the
120 moult associated with thermoregulation and the choice of habitat type when hauling out. An increased
121 metabolic rate during the moult has been demonstrated in previous studies (Slip et al. 1992; Boyd et al.
122 1993; Paterson et al. 2012; Paterson et al. 2021). This increased energetic demand is compounded by the
123 fact that animals fast on land (Slip et al. 1992; Hindell et al. 1994). As a result, body condition decreases
124 as blubber reserves become depleted during the moult (Hindell et al. 1994; Carlini et al. 2005).
125 Meteorological conditions and choice of habitat that increase heat loss from animals to the ground and air

126 will increase energy costs as a greater metabolic rate will be required to maintain high skin temperatures
127 necessary for hair and skin growth.

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

134

135 **2. Materials and methods**

136

137 **2.1. Study animals**

138 Study SES were captured during the early part of the moult, shortly after they arrived onshore and as they
139 moved away from the beach passing through vegetation en route to the wallows. Where recaptures were
140 possible in the latter part of the moult, animals were captured either while still in wallows or when they
141 had moved back to the beach and were likely to leave. A total of 18 adult females, 4 sub-adult females
142 and 1 sub-adult male SES were sampled between 14/01/2014 and 26/02/2016 at Point Suzanne,
143 Kerguelen Islands (49°26'S, 70°26'E) during this study. Animals were anaesthetised with a 1:1
144 combination of Tiletamine and Zolazepam (Zoletil® 100), either administered intramuscularly with a
145 blow dart at a dose rate of 1ml/100kg or intravenously at a dose rate of 0.5ml/100kg (Baker et al. 1990).
146 Moult stage of each individual was estimated at capture and recapture based on the percentage area of the
147 body over which old skin and hair had been shed and new hair was growing through (Chaise et al. 2019).
148 Upon capture when animals were heavily moulting and recapture when the moult process was complete,
149 individuals were weighed ($\pm 0.5\text{kg}$) using a tripod and scales (HST Mini-Weigher, HST Scales, Milton
150 Keynes, UK). Measurements of body length ($\pm 1.0\text{cm}$) from nose to tail were also taken (Table 1).

151 SES work (Program IPEV 1037 HENERGES) was approved by The Antarctic Committee for
152 Environmental Protection and the Ethics Committee (Cometh ANSES/ENVA/UPEC n°16: n°14-055 and
153 n°15-061). The program was also authorised by the French Southern and Antarctic Lands (Decree 2014-
154 131, 15th October 2014; Decree 2015-110, 4th September 2015). All applicable international, national
155 and institutional guidelines for the care and use of animals were followed. All procedures performed in
156 studies involving animals were in accordance with the ethical standards of the institution or practice at
157 which the studies were conducted.

158 **2.2. Heat flux measurements**

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

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

179

180 **2.3. Conversion of heat flux measurements to whole body heat flux**

181 To extrapolate measurements of heat flux taken on the dorsal and ventral surfaces to the whole body
182 surface required a measure of the whole body surface area of animals. Previously, this has been done by
183 predicting maximal surface area based on mass according to the following allometric equation developed
184 for phocid seals by Innes et al. (1990): $\log A = \log 0.14 + 0.51 * \log m$ where A is body surface area (m²)
185 and m is the mass (kg) of the animal. This allometric relationship was based on post-mortem measures of
186 surface area of 56 skins removed from individuals of five different seal species including harbour seals,
187 harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), ringed seals (*Pusa hispida*)
188 and grey seals.

189 A photogrammetry method was developed to test whether the previous equation held true for SES by
190 creating fully scaled 3D models using the software package AutoDesk® Photo Recap™. To create 3D
191 models, approximately 40 photographs were taken at different angles around the circumference of
192 animals while they were anaesthetised. Accurate 3D models of animals were then generated and scaled
193 using nose to tail length measurements taken during captures. Fig. 2 shows examples of 3D models
194 generated for animals in each of the three habitat types; vegetation, beach and wallow.

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

204

205 **2.4. Body surface temperature measurements**

206 Measurements of body surface temperature for the duration between capture and recapture were recorded
207 ($\pm 0.5^{\circ}\text{C}$) using miniaturised temperature loggers (iButton® DS1922L-F5, Maxim Integrated, San Jose,
208 USA). In 2014 and 2015, average temperature was sampled at an interval of 10 minutes. However, in
209 2016 this was increased to an interval of every one minute. This type of logger was chosen due to its
210 small size (diameter = 17.4mm, thickness = 5.9mm, weight = 3g) and its reliable use in a range of other
211 studies (McCafferty et al. 2015). Each logger was located over newly grown hair on either flank, dorsal to
212 the fore flipper and held in place by covering with a fine nylon mesh and a layer of two-part epoxy
213 (Araldite® AW 2101, Huntsman International LLC, Texas, USA) (Fig. 3).

214

215 **2.5. Environmental measurements**

216 Environmental conditions were recorded within one metre of animals during captures. Air temperature (\pm
217 0.1°C), ground temperature ($\pm 0.1^{\circ}\text{C}$), relative humidity ($\pm 1\%$), wind speed ($\pm 0.1\text{ms}^{-1}$) and solar
218 radiation ($\text{W}\cdot\text{m}^{-2}$ error $\pm 5\%$) were all measured using handheld instruments (Kestrel 3000 Pocket
219 Weather Meter, Kestrel Instruments, Pennsylvania, USA; Pyranometer SKS111, Skye Instruments Ltd.,
220 Llandrindon Wells, UK). Measurements were taken at the beginning and end of captures with the average
221 of those two values being used.

222 Environmental conditions in the vicinity of the study site (air temperature ($\pm 0.1^{\circ}\text{C}$), relative humidity (\pm
223 1%), wind speed ($\pm 0.1\text{ms}^{-1}$) and solar radiation ($\text{W}\cdot\text{m}^{-2}$ error $\pm 5\%$)) were recorded as spot measurements
224 every 30 minutes. Rainfall (mm error $<6\%$) was recorded as the total every 30 minutes. These
225 environmental conditions were logged using an automatic weather station (Minimet, Skye Instruments
226 Ltd., Powys, UK) in a fixed location.

227 All means reported in the results below are given as \pm SE.

228

229

230 **2.6. Statistical analyses**

231 **2.6.1. 3D models and predictions of surface area**

232 3D models generated for animals caught in 2016 were used to estimate whole body surface area. A
233 multiple linear regression model was used to predict whole body surface area (m^2) as a function of mass
234 (kg), length (cm) and girth (cm). Results were compared to predictions of surface area derived from
235 Equation 1 developed by Innes et al. (1990) which relied solely on mass as the predictor. All dependent
236 and explanatory variables were log-transformed for multiple regression analyses. The full model used for
237 selection was therefore $\log(\text{surface area}) \sim \log(\text{mass}) + \log(\text{length}) + \log(\text{girth})$ with all variables being
238 treated as continuous. Model selection was performed in a step-wise backwards selection process
239 dropping non-significant explanatory variables as appropriate. The final model could then be used to
240 predict surface area while accounting for variation in morphometrics. Table 1 summarises captures during
241 which photogrammetry images were taken that were then developed into 3D models.

242

243 **2.6.2. Heat flux**

244 Whole body heat flux (W) was converted to kcal/day. This allowed for comparisons with estimations of
245 resting metabolic rate based on mass according to Kleiber (1932): $RMR = 70 * M^{0.75}$

246 where RMR is resting metabolic rate in $kcal.day^{-1}$ and M is mass (kg). Estimations of metabolic rate were
247 expressed as a multiple of resting metabolic rate (RMR multiplier), defined as dividing whole body heat
248 flux ($kcal.day^{-1}$) based on measurements by predictions of RMR ($kcal.day^{-1}$) from Kleiber's equation. In
249 this definition, Kleiber's prediction is referred to as 1 x Kleiber.

250 Analysis of co-variance (ANCOVA) was used to determine differences in the continuous response
251 variable, RMR multiplier, dependent on habitat type consisting of three levels; vegetation, wallow and
252 beach. A post-hoc Tukey's test was used to make pairwise comparisons of RMR multiplier across the
253 three habitat types. To reduce the number of explanatory variables used, air temperature and wind speed
254 were combined to create the variable windchill, defined by the equation: $windchill = 13.12 + (0.6215 * Ta) -$
255 $11.37 * (v^{0.16}) + (0.3965 * Ta * v^{0.16})$ where Ta is air temperature ($^{\circ}C$) and v is wind speed (kmh^{-1})
256 (Environment and Climate Change Canada, Government of Canada; NOAA's National Weather Service,
257 USA). The environmental variables included as covariates were therefore windchill, ground temperature,
258 relative humidity and solar radiation. Time since initiation of general anaesthesia (minutes) was also

259 included as a continuous covariate to determine how changes in body temperature associated with
260 anaesthesia may have influenced recorded heat flux. Moulting stage at capture (20-60% of old skin and hair
261 shed) and recapture (90-100% of old skin and hair shed) was treated as a two-level factor. The full model
262 before selection was $\text{RMR multiplier} \sim \text{habitat type} + \text{windchill} + \text{ground temperature} + \text{relative humidity}$
263 $+ \text{solar radiation} + \text{time since anaesthesia} + \text{moulting stage}$. ANCOVA model selection was performed in a
264 step-wise backwards selection process dropping non-significant explanatory variables as appropriate.

265

266 **2.6.3. Body surface temperature**

267 Changes in body surface temperature (response variable) dependent on body condition were modelled
268 using a Generalised Additive Model (GAM) approach from the mgcv library (Wood 2004). In this case, a
269 proxy for body condition was used which was body mass index ($\text{BMI} = \text{mass (kg)/length}^2 \text{ (m)}$). This
270 index was chosen for consistency with a previous study of habitat use and movements of the same study
271 animals (Chaise et al. 2018). Calculations of BMI between captures assumed that mass changed linearly
272 between measurements at capture and recapture. In the full GAM model, body surface temperature was
273 fitted as a smooth (thin plate regression spline) over values of BMI. Pre-screening of the measured
274 environmental variables showed that air temperature and solar radiation were correlated (Pearson, $r=0.55$,
275 $p<0.001$). Air temperature was therefore used and solar radiation was excluded from the analysis. To
276 further reduce the number of explanatory variables used, air temperature and wind speed were combined
277 to create the smoothed variable windchill (as above). Rainfall was included as a continuous explanatory
278 variable and relative humidity as a smoothed explanatory variable. Moulting stage was included as a
279 continuous explanatory variable which was estimated at capture and recapture as the percentage of body
280 surface where old skin and hair had been shed and new hair growth was evident. Animals were assumed
281 to shed and renew skin and hair linearly between those observations allowing moulting stage to be treated as
282 a continuous variable rather than a categorical variable as in the heat flux analysis. Similarly, rate of
283 change of moulting was also included as a continuous explanatory variable calculated as the change in
284 percentage moulting per day between capture and recapture. The full GAM model before selection was body
285 $\text{surface temperature} \sim \text{smooth(BMI)} + \text{moulting stage} + \text{rate of moulting} + \text{s (windchill)} + \text{rainfall} +$

286 smooth(relative humidity). Model selection during GAM analyses were performed by step-wise
287 backwards selection of candidate models with the lowest AIC scores.

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

289

290 **3. Results**

291

292 **3.1. Environmental measurements**

293 Environmental measurements taken with handheld instruments during captures averaged: air temperature
294 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 %
295 and solar radiation 320.8 ± 33.5 Wm⁻² respectively (Table 2). Longer term measurements from the fixed
296 weather station were air temperature 7.3 ± 0.1 °C, wind speed 6.0 ± 0.1 ms⁻¹ and relative humidity $76.2 \pm$
297 0.2 %. Solar radiation during daylight hours averaged 313.6 ± 6.9 W.m⁻² and there were 34 days of rain
298 (>0.2mm) with a total rainfall of 122.0 mm.

299

300 **3.2. 3D models and predictions of surface area**

301 A total of 18 scaled 3D models involving 12 individuals were created for animals captured in 2016 (Table
302 1). The mean surface area measured using photogrammetry and 3D modelling software (3.20 ± 0.08 m²)
303 was higher than that predicted using equation by Innes et al. (1990) (2.54 ± 0.04 m²). Similarly, mean
304 surface area in contact with the ground measured using 3D modelling software was 1.27 ± 0.04 m²,
305 equivalent to 39.7% of total surface area and greater than an assumed 20% of total surface area used
306 previously (0.64 ± 0.02 m²) (Luecke et al. 1975, Paterson et al. 2012).

307 Model selection during multiple linear regression analyses showed that girth measurements did not
308 explain a significant amount of the observed variation in surface area. After omission of girth
309 measurements during the selection process, the final model was $\log(\text{surface area}) \sim \log(\text{mass}) + \log$
310 (length) . The explanatory variable $\log(\text{mass})$ was also not found to be significant during model selection

311 (t(15) = 0.85, p=0.41) but was retained due to it being the primary explanatory variable of interest. The
312 final model showed that surface area had a positive relationship with mass, increasing by 0.16 (SE = 0.19)
313 units of log (surface area) for every unit of log (mass) when controlling for length (Fig. 4). Surface area
314 was related to length, increasing by 1.34 (SE = 0.40) units of log (surface area) for every unit of log
315 (length) when controlling for mass (Fig. 5). The final model explained 59% of the variation in log
316 (surface area) overall (F = 10.93, df = 2,15, p=0.001). This final model was then used to predict surface
317 area using mass and length measurements for the animals captured throughout the study period that were
318 subsequently used for heat flux analyses.

319

320 **3.3. Heat flux**

321 Of the 23 SES used in this study overall, a total of 18 individuals (13 adult females, 4 juvenile females
322 and 1 juvenile male) were used for measuring heat flux to the environment (Table 1). During model
323 selection, time since start of anaesthesia was not found to be a significant explanatory variable and was
324 subsequently excluded. The final model after selection was therefore RMR multiplier ~ habitat type +
325 windchill + ground temperature + relative humidity + solar radiation + moult stage. ANCOVA results
326 showed that RMR multiplier was different between the three habitat types sampled (F = 21.86, df = 2,77,
327 p<0.001). Post-hoc Tukey comparisons indicated that the RMR multiplier was greater for animals on the
328 beach (2.3 ± 0.1) than in both vegetation (1.3 ± 0.1) (p<0.001) and willow (1.8 ± 0.1) (p<0.001) habitats
329 and greater in willows compared with vegetation (p=0.001). Across all habitat types, the mean predicted
330 RMR multiplier was 1.8. There was a decrease in RMR multiplier with increasing windchill (F = 20.53,
331 df = 1,77, p<0.001), ground temperature (F = 19.19, df = 1,77, p<0.001), relative humidity (F = 6.40, df =
332 1,77, p=0.013) and solar radiation (F = 4.40, df = 1,77, p=0.039). The RMR multiplier increased (F =
333 4.89, df = 1,77, p=0.030) as animals progressed in their moult stage. Mean RMR multiplier with 95%
334 confidence intervals adjusted for the effects of covariates are presented for each habitat type in Fig. 6. The
335 final model explained 51.4% of the variation in RMR multiplier across the three habitat types. The final
336 ANCOVA model was checked and found to meet assumptions of homogeneity and normal distribution of
337 residual errors.

338

339 **3.4. Body surface temperature**

340 A total of 10 adult females were instrumented with iButton® temperature loggers with a mean
341 deployment duration of 5.1 ± 0.7 days, resulting in 59900 individual measurements (Table 1). A further
342 14 deployments were attempted but instruments were either quickly lost due to hair not being strong
343 enough to support device attachment or water damage causing instruments to fail. During model
344 selection, all explanatory variables were retained, meaning the final GAM model selected was body
345 surface temperature \sim smooth(BMI) + moult stage + rate of moult + s (windchill) + rainfall + s (relative
346 humidity). GAM model predictions showed there to be an overall non-linear decrease in body surface
347 temperature with decreasing BMI ($p < 0.001$). Animals with a BMI of between 55 and 66 kg m^{-2}
348 maintained a surface temperature of between 26.7°C and 28.8°C which then rapidly declined to 9.0°C
349 when animals had a BMI of between 47 and 54 kg m^{-2} (Fig. 7). Body surface temperature decreased
350 linearly with increasing moult stage ($p < 0.001$) and rainfall ($p < 0.001$) and increased linearly with
351 increasing rate of moult ($p < 0.001$). BMI, windchill and relative humidity were all significant smooth
352 terms (all $p < 0.001$) included in the final model. The amount of variability in body surface temperature
353 explained by the final GAM model was 19.5% indicating that the extent to which external conditions
354 affect surface temperature is relatively small and that other behavioural/physiological factors may be
355 more important.

356

357

358

359

360 **4. Discussion**

361 SES that come ashore to moult have been shown previously to initially reside in vegetation before
362 seeking out muddy wallows (Boyd et al. 1993; Chaise et al. 2017) where they aggregate in tight groups
363 (Riedman 1990; Cruwys and Davis 1995). When the moult is nearing completion, they move towards the

364 beach before eventually going to sea (Boyd et al. 1993; Chaise et al. 2017). In this study, animals showed
365 a similar temporal and spatial pattern of behaviour while moulting in that the initial part of the moult was
366 characterised by movements across vegetation towards wallows when initial captures were carried out.
367 Having completed the moult, animals then left the wallows and moved back through vegetation towards
368 the beach where they would reside for several days before leaving the study site (Chaise et al. 2017). All
369 second captures of animals took place either as animals were in wallows or on the beach as they were
370 getting ready to leave. This study sought to determine possible drivers of these behaviours by examining
371 heat loss in each of the three different habitat types and by assessing temperature profiles of animals as
372 body condition decreased during the moult fast.

373 Heat loss from animals to their surrounding environment resulted in predictions of RMR multiplier that
374 were 38% higher in individuals that had already moved to wallow habitat (1.8 x Kleiber) compared with
375 those that were moving towards wallows through vegetation (1.3 x Kleiber). This may be partly explained
376 by the fact that the largest visual changes in terms of renewing skin and hair occurred while animals were
377 in wallows and so could be considered to be at the peak of moulting. At this time, phocid seals are
378 expected to be maximally perfusing blood to the skin surface which facilitates the renewal of skin and
379 hair (Paterson et al. 2012). Animals captured around wallows may therefore simply have had a higher
380 skin temperature gradient with the surrounding environment because they were at the peak of the moult,
381 resulting in higher heat flux measurements. Conversely, animals moving towards wallow habitat through
382 vegetation had lower heat fluxes. This could have been due to the fact that animals were at an earlier
383 stage in the moult process and so elevation of skin temperature was less evident. Additionally, the thermal
384 properties of vegetation may mean that conduction of heat from animals' bodies was reduced.

385 Heat loss from animals to the surrounding environment resulted in predictions of RMR multiplier that
386 were 77% higher when animals had appeared visually to have completed the moult and moved to beach
387 habitat (2.3 x Kleiber) compared with vegetation habitat (1.3 x Kleiber), and 28% higher compared with
388 wallow habitat (1.8 x Kleiber). Visually, study animals appeared to have completed the moult process
389 when they left wallow and vegetation habitats and arrived at the beach. However, previous studies on
390 other phocid species have shown that the period during which hair follicles are active extends beyond the
391 point when visual signs of moulting are apparent (Ashwell-Erickson et al. 1986; Ling 2012). It is

392 therefore likely that animals captured in the beach habitat were still actively moulting despite appearing to
393 have completed the moult process. RMR on the beach, measured at 2.3 x Kleiber, approached the 2.8 x
394 Kleiber reported by Boyd et al. in 1993 for animals captured at a lower latitude in South Georgia.
395 However, the average RMR across the three habitats in the present study was lower overall at 1.8 x
396 Kleiber, which may be partly due to study animals moulting in a less extreme environment at a higher
397 latitude.

398 Predictions of heat flux expressed as RMR multiplier in different habitat types were performed using a
399 modelling approach that accounted for the effects of environmental variables. Choice of habitat type
400 would therefore appear to influence how heat is lost to the environment in moulting SES. Behavioural
401 adaptations to reduce heat loss are rarely assessed in hauled out phocids, though lair use in ringed seals
402 (*Phoca hispida*) (Kelly and Quakenbush 1990) represents a rare example. A lack of research in this area
403 may be due to the thick insulating blubber layer in phocid seals being considered to provide sufficient
404 insulation in cold environments (Hart and Irving 1959; Hansen et al. 1995). However, the results of this
405 study suggest that differences in heat conduction between habitat types was enough to influence where
406 animals chose to reside at certain stages of the moulting process. Mellish et al. (2015) predicted that in
407 Weddell seals (*Leptonychotes weddellii*), conduction of heat to the substrate accounted for 28% of total
408 heat loss while hauled out on ice. In the present study, average conduction of heat to the substrate was
409 found to average 37% after accounting for the increased surface area in contact with the ground shown by
410 3D models. It may therefore be the case that differential conduction of heat away from animals dependent
411 on substrate type and localised environmental conditions was a significant driver of habitat choice while
412 animals were moulting. The data also suggest that the relatively high energetic cost of moulting in SES
413 described by Boyd et al. (1993) may be more evident when animals have established themselves in
414 wallows and when they are on the beach before heading out to sea.

415 Surface temperature decreased with decreasing BMI between capture and recapture. The body condition
416 and thickness of blubber of animals that come ashore to begin moulting is expected to be relatively high
417 and decrease thereafter as the moult proceeds (Slip et al. 1992; Hindell et al. 1994). This is
418 physiologically important as the blubber layer is the primary means of insulation due to its low thermal
419 conductivity and high insulative properties when not perfused (Ling 1968; Kvadsheim and Aarseth,

420 2002). However, the insulative properties of blubber may be bypassed to some extent through venous
421 return from the skin surface when animals must lose excess heat (Kvadsheim and Folkow 1997; Mauck et
422 al. 2003). Heat may also be lost by perfusion of blood through anastomoses at the skin surface to facilitate
423 hair renewal during the moult (Paterson et al. 2012). Mean mass loss in the present study was 3.6 ± 0.3 kg
424 day^{-2} which was similar to that found for moulting SES in other studies (Carlini et al. 1999; Chaise et al.
425 2019). The fact that body surface temperature decreased at BMI values of less than 54 kg m^{-2} suggests
426 that perfusion of blood to the skin surface was reduced beyond this point. However, it is unlikely that a
427 lowered BMI and a resultant reduction in blubber layer thickness would occur to the extent that animals
428 were forced to reduce perfusion of blood to the skin surface as a thermoregulatory response. It is therefore
429 more likely that that lower body surface temperature at the end of the moult was the result of a reduced
430 need to elevate skin temperature for hair and skin growth.

431 Higher body surface temperatures at the beginning and middle of deployments were likely a reflection of
432 increased perfusion of blood to the skin surface as part of the moult process. Additionally, behavioural
433 changes associated with moulting in SES could have contributed to elevated body surface temperatures.
434 SES huddle during the moult (Riedman 1990; Cruwys and Davis 1995; Chaise et al. 2019) which results
435 in a large proportion of the body being in contact with other individuals and not the ground or air. The
436 behavioural adaptation of aggregating (huddling) in wallows by SES is considered to minimise heat loss
437 through sharing body heat from other individuals (Riedman 1990). However, Chaise et al. (2019) found
438 that stomach and skin temperature were in fact lower in aggregated seals compared with solitary ones.
439 Huddling animals may be able to reduce core and skin temperature as a means of saving energy while
440 also benefitting from heat shared between individuals in contact with each other. Animals in the present
441 study were likely to have been huddling some of the time in wallow habitats and vegetation but no
442 behavioural observations between capture and recapture were recorded.

443

444 **5. Conclusions**

445 This study showed that heat transfer between skin surface and the surrounding environment in SES was
446 dependent on habitat selection. Moving from the haulout beach to aggregate in wallows or in vegetation

447 may have allowed animals to increase skin surface temperature while minimising heat loss. The relatively
448 high body condition of animals during the initial stages of moult would have afforded animals higher
449 energy stores to cope better with the thermoregulatory costs at this time. As the moult proceeded, body
450 condition declined which was concomitant with a lowering of skin surface temperature. In late moult, this
451 may have been due to vasoconstriction of anastomoses in the skin to minimise heat loss when moving
452 back to the beach before heading out to sea. However, the main reason for reduced skin temperatures was
453 likely a reduced need to perfuse blood to the skin surface as the moult was nearing completion. This study
454 provides valuable insight into the ecophysiology of the catastrophic moult in SES, showing that the
455 behaviour of animals coming onto land and moving from the beach across vegetation and into wallows
456 influences heat transfer as they make that transition. Longitudinal behavioural observations concurrent
457 with heat flux and surface temperature measurements are recommended as the next step to examine more
458 fully the relationship between behavioural and physiological adaptations that facilitate the moult process.
459 This research may be particularly relevant for SES adapted to changes in environmental conditions in
460 polar regions.

461

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475 accordance with the ethical standards of the institutions or practice at which the studies were conducted.

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633 **Tables**

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Animal sex	Date		Mass (kg)		Length	Girth (cm)		iButton® (°C)	Heat flux (W.m ⁻²)	
	Capture	Recapture	Capture	Recapture		Capture	Recapture		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	NA
31 J ♀	24/12/2014	NA	222.0	NA	212	150	NA	NA	115.67 ± 8.63	NA
32 J ♀	24/12/2014	NA	268.0	NA	207	170	NA	NA	185.62 ± 4.46	NA
33 J ♀	24/12/2014	NA	183.0	NA	192	144	NA	NA	167.10 ± 6.67	NA
34 J ♀	25/12/2014	NA	185.0	NA	166	153	NA	NA	175.15 ± 4.04	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	NA
44 A ♀	25/01/2016 (P)	NA	326.5	NA	247	177	NA	NA	96.00 ± 2.15	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	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
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	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	NA
52 A ♀	28/01/2016 (P)	02/02/2016 (P)	265.5	250.5	230	154	167	NA	103.54 ± 4.72	NA
53 A ♀	28/01/2016 (P)	NA	284.0	NA	227	170	NA	NA	134.07 ± 6.50	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	NA
56 A ♀	16/02/2016	22/02/2016 (P)	308.5	290	228	170	171	NA	NA	277.22 ± 4.18
57 A ♀	17/02/2016 (P)	NA	420.0	NA	250	193	NA	NA	NA	145.18 ± 2.93
58 A ♀	17/02/2016 (P)	25/02/2016 (P)	265.5	248.0	203	210	165	NA	132.82 ± 1.81	128.86 ± 3.11
59 A ♀	21/02/2016	26/02/2016	NA	383.5	253	NA	187	NA	146.39 ± 1.75	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 (W.m⁻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. P next to dates indicates 3D photogrammetry. NA values indicate no data were collected.

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Environmental measure	Habitat type		
	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)

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

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658 **Figure Captions**

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

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

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

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

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

677 **Fig. 6.** ANCOVA predictions of corrected mean multiple of resting metabolic rate (RMR multiplier) according
678 to allometric equations by Kleiber (1932) (left y-axis) in three different habitat types; vegetation, wallow and
679 beach (x-axis) based on heat flux calculations. Also shown are predicted values for RMR multiplier converted to
680 $\text{kJ}\cdot\text{day}^{-1}$ (right y-axis). 95% confidence intervals of corrected means are also shown.

681 **Fig. 7.** Predictions (solid black line) of body surface temperature ($^{\circ}\text{C}$) (y-axis) dependent on body mass index
682 ($\text{BMI} (\text{kg}\cdot\text{m}^{-2})$) (x-axis). 95% confidence intervals of predictions (grey) are also shown. Black circles indicate
683 mean body surface temperature for each value of BMI.

684



Fig. 1



Fig. 2

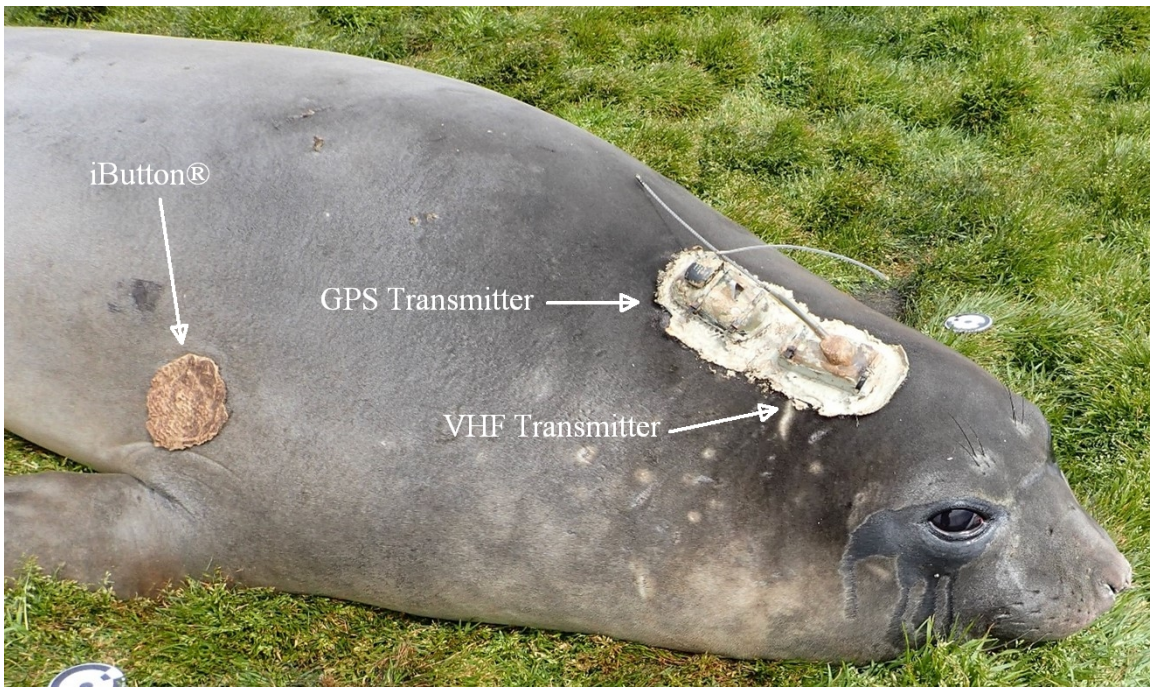


Fig. 3

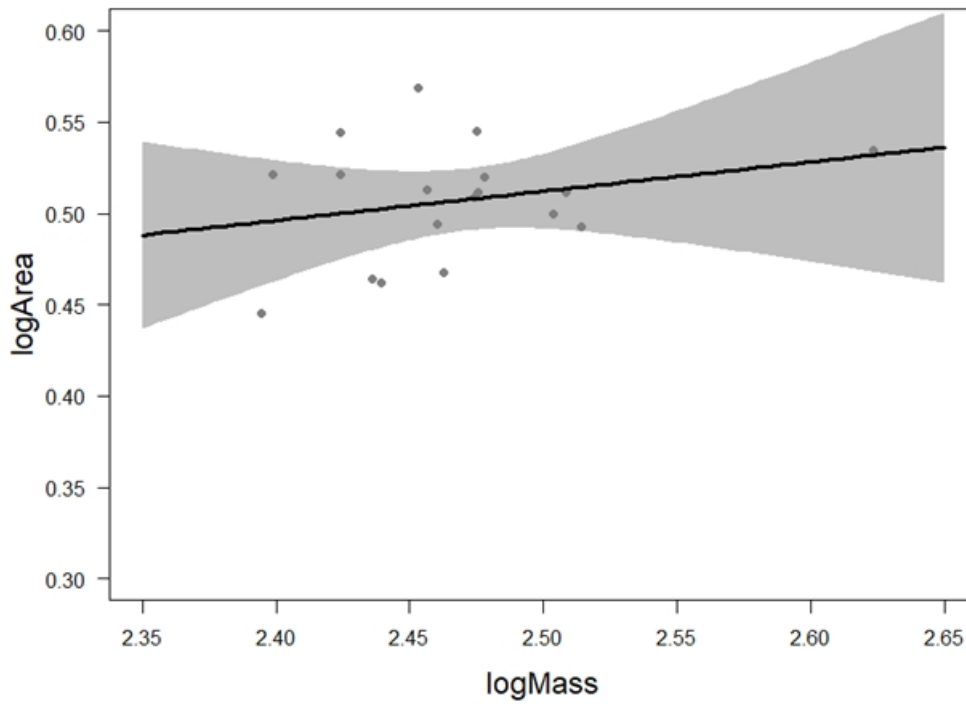


Fig. 4

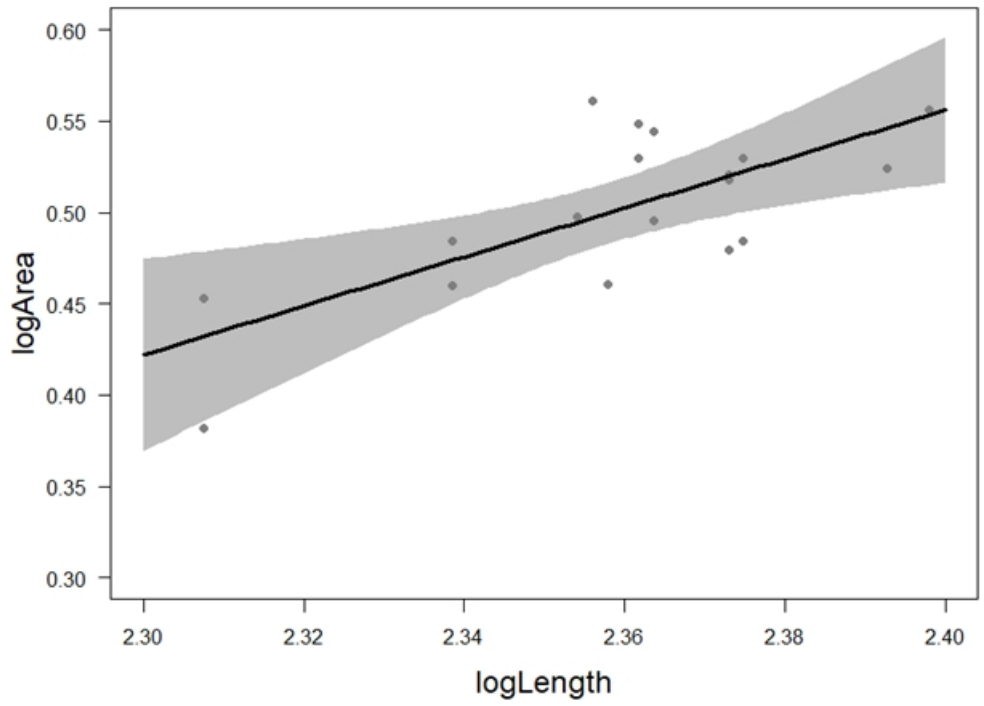


Fig. 5

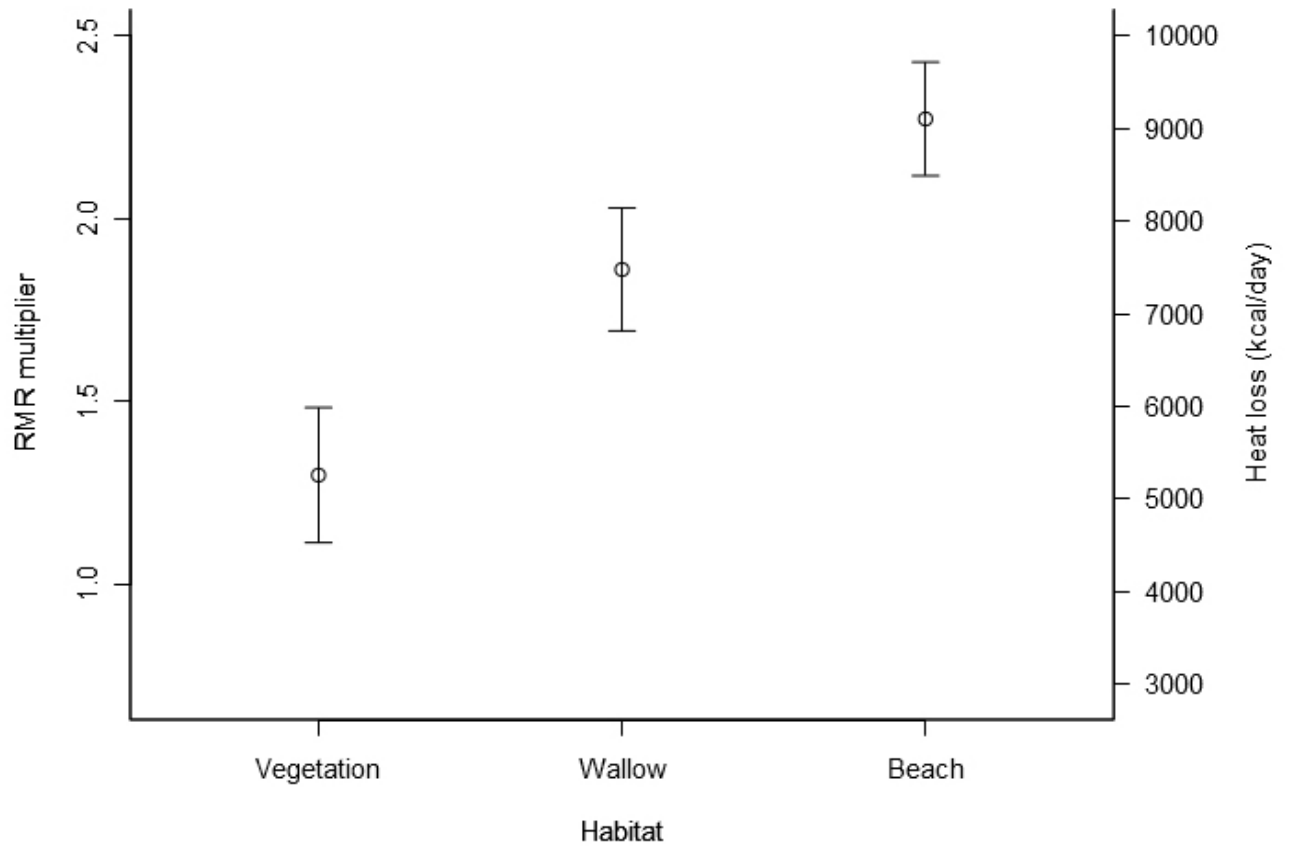


Fig. 6

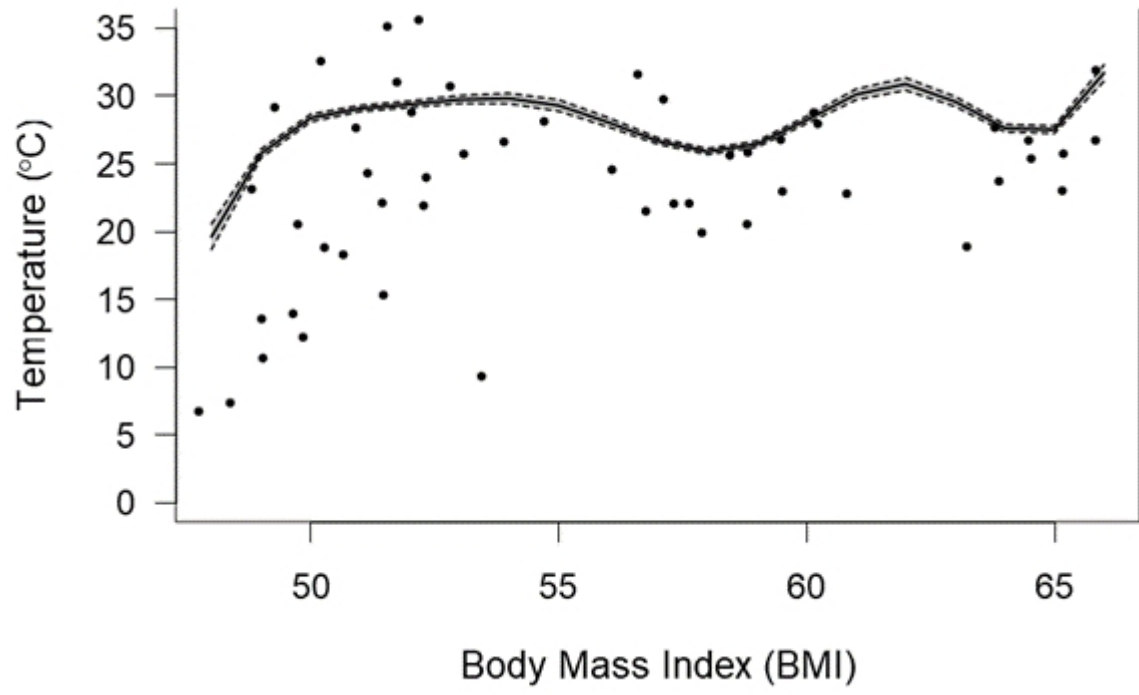


Fig. 7