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1 **Title**

2 Breaking the fast: First report of dives and ingestion events in molting southern elephant seals.

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17

18 **Abstract**

19 Southern elephant seals (SES) experience a 'catastrophic molt', a costly event characterized by the
20 renewal of both hair and epidermis that requires high peripheral vascular circulation. Molting animals
21 are therefore constrained by high metabolic heat loss and are thought to fast and remain on land.

22 To examine the ability of individuals to balance the energetic constraints of molting on land we
23 investigate the stomach temperature and movement patterns of molting female SES.

24 We find that 79% of females swam and 61% ingested water or prey items, despite the cost of cold-water
25 exposure while molting. This behavior was related to periods of warm and low wind conditions, and
26 females that dived and ingested more often, lost less body mass.

27 We conclude that the paradigm of fasting during the molt in this species, and the fitness consequences
28 of this behavior should be reconsidered, especially in the context of a changing climate.

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Introduction

Molting is an important physiological event of partial or total renewal of integuments, which is influenced by season, growth, age, and environmental conditions^{1,2}. This process occurs in a large variety of species, including mammals³⁻⁵, birds^{5,6}, reptiles^{7,8}, fishes⁹ and arthropods¹⁰. Molting is involved with a change in coat or plumage color, that may be related to reproductive success and camouflage in the environment^{5,11}, growth¹⁰, thermoregulation¹², and defense against parasites or pathogens⁷, hence playing an important role in the fitness of an individual. However, molt is an energy demanding process¹³ requiring high peripheral vascular circulation to promote skin cell proliferation and tissue growth¹⁴, and a high metabolic rate to balance heat loss^{15,16}.

Most Antarctic and sub-Antarctic phocid seals undergo an annual molt⁴. While seals are well adapted for an aquatic life, they are obliged to come ashore (on land or ice floe) to molt^{17,18}. In phocids, regrowth of skin and fur requires a skin temperature above 17°C¹⁹. Maintenance of this warm temperature in polar regions leads to elevated metabolic rate^{15,16,20}. To reduce energy expenditure during the molt, seals are insulated with thick subcutaneous blubber^{21,22}, regulate peripheral blood flow, and avoid even higher heat loss by hauling out to minimize time in cold water, where heat loss is 25 times faster than in air^{23,24}. Even with these actions, molting metabolic rate is 2-3 higher than resting metabolic rate^{14,24}. The extent to which time in water, particularly during the molt, may affect thermoregulatory costs is poorly understood.

Southern elephant seals (SES) are one of only four species of phocids that undergo a 'catastrophic molt', during which they renew both their hair and cornified epidermis^{25,26}. Of the four species, they are the only one to undergo the molt in a polar environment (other species: northern elephant seal (NES), *Mirounga angustirostris*²², Hawaiian monk seal (*Monachus schauinslandi*)²⁷, and Mediterranean monk seal (*Monachus monachus*)²⁸). During this period, like other phocids, they lose a large proportion of their body mass (23% SES²⁹, 25%, NES²², 17%, gray seals *Halichoerus grypus*³⁰). This large change, combined with the increased peripheral circulation which would result in high heat loss in water, led to the conclusion that elephant seals fast and remain on land during the molt^{22,31-33}. While ashore, they are exposed to a range of meteorological conditions. SES molt on subantarctic islands, they experience cold, wet, and windy conditions during the approximately one-month haulout³⁴. Environmental conditions strongly influence heat flux between an animal and the environment. SES minimize heat loss through social thermoregulation in large aggregations and through choice of different beach habitats such as grass or mud pools^{35,36}. Therefore, we would predict that only animals with sufficient energy reserves to cover the cost of fasting, molting, and cold-water contact would be able to go to sea during the molting period.

69 A high energetic cost during the molt increases the depletion of energy reserves in blubber, with
70 possible fitness consequences, such as lower survival or reproductive success for seals^{37,38}. Climate in the
71 Southern Ocean is rapidly changing, and environmental conditions are known to impact heat loss and
72 molting phenology in phocids^{15,39}. In this context, understanding how energetic constraints and
73 individual strategies may help reduce metabolic costs of animals during key stages of their lifecycle is
74 important. While it is commonly agreed that molting SES remain on land and rely on their reserves,
75 breaking the fast has already been suggested as a mechanism to mitigate physiological costs while
76 molting by restoring blubber reserves or limiting metabolic water production³¹. However, few studies
77 examined movement and potential drinking or feeding behavior in this species throughout the molt. One
78 way to investigate at-sea feeding or dinking behavior is to combine stomach temperature measurements
79 with time-depth recorders (TDRs). This allows detection of possible cold water or prey item ingestion
80 through stomach temperature changes and to record the depth and location of ingestion events. This
81 approach has previously been used in seabird research (penguins, cormorants, albatrosses⁴⁰⁻⁴³, and
82 captive or non-captive pinnipeds (NES and Californian sea lions^{20,44}), but not during the molt.

83 In this study, we investigated the behavior of adult female SES during the molt. Females were
84 instrumented with TDRs to document diving behavior and stomach temperature pills to document
85 ingestion events. We hypothesized that female SES would remain on land, either in mud pools or on the
86 beach, fasting, at least in the early stages of the molt to minimize heat loss. If seals did spend time at sea,
87 we investigated if weather conditions influenced this behavior. Last we hypothesized that only females in
88 good body condition would spend time at sea, as they have sufficient energy reserves to compensate for
89 high heat loss.

90

91 **Results**

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93 Combining diving analysis and stomach temperature recording, the monitoring duration was
94 7.0 ± 2.9 days of analyzed data (between 2 and 14 days of recording). Females arrived on land with a
95 body mass of 314.7 ± 41.4 kg (BMI of 59.4 ± 5.1 kg/m²). Molt stage when animals were equipped was 54
96 $\pm 25\%$ with 41% of the females caught at the initial stage ($n = 16$), 41% at the mid stage ($n = 16$), and 18%
97 at the final stage of molt ($n = 7$). Body mass at the end of the monitoring averaged 294.5 ± 37.7 kg,
98 resulting in a daily body mass loss of 3.2 ± 1.4 kg per day. At this point all females were at the final stage
99 of molt, with more than 90% of hair renewed. During the monitoring period, the mean daily wind speed
100 was 8.8 ± 2.7 m/s (ranging from 2.8 to 18.4 m/s), mean daily air temperature was 8.4 ± 2.4 °C (ranging
101 from 4.4 to 15.3 °C), mean daily total sunshine duration was 355.3 ± 219.9 minutes (ranging from 0 to
102 855 minutes) and mean daily relative humidity was $70.2 \pm 7.7\%$ (ranging from 50.7 to 91.6%).

103

104 Diving and surface swimming behavior

105 Between 2014 and 2022, 39 female elephant seals were captured and monitored and 79% went
 106 to sea (n = 31). A total of 660 dives were recorded, grouped in 77 dive cycles (Table 1), for 39% of the
 107 monitored females (n = 15). Mean dive duration was 7.7 ± 3.6 minutes, with a mean time to reach
 108 maximum depth of 3.2 ± 3.1 minutes, followed by a mean surface phase duration of 2.2 ± 2.5 minutes.
 109 Dive cycles had an average duration of 1.4 ± 1.7 hours.

110 We detected a total of 375 surface swimming events with an average duration of 1.8 ± 2.6 hours
 111 grouped in 226 surface swimming cycles. Seventy-seven percent of monitored females (n = 30)
 112 performed surface swimming. Fourteen animals dived and surface swam. One female only dived.

113 On average, instrumented females spent time in the water (diving or surface swimming) every other day
 114 (% of monitored days with at-sea events = $49.2 \pm 23.9\%$). The amount of time they spent in the water
 115 ranged from 9.0 to 92.8% of the day.

116 At-sea behavior was more diurnal, as 57% of the dives and 66% of the surface swimming occurred during
 117 the daytime.

118

119 **Table 1: Summary of diving parameters from 31 female southern elephant seals during the molt**

120 Among 31 female who went at sea, 15 dived (n = 660 dives, 77 dive cycles and 226 episodes of surface
 121 swimming; 2014-2022). ‘At-sea events’ include both surface swimming and diving.

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	Mean (SD)	Min - Max
Estimated time spent at sea per day per individual (min)	109.32 (98.3)	1.0 – 391.0
Mean number of at-sea events per day per individual	1.1 (0.8)	0.1 – 2.8
Total number of dive cycles per individual	5.1 (5.5)	1 - 22
Total number of dives per dive cycle	8.6 (10.8)	1 - 49
Total number of dives per individual	44.0 (55.0)	1 - 157
Maximum dive depth (m)	12.5 (7.3)	5 - 43
Dive duration (min)	7.7 (3.6)	0.2 – 22.5
Time at surface (min)	2.2 (2.5)	0.3 - 19.3
Surface swimming duration (h)	1.8 (2.6)	0.2 – 26.7

129 Stomach temperature

130 Excluding temperature drops during the ingestions, mean at-sea stomach temperature was
 131 higher than on land (at sea = $37.1 \pm 0.3^\circ\text{C}$, on land = $36.5 \pm 0.2^\circ\text{C}$, Student test, $t = -7.3$, $df = 49.6$, p -value
 132 < 0.0001). On land temperature analysis revealed hyperthermia events (from 1 to 3 events per
 133 individual) for 61.5% of the animals ($n = 24$), with a mean stomach temperature of $38.1 \pm 0.3^\circ\text{C}$. In total,
 134 33 hyperthermia events of 110 ± 39 min were analyzed, and the first at-sea event occurred within
 135 24.5 ± 21.0 hours after.

136 A summary of ingestion event variables is available in Supplementary Table S1. We recorded a
 137 total of 87 ingestion events (Table 2), from 80% of individuals ($n = 31$ from total $n = 39$), with an average
 138 of 2.8 ± 2.1 ingestions per individual. Among these events, 70% occurred during the daytime.

139 A total of 10 ingestion events were detected during a dive (12%) and 42 events occurred during surface
 140 swimming (49%). Due to bad Argos locations, the remaining 37 events (39%) were not clearly
 141 characterized as at sea or on land, but were not associated with complete submersion of the animal
 142 according to wet and light sensors. These ingestion events could have happened strictly on land or in the
 143 tidal zone.

144 Results of the different methods from the literature⁴⁴ are reported in Table 2 and based on the different
 145 methods, 25 to 53% of the ingestions were classed as potential prey ingestions.

146

147 **Table 2: summary of ingestion type based on Kuhn and Costa (2006) results, from 31 female southern**
 148 **elephant seals monitored between 2014 and 2022 ($n = 87$ events).**

149 T_1 is the initial stomach temperature and T_2 the minimum temperature during the ingestion event.

Method	Threshold for feeding events	Number of feeding events
Index of rate of temperature recovery I ($\text{s}\cdot^\circ\text{C}^{-1}$)	$I \text{ value} > 250 \text{ s}\cdot^\circ\text{C}^{-1}$	$n = 39$ (44%)
Area above the curve ($\text{s}\cdot^\circ\text{C}$)	Integral $> 3000 \text{ s}\cdot^\circ\text{C}$	$n = 25$ (29%)
Time of temperature recovery (Δt between T_2 - T_3)	$t_{\text{rec}} > 35 \text{ min}$	$n = 46$ (53%)
Delta temperature T_1 - T_2	$\Delta T > 4.7^\circ\text{C}$	$n = 22$ (25%)

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151 Determinants of female SES behavior

152 At-sea behavior was not determined by initial physiological parameters; individual swimming
 153 score and the number of ingestions per female were influenced neither by BMI nor molt stage (Tables 3
 154 and 4).

155 Environmental conditions played a role in SES behavior. We found a positive effect of
 156 temperature and a negative effect of wind speed on the probability of surface swimming (Table 5).

157 Females tended to do more surface swimming during days of high temperature and days of low wind

158 speed (Figures 1A and 1B). The probability of diving was not related to meteorological conditions
 159 (Table 5).

160 We also found a positive effect of sunshine duration on the probability of ingestion. The probability of
 161 recording individuals that ingested increased during days with high total sunshine duration (Figure 1C).
 162 The effect of relative humidity and wind speed on ingestion was not significant (Table 5).

163

164 **Table 3. Best models to explain female southern elephant seals swimming score variability**

165 ANOVA table of the best linear mixed effect models for at-sea behavior (PC1 and PC2): diving (n=15) or
 166 surface swimming (n=31).

Response variable	Behavior / group	Explanatory variables	X ²	Df	P	AICc
PC1	Diving	Monitoring duration	13.43	1	< 0.001 ***	63.3
PC2	Surface swimming	Monitoring duration	0.34	1	0.56	56.5

167 *** : p-value < 0.001

168

169 **Table 4. Best models to explain female southern elephant seals ingestion behavior variability**

170 Summary of coefficients and goodness-of-fit indices from the best models for the number of ingestions
 171 (generalized linear models fitted with negative binomial law), at-sea (n=32) or on land (n=7).

Response variable	Location	Explanatory variables	Coefficient ± SE	Z	P
Number of ingestions	At-sea	Intercept	0.54 ± 0.43	0.95	0.20
		Monitoring duration	0.03 ± 0.05	1.07	0.51
	On land	Intercept	-1.95 ± 2.95	-0.66	0.51
		Monitoring duration	0.29 ± 0.48	0.60	0.55

172

173 **Table 5. Summary of coefficients and goodness-of-fit indices from the best models for environmental
 174 conditions effect on female southern elephant seals behavior**

175 Generalized linear models were fitted with binomial (probability of ingesting) or quasibinomial
 176 (probability of diving and surface swimming) law. Females behavior is separated as diving behavior (n=15
 177 females), swimming behavior (n=31 females), ingesting behavior (n=31 females).

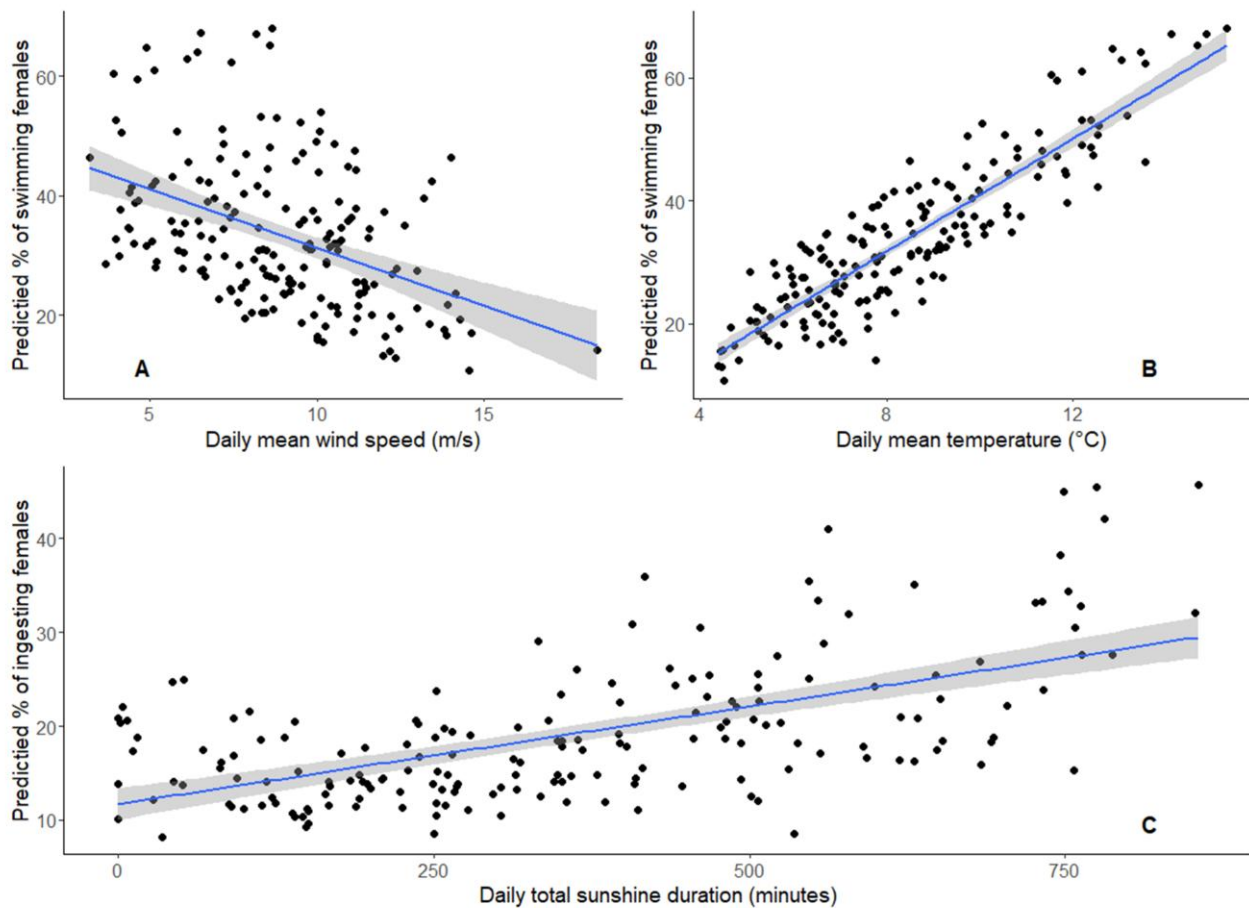
Response variable	Explanatory variables	Coefficient ± SE	t	P
Daily proportion of diving females	Intercept	-1.7 ± 0.8	-2.0	0.04 *
	Temperature	0.06 ± 0.08	0.8	0.44
	Wind speed	-0.09 ± 0.06	-1.4	0.16
Daily proportion of surface swimming	Intercept	-1.6 ± 0.6	-2.7	0.008 **
	Temperature	0.21 ± 0.06	3.7	<0.001 ***

females	Wind speed	-0.10 ± 0.05	-2.1	0.03 *
Daily proportion of ingesting females	Intercept	-3.7 ± 1.7	-2.1	0.03 *
	Sunlight	0.001 ± 0.0006	2.8	0.02 *
	Humidity	0.03 ± 0.02	1.7	0.09
	Wind speed	-0.09 ± 0.05	-1.8	0.07

178
179 * : p-value < 0.05; ** : p-value < 0.01; *** : p-value < 0.001

180
181 **Figure 1: Relationships between meteorological conditions and behavior of female southern elephant**
182 **seals using.**

183 A: GLM predicted daily proportion of swimming females with daily mean wind speed (m/s). B: GLM
184 predicted daily proportion of swimming females with daily mean temperature (°C). C: GLM predicted
185 daily proportion of females that ingest with total daily sunshine duration (min/day).



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188 Consequences on female SES condition

189 Female SES condition at the end of the molt was influenced by their behavior. For females going
190 to sea, we found a positive relationship with the swimming score (PC1) and of the number of ingestions
191 on daily body mass loss (Table 6). Females that dived and ingested more often were in better body
192 condition at the end of the molt (Figures 2A and 2B).

193

194 **Table 6. ANOVA table of the best linear mixed effect models for female southern elephant seals**
 195 **condition at the end of the molting period.**

196 Body mass loss is used as a proxy for female southern elephant seals condition. Females are grouped by
 197 location: on land (n=6) or at sea (n=12).

Response variable	Location	AICc	Explanatory variables	χ^2	Df	P
Body mass loss	On land	46.9	Mass start	0.38	1	0.53
			Length	0.27	1	0.61
			Monitoring duration	1.41	1	0.24
	At-sea	126.7	Mass start	0.02	1	0.89
			Length	0.37	1	0.54
			PC1	8.19	1	0.004 **
			Number of ingestions	4.42	1	0.03 *
			Monitoring duration	10.65	1	0.001 **

198 * : p-value < 0.05; ** : p-value < 0.01

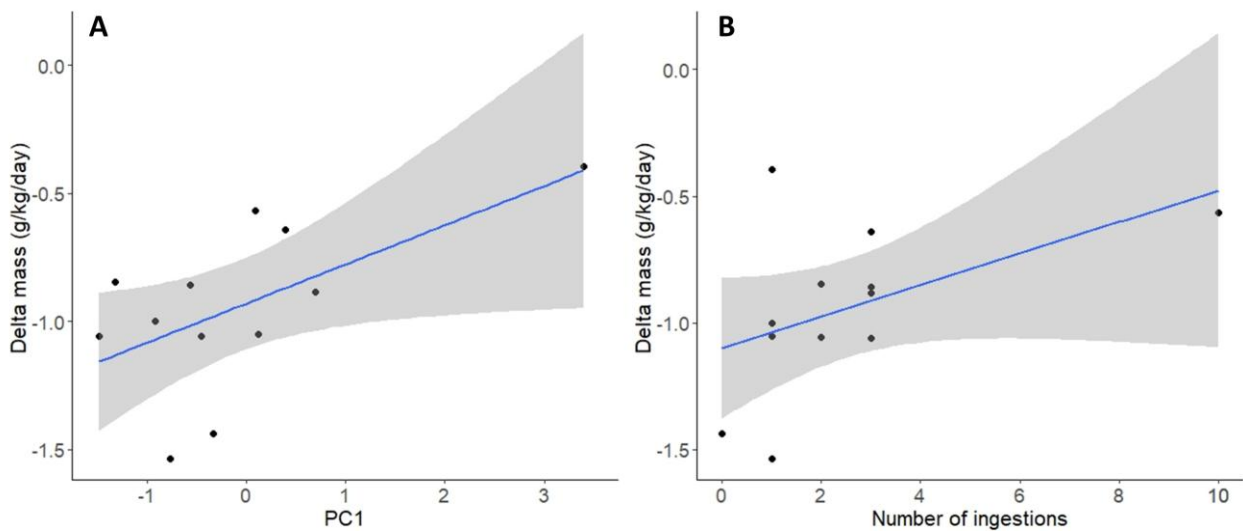
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200

201 **Figure 2: Daily mass loss per unit of body mass (g/kg/day) of female southern elephant seals according**
 202 **to their behavior.**

203 A. Diving score (PC1 as individual values on the first component of the PCA) and B. Number of ingestions
 204 per individual. Individuals with high PC1 values perform more dives, that last longer, and show more
 205 surface swimming.

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211 **Discussion**

212 Through the use of TDRs and STP, we identified surface swimming, diving, and ingestion events
213 during the molt of female SES. To our knowledge, this study is the first to show evidence of SES breaking
214 the fast during this energetically costly molt period.

215 We found no evidence of adverse effects of the STP on the behavior and body condition of animals at
216 the end of the monitoring period. The STP assembly remains in the stomach, and the potential effect on
217 satiety or ability to ingest was not possible to test. However, no such adverse effects have been
218 described in experimental studies on pinnipeds⁴⁴, probably due to the short retention time and small size
219 of the STP compared to the volume of the stomach.

220

221 Our data revealed that female SES went to sea during the molt, as reported in Table 1 and
222 Figure S1. Indeed, nearly half of equipped individuals performed several dives, from 5 to 43 m.

223 To our knowledge, this behavior has not been reported yet in a species displaying a 'catastrophic' molt,
224 including aquatic birds and mammals⁴. In marine mammals, pinnipeds undergoing such an extreme
225 physiological event, such as elephant seals^{22,31-33,45}, have always been thought to rely exclusively on
226 energy reserves in blubber during the molt. All birds experiencing catastrophic molt are known to fast
227 and avoid cold water contact, as demonstrated in cormorants⁴⁶ and penguins⁴⁷. Few diving birds are
228 known to break the fast and dive during the molting period, but they undergo a rapid simultaneous molt
229 that is not reported as 'catastrophic' (common eider *Somateria mollissima*⁴⁸, lesser snow geese *Chen*
230 *caerulescens caerulescens*⁴⁹, and grebes *Podiceps sp.*⁵⁰). Therefore, our results reveal that SES may be the
231 first recorded case of a species experiencing a catastrophic molt while also spending time at sea, despite
232 the potential energetic costs.

233 Although female SES dove during their molting fast, diving parameters differ from diving foraging
234 parameters. Indeed, most of the dives were not deeper than 11.5 m and lasted on average for almost
235 7 minutes, compared to average foraging dive depth and durations of 400 m and 30 minutes⁵¹⁻⁵⁴,
236 respectively. SES are known to perform deeper dives according to prey distribution, migration, or
237 predation avoidance⁵⁵⁻⁵⁷. Cold water exposure at shallow depths during this period thus requires further
238 investigations to better understand the reasons for such behavior.

239 According to our data, female SES dive during the molt but also ingest water and/or food, which
240 challenges the paradigm of fasting. Indeed, stomach temperature clearly shows that 80% of diving
241 females ingest water and/or prey. Such behavior has already been suggested³¹ as metabolic rate
242 calculations based on water flux during the molting period indicate that water ingestion takes place, but
243 no food was found in the stomachs of females. In our study, the type of ingestion (water and/or prey)
244 remains unclear. Indeed, the results differ between the different methods of estimation, as supposed
245 feeding events represent approximately 25 to 53% of ingestion events (Table 2), which is greater than
246 previously described through behavioral and movement patterns⁵⁸.

247 It is difficult to distinguish between water or prey ingestion events in pinnipeds. While index I values
248 (index of the rate of stomach temperature recovery, see Method section) of less than $30 \text{ s} \cdot ^\circ\text{C}^{-1}$ always
249 denoted water ingestion for albatrosses²³, for pinnipeds, this distinction was more complicated⁴⁴. In a
250 previous experimental study, index I values for prey ingestion ranged from 55.1 to $4380.0 \text{ s} \cdot ^\circ\text{C}^{-1}$, while
251 water ingestion ranged from 37.8 to $764.0 \text{ s} \cdot ^\circ\text{C}^{-1}$. The previous study used a threshold of $250 \text{ s} \cdot ^\circ\text{C}^{-1}$ to
252 distinguish fish from water consumption, as this value lowered the error rate of identification, but
253 uncertainty remained⁴⁴. We used the same threshold in our study but as sea surface temperature was
254 different (around 14°C in the experimental study⁴⁴, and 8°C in Kerguelen during the molting period³⁴), it
255 may distort variable calculations and so ingestion type. In our study, as 49% of ingestion events occurred
256 during surface swimming (i.e., depth between 0 to 5 m), and regarding prey repartition⁵⁶, half of
257 ingestion events may likely involve water.

258 Across taxa, catastrophic molts in birds and mammals have always been associated with fasting⁴. It
259 appears that SES may be the first species reported to break the fast during this energetically costly
260 period, but why?

261

262 In this study, we found that meteorological conditions influenced the behavior of molting female
263 SES. The weather effect on social thermoregulation and habitat preference has already been described
264 during the molt in this species^{35,59}. Meteorological conditions influence the behavior of molting
265 pinnipeds, such as haulout frequency and time spent on land, but it has only been investigated in species
266 of phocid seals that do not undergo a catastrophic molt and keep foraging at sea during this period^{15,39}.
267 Our data revealed that during days with low wind speed and days with high air temperature, female SES
268 tend to swim more often. The same parameters were reported to influence the number of molting
269 Weddell seals (*Leptonychotes weddellii*) hauling out on ice, but surprisingly, it was the opposite behavior,
270 as Weddell seals tend to remain in the water when wind speed is elevated and air temperature are low³⁹.
271 Meteorological conditions strongly differ between Kerguelen and Antarctica, where Weddell seals are
272 found. If daily wind speed is nearly equal ($8.8 \pm 2.7 \text{ m/s}$, ranging from 2.8 to 18.4 m/s in Kerguelen and
273 $5.3 \pm 4.2 \text{ m/s}$, ranging from 0.7 to 19.8 m/s in Syowa station), air temperature does not go below 0°C
274 during the molting period in Kerguelen ($8.4 \pm 2.4^\circ\text{C}$, 4.4 to 15.3°C versus $-8.3 \pm 5.3^\circ\text{C}$, with a maximum
275 of 1.7°C in Syowa). Weddell seals and SES are not exposed to the same environmental conditions during
276 their molting period, but both could lead to thermal discomfort. The thermoneutral zone (TNZ) is a range
277 of temperature between a lower and upper threshold, between which the metabolic cost associated
278 with thermoregulation is the lowest⁶⁰. Out of this range, animals are hypo- or hyperthermic, resulting in
279 higher metabolic costs (thermogenesis) or heat dissipation (thermolysis) to avoid deleterious effects of
280 overheating on the organism, such as water loss, cell-damage, and disruption of reproductive
281 function^{61,62}. Consequently, any supplementary energetic cost required for thermogenesis or thermolysis

282 in both hypothermia or hyperthermia may increase energy depletion^{37,38}. Moreover, as phocid seals
283 obtain their water requirements from the metabolism of fat reserves^{63,64}, compensating for metabolic
284 water loss triggered by heat stress could be extremely costly. Going to sea could be a way to avoid
285 extreme weather events when seals are out with their TNZ, leading to thermal discomfort and to other
286 physiological effects. As SES remain in a warmer environment, they should avoid overheating and
287 minimize elevated metabolism and increased water loss on warmer days, while Weddell seals, exposed
288 to colder conditions, would go to sea to reduce metabolic costs of thermogenesis in bad weather
289 conditions.

290 We were not able to obtain solar radiation in W/m^2 , but instead used sunshine duration (minute per
291 day), which is a less precise estimate of the thermal power received at the surface of the skin. The effect
292 of sunshine duration was not significant in initiating at-sea movements in our females, but solar radiation
293 was already reported to be positively correlated with swimming behavior during the breeding period of
294 females NES⁶⁵ and other pinnipeds^{66,67}. Heat dissipation is maximized by peripheral vasodilatation and by
295 an important thermal gradient through thermal windows (surface temperature-air temperature⁶⁸). If
296 peripheral circulation is already increased during the molt, and solar radiation heats blood at the skin
297 surface, heat loss by radiation or convection may not be sufficient to cool down and prevent thermal
298 stress during warm days. Because of the high cooling capacity of water, going to sea would be the most
299 efficient method to dissipate heat⁶⁶. This suggests that SES could be subject to thermal stress and go into
300 the water to avoid overheating, especially during the molt when vasodilatation at the skin surface
301 occurs.

302 Total sunshine duration was correlated with the number of ingestion events in our females. As ingestion
303 events were rare during a dive (12% of ingestion events), this would be more consistent with drinking
304 than foraging. Drinking at sea has already been reported in gray seals⁶⁷ and would be in line with a
305 behavioral response to thermal stress to avoid supplementary metabolic costs and blubber depletion
306 needed to restore hydration if they remain on land.

307 Although the majority of our results confirm a behavioral response to thermal stress, few hyperthermia
308 events were detected (from 1 to 3 events for 61.5% of the animals) and were not related to an
309 immediate at-sea event (first at sea event within 24.5 ± 21.0 hours after a detected hyperthermia). In
310 breeding NES, a strong effect of solar radiation on surface temperature was reported and was related to
311 at sea movement⁶⁵. As heat is gained by radiation, an increase in surface temperature may be most
312 relevant to hyperthermia events. Considering the blubber thickness in phocid seals⁶⁹⁻⁷¹, behavioral
313 responses to high surface temperature (i.e. going to sea) may occur rapidly after an increase in surface
314 temperature, probably before stomach temperature increased through heat diffusion by conduction.
315 This may question the relevance of using stomach temperature for detecting overheating in response to
316 environmental factors in this species.

317 Finally, our data did not show any link between at-sea movements and stage of molt, where we expected
318 more at sea movements when heat loss is reduced at the end of the molt¹⁵. This may indicate that heat
319 loss and the metabolic cost of cold-water immersion are not limiting factors for this behavior, in line with
320 possible thermal stress events and the need for heat dissipation rather than conservation.

321

322 Considering high energetic constraints triggered by cold water contact and previous studies
323 reporting that body condition could influence molting duration⁷², we thought female SES with a high BMI
324 would be less constrained by energetic trade-off and spend more time at sea than females in lower body
325 condition. However, our data did not find any evidence that body condition influenced the behavior of
326 molting females, neither at-sea movements nor ingestion events. Molt stage also did not influence
327 female behavior despite less energetic constraints at the end of the molt¹⁵, which suggests an
328 environmental rather than a physiological driver of this behavior.

329 Moreover, going to sea during the molt might not be as costly as we believed. Daily specific body mass
330 loss of our females was a good indicator of energetic loss during the molt. A previous study reported that
331 the mass loss of female elephant seals averages 4.7 kg/d, during 25 to 30 days of molting³¹. Surprisingly,
332 females that went to sea did not lose more body mass than females remaining on land but had higher
333 stomach temperatures, which could reflect a higher metabolic rate, hence higher energy loss at sea.
334 However, previous studies on molting Arctic seals (ringed *Pusa hispida*, spotted *Phoca largha*, and
335 bearded seals *Erignathus barbatus*) reported that metabolic rates were similar when resting in air and
336 water¹⁶. An increase in stomach temperature might be detected at the onset of diving as a result of heat
337 generated by muscles during swimming⁷³, which questions the reliability of STP to estimate metabolic
338 variation.

339 According to our results, females may benefit from trips to sea. Among the females that went to sea, the
340 more they dived and ingested, the less mass they lost. The diving profile of these females was very
341 similar to foraging diving profiles, suggesting they could ingest prey items during their trip. Although
342 depth and duration are very different from typical foraging dives, high shallow biomass sites related to
343 phytoplankton bloom have been located in the vicinity of the Kerguelen Plateau during spring and
344 summer, with a peak between December-February⁷⁴. Many studies have shown that juvenile SES
345 perform shallower dives during their first year at sea and that their diet is mainly composed of krill
346 (*Euphausia sp.*)⁷⁵⁻⁷⁷. As molting females are constrained to stay close to the island until the end of the
347 molting process, they could be limited by the bathymetry and benefit from shallower prey such as krill,
348 which could restore body reserves if the molting period is too long or too costly to rely on body fat. As
349 these are very small prey items, that could also explain the difficulty of distinguishing between water and
350 prey items from ingestion curves. However, no precise information on what was ingested could be
351 determined with this method, and thus this question requires further investigation. Other methods such

352 as sonar tag or video camera⁷⁸⁻⁸⁰ could collect further important information which would determine
353 precisely what is ingested during these trips to sea during the molt

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355 Energetic constraints and metabolic costs associated with molting behavior, as well as the possible
356 fitness consequences, still remain unclear.

357 Whether seals remain on land to limit heat loss and metabolic costs from unavoidable perfusion during
358 the molt or whether this behavior allows a faster molt remains uncertain. Avoiding cold water would
359 limit energy expenditure and blubber depletion, while a faster molt would limit fasting duration and
360 extend the next foraging period⁷², resulting in higher at-sea body condition, survival, and reproductive
361 success^{37,38}. Previous studies on ringed and spotted seals did not report supplementary energy
362 expenditure at sea¹⁶, and our data did not show any difference in body mass loss between at-sea and on-
363 land females. This highlights that the physiological cost of molting, i.e., for tissue regeneration, may be
364 greater than the cost of heat loss in cold water. Spending an extended time at sea would be costly by
365 slowing down the molt. Unfortunately, because the molting stage is difficult to determine and to assess
366 without regular visual checks, we were not able to investigate to what extent the amount of time spent
367 at sea influenced the duration of the molting period. This would be of strong interest as this equilibrium
368 of haul out frequency and molt duration may be compromised by current global changes and rapid
369 warming at the poles⁸¹. Thermal stress could affect the behavior of seals, increasing molt duration and
370 causing a greater depletion of blubber reserves. In this context, knowing how molt duration impacted
371 ingestion behavior in females is of interest. Seals with a slower molt may need to restore their body
372 reserves to make sure they end the molting process with sufficient body condition to ensure good
373 foraging success and survival during their next post-molt foraging trip. Thus, the link between energetic
374 constraints, molting phenology, and behavior of SES on land needs further investigation.

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376 This study found that female SES travel at sea during the molt, performing shallow and short
377 dives or surface swimming, and these behaviors were associated with ingestion events. This shows that,
378 SES frequently break the fast and may not always remain on land relying exclusively on blubber reserves.
379 While environmental factors responsible for heat stress were determinants of swimming behavior and
380 likely water ingestion, physiological and fitness consequences of diving and ingestion events need to be
381 further investigated. This will allow a better understanding of the energetic constraints that drive this
382 critical period and the extent to which thermal stress may impact SES. Considering rapid changes in polar
383 climates and possible fitness consequences, the effect of warmer conditions is of particular interest for
384 the conservation of polar phocids.

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386 **Methods**

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Data collection and analysis

All scientific procedures were approved by the Ethics Committee of the French Polar Institute. Data were collected during the austral summer molt (December-February) between 2014 and 2022. The field work took place at three colonies within the Kerguelen Archipelago: Pointe Suzanne (49°26'S, 70°26'E) between 2014 and 2019, Estacade (49°16'S, 70°32'E) in 2020 and 2022, and Port-Aux-Français (49°34'S, 70°21'E) in 2021.

Female elephant seals were captured during the molt and anesthetized using tiletamine and zolazepam (Zoletil® 100^{59,82}). Individuals were equipped with devices provided by Wildlife Computers (USA): TDRs (TDR10-LX-340, 57 x 38 x 30 mm, 75 g in air), Argos satellite transmitters (SPLASH10-L-309D, 76 x 55 x 32 mm, 125 g in air) and Stomach Temperature Pills (TDR-STP-207D, 63 x 21 mm, 31 g in air). Argos location was obtained each day from resulting transmissions. Locations are classified as 3, 2, 1, 0 according to the error radius (<250m, 250-500m, 500-1500m, >1500m). We show an example of good at-sea locations in Supplementary Figure S1. Stomach temperature pills (STP) were placed in the stomach under anesthesia using a lubricated flexible tube, and SPLASH10/TDR10 tags were glued on the head with epoxy bi-component glue (Araldite®). Data-logging tags were set to measure depth (resolution of 0.5 m with an accuracy of 1% of reading), light-level (range from 5×10^{-12} W/cm² to 5×10^2 W/cm² with a resolution of 20 units/decade), stomach temperature (resolution: $\pm 0.1^\circ\text{C}$; accuracy: $\pm 0.3^\circ\text{C}$), and wet/dry sensor every 10 s. Tags were retrieved at recapture, while remaining STP were naturally ejected later at sea or on land. Individuals were recaptured between the completion of the molt and their final departure to sea.

Of the 55 instrumented seals, we obtained stomach temperature data over 2 days from 39 of the seals. Data were analyzed starting from 6 hours following capture (to discard the effects of anesthesia) until the STP was ejected or the seal was recaptured. For each individual, the molting stage was visually estimated at both capture and recapture and during daily monitoring (0-40%: initial stage; 50-80%: mid stage; >90%: final stage, as described in previous study³⁵). Eighteen of the instrumented seals were weighed at capture and recapture, allowing us to calculate the daily mass loss (kg/day). Length (m) was calculated from the mean length measured at capture and recapture. From this, we calculated a body mass index (BMI, kg/m²).

Local meteorological data was retrieved from Météo-France base station archives in Port-aux-Français (Kerguelen archipelago). These data included temperature under cover (°C), relative humidity (%), sunshine duration (min), and wind speed (m/s). Data were recorded per hour and summed per day for sunshine duration.

Data were processed and analyzed using “pandas”, a Python data analysis package (versions: Python 3.10; pandas 1.5.0), and R software (R version 4.1.2).

423 Diving pattern analysis

424 Because Argos locations were poor, diving patterns were analyzed only from depth, light level,
425 and wet/dry sensor data. When necessary, a depth-zero correction was made on land at the time of
426 capture. Diving behavior was determined using a Python algorithm especially developed for this study
427 (Hex·Data, France). To make sure light level variations involved depth and not daily changes, day-night
428 light-level variations were removed using a seasonal decomposition function based on moving averages
429 (function "seasonal decompose" from Python package "statsmodels"; version 0.13.2). We combined a
430 depth threshold of 0.5 m and a "wet" display to spot the start of a dive. To distinguish mud pools
431 (wallows) from sea-water baths, we made sure the light level varied by more than 5 units (values ranging
432 from 0 to 255) during the presumed dive.

433 At-sea behavior was characterized by 1) a submerged phase, 2) a maximum depth, and 3) a
434 surface phase. We distinguished surface swimming and diving behavior according to maximum depth.
435 Surface swimming was defined to occur between 1 and 5 m, with a maximum surface time of 20 minutes
436 between two submerged phases (based on our own data exploration, Figure 3A). Dives were described
437 by a descent, a bottom, and an ascent phase with a maximum depth greater than 5 m and showed
438 different profiles (Figures 3B, 3C, 3D). A dive cycle was characterized by at least two successive dives
439 separated by less than 20 minutes at the surface, as surface duration intervals showed a break around
440 17 minutes. Events were described by their mean duration, mean and maximum depth, and frequency.

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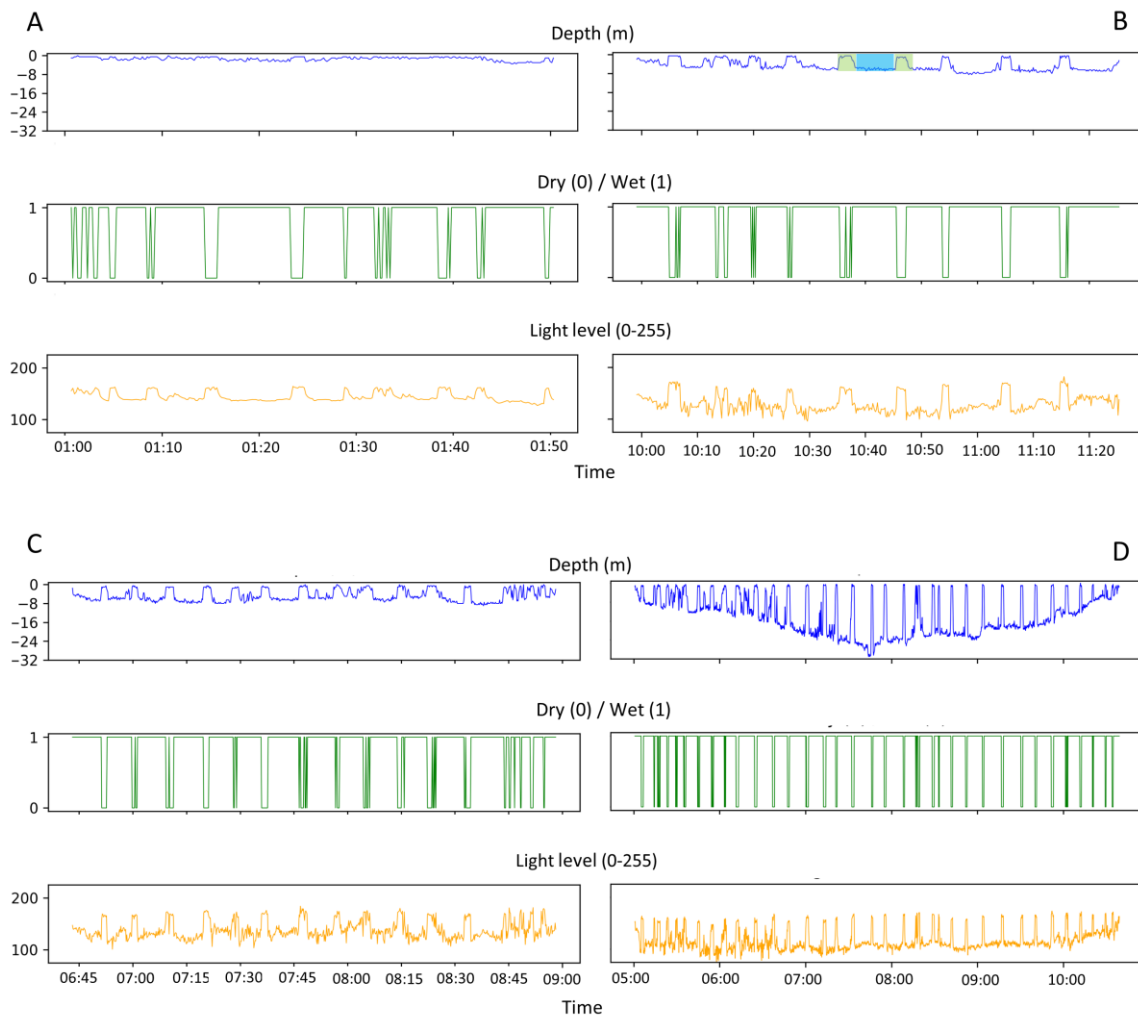
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461 **Figure 3: Diving parameters during different at-sea behaviors; diving or surface swimming.**

462 Surface swimming occurs between 1 and 5 m, while a dive is characterized by a maximum depth of more
463 than 5 m. A dive or a surface swimming cycle is characterized by at least two successive dives or surface
464 swimming separated by less than 20 min at the surface. Fig 3A. represents a surface swimming cycle and
465 different profiles of dive cycles (B, C, D) of a female southern elephant seal in 2017. Each dive is defined
466 by the succession of a submerged phase (blue area) and a surface phase (green area) (B).



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469 Stomach temperature analysis

470 Ingestion events were identified by a sharp decline in stomach temperature followed by a logarithmic
471 increase (Figure 4A, 4B, 4C, 4D). The ingestion detection algorithm identified:

- 472 1. The minimum temperature below 36.5°C (under the lowest core temperature described for
473 elephant seals^{36,44}), referred to as T_2
- 474 2. The previous stable temperature before the drop (T_1 , backward from T_2)
- 475 3. The point at which temperature returned to baseline for at least 10 minutes^{44,83} (T_3 , forward
476 from T_2)

477 T_1 , T_2 and T_3 are illustrated in Figure 4A. Events that were close together were merged into a single event.
478 Each ingestion event was assigned to a female behavior: on land, diving, surface swimming, or unknown.
479 Following the algorithm analysis, a visual check of ingestion curves led to the removal of 12 anomalous
480 events (non-logarithmic curves or abrupt variations consistent with STP measurement errors). The STP
481 was considered lost when the stomach temperature reading remained constant for at least 3 hours.
482 Outliers were deleted using a filter based on the rolling average and bounded by the 1st and 3rd quartiles.

483 To examine STP temperature drift over time, we downsampled the data to one measurement
484 every 15 minutes (factor of 100) and examined the trend in temperature over time using Kendall's tau
485 correlation coefficient. The temperature increased for 16 individuals, decreased for 12 individuals, and
486 did not change for the remaining 11 individuals. The mean absolute value of the correlation coefficient
487 was $\tau = 0.11 \pm 0.09$, with the mean absolute value of the slope estimator $s = 5.1 \cdot 10^{-7} \pm 6.2 \cdot 10^{-7}$,
488 corresponding to a variation of $\pm 0.1^\circ\text{C}$ every 10 days (for 72% of the 39 individuals; $n = 31$). Therefore,
489 based on the temperature pill accuracy ($\pm 0.3^\circ\text{C}$) and mean survey duration (over a week), we considered
490 that the signal drift was trivial and chose not to apply a correction.

491 STP were synchronized with diving patterns, that were filtered with a seasonal decomposition of
492 light-level function to cancel the effect of the day/night cycle. As this function required 48 hours to work,
493 six animals with less than 2 days of recording were discarded ([R documentation](#)). Eight seals ejected the
494 pill before recapture. In total, 80% of monitored seals were recaptured with the temperature pill still
495 recording ($n = 31$), with an average retention duration of 7.2 ± 2.9 days.

496 To distinguish between water and prey ingestions, we followed two published methods^{43,44},
497 using the index of the rate of stomach temperature recovery (I , $\text{s} \cdot ^\circ\text{C}^{-1}$), calculated as follow:

$$498 \quad I = t_{0.5} / (T_1 - T_2)$$

499 where T_1 ($^\circ\text{C}$) is the initial stomach temperature before the drop due to the ingestion of sea water, T_2 ($^\circ\text{C}$)
500 is the minimum temperature reached during the drinking or feeding event, and $t_{0.5}$ (seconds) is the time
501 from the beginning of the temperature decrease to the point of half recovery (half-way temperature
502 between initial T_1 and minimum T_2 ; Figure 4A). The threshold of $250 \text{ s} \cdot ^\circ\text{C}^{-1}$ was used to distinguish
503 between fish and water consumption, as previously reported⁴⁴.

504 We also calculated the area above the curve (integral) of drop in stomach temperature during ingestion
505 events, as it may be related to ingested mass in NES, based on the trapezoid method^{44,73} (for more
506 details, see Supplementary Figure S2).

507 Ingestion events were compiled with dry/wet and light sensor to identify whether they occurred at sea
508 or on land (mud pools).

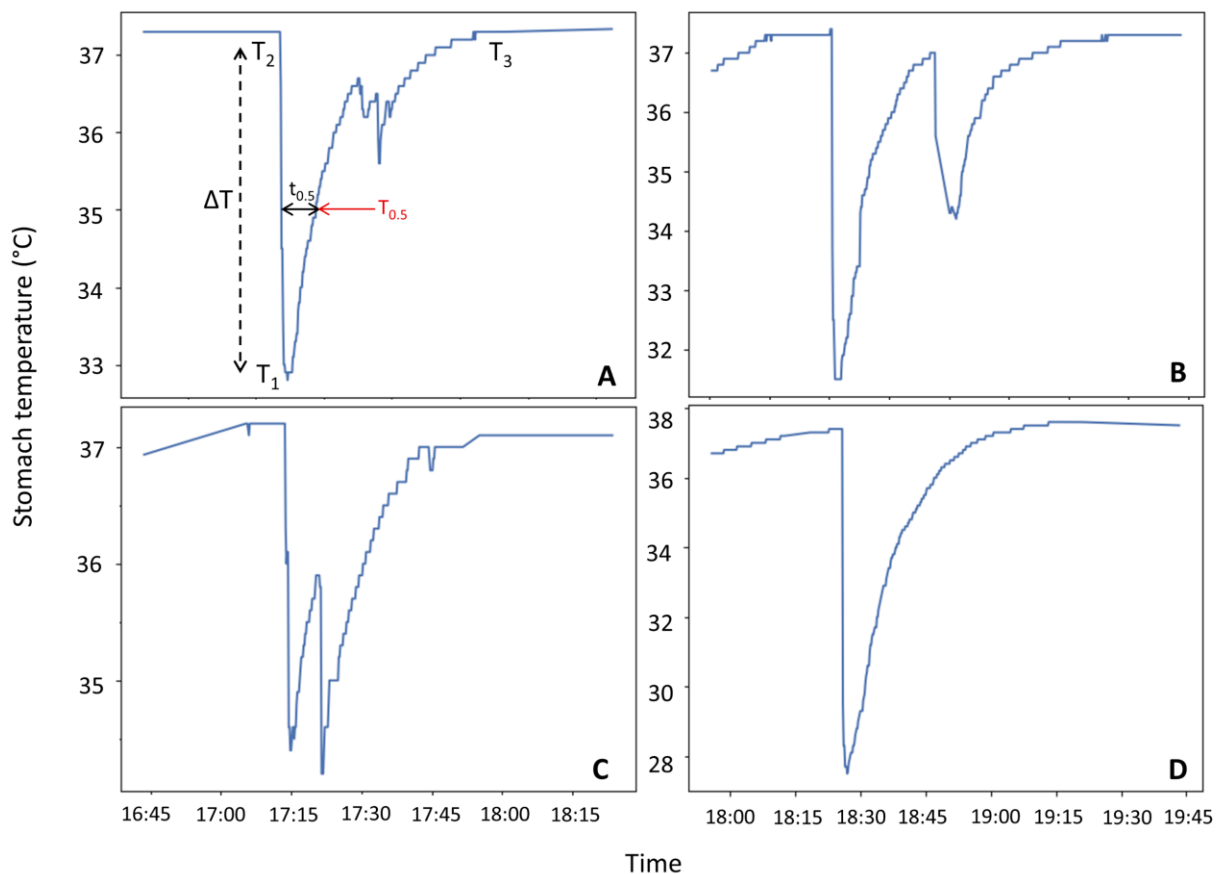
509 We investigated on-land stomach temperatures to detect hyperthermia events that could have
510 initiated at sea movements. We calculated the mean stomach temperature on land ($36.6 \pm 0.2^\circ\text{C}$) and
511 considered hyperthermia if values were higher than the 97.5% quantile for more than one hour.

512

513 **Figure 4: Stomach temperature variations ($^\circ\text{C}$) during ingestion events recorded for two female**
514 **Southern elephant seals in 2014 and 2019.**

515 A: standard temperature variation. B, C: double ingestions. D: extreme temperature variations

516 T_1 is the initial temperature, T_2 the minimum temperature, T_3 the recovery temperature, ΔT the
517 difference of temperature between T_1 and T_2 , $T_{0.5}$ the half-way recovery temperature between T_1 and T_2
518 ($T_{0.5} = T_2 + \Delta T/2$) and $t_{0.5}$ the time of half-way recovery (black arrow: $t_{0.5} = t_{T_{0.5}} - t_{T_1}$). The area above the
519 curve (integral) was calculated from the asymptote.



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523 Statistics and Reproducibility

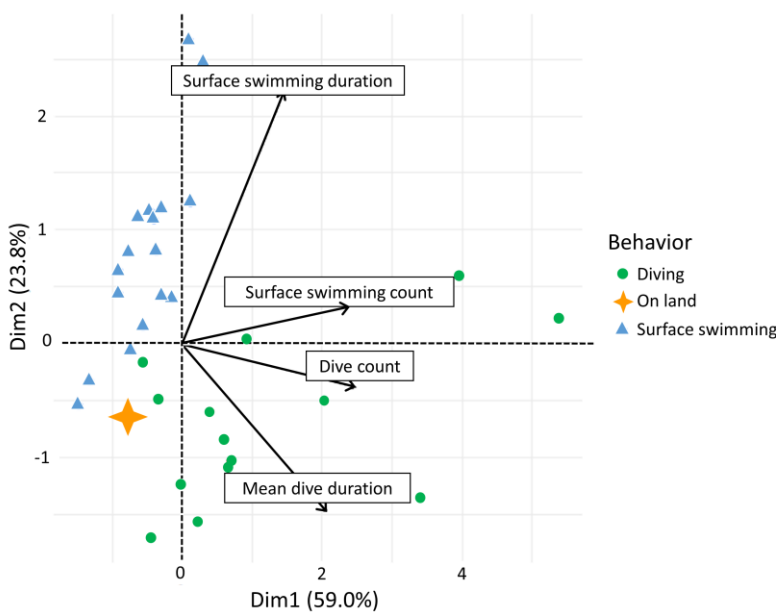
524 Statistical analyses were performed with R software (R version 4.3.1). Results are expressed as
525 mean \pm standard deviation (minimum to maximum), unless otherwise specified.

526 As at-sea behavior and diving parameters were variable among individuals, we defined a swimming score
527 to determine the amount of time spent in water, including surface swimming and diving. To do so, we
528 used a centered-scale Principal Component Analysis (PCA) to account for diving parameters (number of
529 dives per individual, number of surface swims per individual, and mean dive or surface swimming
530 duration). The first component (PC1) accounted for 59.0% of the variation, and the second component
531 (PC2) accounted for 23.8% of the variation. PC1 was characterized by the number of dives, the number
532 of surface swims, and the mean dive duration. PC2 was defined by the surface swimming duration. We
533 decided to define three groups according to the behavior of each female (diving, surface swimming, on
534 land, Figure 5) in the models when group size was sufficient. As an animal's behavior was well separated
535 by the PCA, PC1 values were kept as a proxy of swimming score for the group Diving, and PC2 for the
536 group Surface swimming.

537

538 **Figure 5: Principal Component Analysis (PCA) including number of dives per individual, number of**
539 **surface swims per individual, and mean dive or surface swimming duration.**

540 The first component (PC1) accounted for 59.0% of the variation and the second component (PC2)
541 accounted for 23.8% of the variation. PC1 was characterized by number of dives, number of surface
542 swims, and mean dive duration. PC2 was defined by surface swimming duration. Individuals are reported
543 on the PCA and identified through their behavior (red circles, diving; orange star, on land; blue triangle,
544 surface swimming only). Orange star represents eight individuals on the same point.



545

546 To investigate the reason for variability in SES swimming score, we used linear mixed models (LMM) with
547 molting stage when equipped, BMI, monitoring duration as explanatory variables, PC1 (group diving) or
548 PC2 (group surface swimming) as response variables. To determine if physiological parameters
549 influenced ingestion behavior, we ran a generalized linear mixed model with molting stage when
550 instrumented, BMI, monitoring duration as explanatory variables, ingestion counts per individual as
551 response variable. To correct for overdispersion, we used a negative binomial distribution⁸⁴. Each time,
552 animal ID was used as random. For each model, an ANOVA type II was performed (Anova function in R
553 library 'car').

554 Then, to determine if weather influenced when seals spent time in the water we ran a generalized linear
555 model with temperature, relative humidity, sunshine duration and wind speed as explanatory variables,
556 and the daily probability of female SES diving, surface swimming, and ingesting as response variables.
557 Models were fitted with a binomial distribution (logistic regressions for probabilities), checked for
558 overdispersion, and adjusted with a quasibinomial distribution if necessary.

559 Last, to determine if changes in SES behavior and molt phenology influenced their condition before their
560 next travel, we used LMM with the swimming score, ingestion counts, body mass/length and molting
561 stage at capture, and monitoring duration as explanatory variables, body mass loss (kg) as response
562 variable, and animal ID as random.

563

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565

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572 Krellenstein, Alex Lathuilliere, Marion Nebot, William Paterson, Julie Pauwels, Baptiste Picard, Erwan
573 Piot, Manon Potin, Camille Toscani, Martin Tournier, Yakov Uzan, Coline Vulliet, Pauline Vuarin). D.M
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575

576 **Author contributions**

577

578 C.G. and A.A. and D.M conceived and designed the overall study. L. Chaise, L. Charlanne and E. P.
579 contributed to field work. L. Chaise and D.S. conceived the algorithm and performed the analyzes. L.

580 Charlanne performed the statistical analyzes and wrote the manuscript. All authors reviewed and agreed
581 on the final content of the manuscript.

582

583 **Competing interests**

584

585 The authors declare no competing interests.

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587 **Data availability**

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589 All diving data are available in the figshare public data at: [10.6084/m9.figshare.24773235](https://doi.org/10.6084/m9.figshare.24773235)

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591 **Code availability**

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593 The Python code is available on request from the authors.

594 The R code can be downloaded from Zenodo⁸⁵.

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Supplementary information

Breaking the fast: First report of dives and ingestions events in moulting southern elephant seals.

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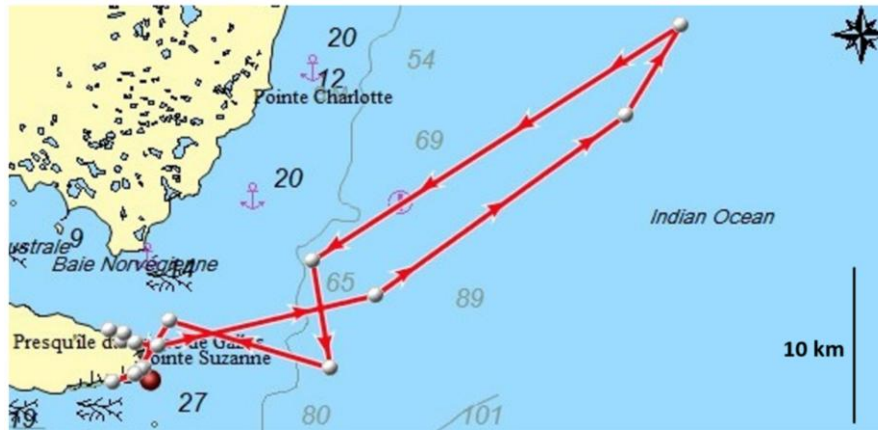
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Supplementary Figure S1. At-sea movement recorded in one monitored female southern elephant seal at mid-stage of moult in 2016, from the site of Pointe Suzanne (49°26'S, 70°26'E), with a corresponding maximum dive depth of 18.5 m. Red arrows represent the direction of travel between the grey dots (Argos locations).



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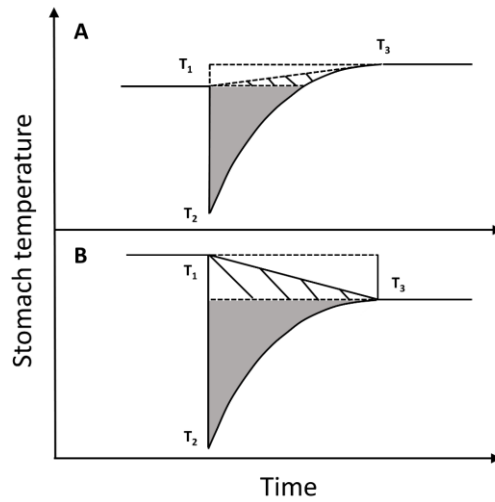
Supplementary Figure S2. Method used to calculate the area above the curve of drop in stomach temperature during ingestion events.

We used the equation:

$$Area_{event} = |area_{trapezoid}| - (|T_3 - T_1| * (t_3 - t_1)) / 2$$

Where $area_{trapezoid}$ was calculated using the integral function "trapezoid()" from Python package "scipy" (version: 1.9.1), and T_1 , T_3 (°C) and t_1 , t_3 (s) are respectively the stomach temperature and time at points T_1 and T_3 (start and end of the ingestion event).

Recovery temperature T_3 can be greater than initial temperature T_1 (A) or lower (B) (based on Kuhn and Costa, 2006): the grey area below corresponds to $area_{trapezoid}$ calculated with the trapezoid method, and hatched area corresponds to half of the additional rectangular area calculated $(|T_3 - T_1| * (t_3 - t_1)) / 2$.



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874 **Supplementary Table S1:** Summary of ingestion event variables from 31 female Southern elephant seals
 875 monitored between 2014 and 2022 (n = 87 events).

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	Mean (SD)	Min - Max
Minimum temperature T_2 (°C)	33.8 (2.0)	27.1 - 36.5
Delta of temperature $T_1 - T_2$ (°C)	3.4 (2.0)	0.5 - 10.7
Time to minimum temperature $T_1 - T_2$ (min)	11.3 (30.4)	0.2 - 182.2
Time to temperature recovery $T_2 - T_3$ (min)	36.9 (17.6)	9.2 - 98.2
Area above the curve (s.°C)	2361 (1536)	151 - 6976
Index of rate of temperature recovery I (s.°C ⁻¹) 1)	474 (840)	13 - 5213

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