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Changes in surface temperatures reveal the thermal challenge associated with catastrophic moult in captive Gentoo penguins

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35 **Abstract**

36 Once a year, penguins undergo a catastrophic moult replacing their entire plumage during a
37 fasting period on land or on sea-ice during which time individuals can lose 45% of their body
38 mass. In penguins, new feather synthesis precedes the loss of old feathers leading to an
39 accumulation of two feathers layers (double coat) before the old plumage is shed. We
40 hypothesize that the combination of the high metabolism required for new feathers synthesis
41 and the potentially high thermal insulation linked to the double coat could lead to a thermal
42 challenge requiring additional peripheral circulation to thermal windows to dissipate extra-
43 heat. To test this hypothesis, we measured the surface temperature of different body regions
44 of captive Gentoo penguins (*Pygoscelis papua*) throughout the moult under constant
45 environmental conditions.

46 The surface temperature of the main body trunk decreased during the initial stages of the
47 moult, therefore suggesting a higher thermal insulation. On the opposite, the periorbital
48 region, a potential proxy of core temperature in birds, increased during these same early
49 moulting stages. The surface temperature of bill, flipper and foot (thermal windows) tended
50 to initially increase during the moult period, highlighting the likely need for extra heat
51 dissipation in moulting penguins. These results raise questions regarding the thermoregulatory
52 capacities of wild penguins during the challenging period of moulting on land in the current
53 context of global warming.

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68 **Keywords:** Thermal challenge - Moult – Thermoregulation – Penguin – Global warming

69 Introduction

70

71 In birds, feathers have many functions including flight, thermal insulation,
72 communication (with plumage coloration; e.g. Bortolotti 2006) as well as tactile sensation
73 (Cunnighams et al. 2011). Plumage provides thermal insulation for endothermic birds helping
74 them to maintain a high core body temperature (Prinzinger et al. 1991). Indeed, the feather
75 layers trap air above the skin (Dawson et al. 1999) and plumage color and microstructure of
76 plumage elements (Wolf and Walsberg 2000) reduce conductive, convective and radiative heat
77 loss between bird and the outside environment (e.g. Calder and King 1974; Bakken 1976; Wolf
78 and Walsberg 2000). This is especially true in aquatic birds such as penguins that show a high
79 density of downy and contour-feathers increasing the water resistance (Pap et al. 2017; Osváth
80 et al. 2018). Penguins have a thick and morphologically specialized plumage (Rutschke 1965;
81 Williams et al. 2015) providing 80-90% of insulation requirements (Le Maho et al. 1976; Le
82 Maho 1977) that enable them to exist in the harshest climates of Antarctica. It is therefore
83 important that penguins are able to maintain high quality plumage (Jenni and Winkler 2020),
84 through the moult: a replacement of the old and damaged feathers by new ones (Humphrey
85 and Parkes 1959).

86 The moult of penguins is described as “catastrophic” (Davis and Darby 2012) and occurs
87 once a year during a fasting period on land or on sea-ice where the heat conductance of air is
88 25 times lower than that of water (de Vries and van Eerden 1995). During this time, individuals
89 replace their entire plumage in two overlapping stages with the synthesis of new feathers
90 preceding the loss of old feathers (Groscolas and Cherel 1992; Fig. 1A). New feathers begin to
91 grow under the skin until they reach 40% of their size, when they emerge through the skin.
92 Between 40% and 60% of the new feather growth, the old feathers remain attached to the
93 new feathers and at this stage birds simultaneously have two feather layers (Fig. 1A). The old
94 feathers then fall off, reducing thermal insulation until the new feathers finish growing
95 (Groscolas and Cherel 1992; Fig. 1A). Moult is an energetically costly period for penguins
96 (Croxall 1982; Adams and Brown 1990), despite their low level of activity while fasting on land
97 (Cherel et al. 1994). Indeed, the metabolic rate increases by a factor of 1.3 and 1.5 in king
98 penguins (*Aptenodytes patagonicus*; Cherel et al. 1994) and in little penguins (*Eudyptula*
99 *minor*; Baudinette et al. 1986) respectively. During this fasting period, macaroni (*Eudyptes*
100 *chrysolophus*) and rockhopper penguins (*E. chrysocome*) lose 44% and 45% of their body mass

101 respectively during a 25-day moult period (Brown 1986). Similarly king and emperor penguins
102 (*Aptenodytes forsteri*) lose approximately 45% of their body mass in 30 days with a peak of
103 daily body mass loss during the final stage of feather loss (Groscolas 1978; Cherel et al. 1988).

104 While Groscolas and Cherel (1992) suggested a decrease in thermal insulation during
105 the loss of old feathers, the preceding overlay of the new and the old feathers could increase
106 the overall thermal insulation of plumage. Metabolic heat production increases during the
107 moult due to feather synthesis and increased peripheral blood flow to grow the feather. During
108 the earlier stages of the moult, when penguins may have a greater thermal insulation due to
109 the double layer of feathers, penguins may face a thermal challenge (Fig. 1A) by being unable
110 to efficiently dissipate metabolic heat, potentially leading to a rise in body temperature. To
111 investigate this hypothesis, we measured surface temperatures of captive Gentoo penguins
112 (*Pygoscelis papua*) using thermal imaging during the entire moulting period. The captive
113 conditions allowed us to measure individuals throughout the full moult period at a uniform air
114 temperature without interferences of solar radiation, wind or precipitations. We measured
115 surface temperature of old and new plumage to represent well-insulated body regions,
116 periorbital region as a proxy of core temperature (e.g. Gauchet et al. 2022), while surface
117 temperature of bill, flipper and the foot correspond to thermal windows (i.e. poorly insulated
118 body areas governed by a vascular system that controls their surface temperature; Tattersall
119 et al. 2009; McCafferty et al. 2013; Lewden et al. 2020). Specifically, we predicted that when
120 penguins possessed two simultaneous feather layers (moulting stages M2 to M5; Fig. 1) there
121 would be a decrease of plumage surface temperature, an increase in surface temperatures of
122 thermal windows and a potential rise in the temperature of the periorbital region.

123

124 **Material and Methods**

125

126 *Study site*

127

128 Twenty-seven Gentoo penguins were studied in captivity at Océanopolis© aquarium, Brest,
129 France. Individuals were identified by a colored plastic ring on the right flipper, and divided
130 into two groups, the first of 18 individuals (7 males and 11 females) and the second of 13
131 individuals (6 males and 7 females). Individuals were maintained within their thermoneutral
132 zone, that is between 8 and 15°C in Gentoo penguins (Taylor 1985; Wilson et al. 1998), in two
133 separate enclosures with similar conditions, *i.e.* a permanent access to free water, unfed

134 during moulting period and with the same number of enclosure cleaning and animal keeper
135 visits. During measurement sessions, air temperature (T_a) and relative humidity (RH) were
136 measured using a weather station Kestrel® 5400 Heat Stress Tracker. The wet-bulb
137 temperature (T_w) was then calculated according to the equation (1) in Stull 2011, to take into
138 account the cooling effect of higher humidity. Enclosures showed a relatively stable T_w during
139 the study period (from July, 30th to October, 20th) with a range of temperature between 7.20
140 and 12.56°C in the first group (Group 1) and between 9.19°C and 14.20°C in the second group
141 (Group 2). However, we measured a small but significant difference between
142 groups/enclosures with a higher T_w in Group 2 (mean \pm standard error of $10.82 \pm 0.39^\circ\text{C}$)
143 compared to Group 1 (mean \pm standard error of $9.38 \pm 0.28^\circ\text{C}$) ($P < 0.005$). Similarly, the ground
144 surface temperature (T_{ground}) in contact with penguin's feet was higher in Group 2 (mean \pm
145 standard error of $14.65 \pm 0.13^\circ\text{C}$) compared to Group 1 (mean \pm standard error of $12.93 \pm$
146 0.09°C) ($P < 0.0001$). Molt lasted 14.0 ± 0.66 days per individual in Group 1 and 12.8 ± 0.97
147 days per individual in Group 2, without significant difference between group ($P = 0.85$).

148

149 *Moult*

150

151 Penguin surface temperatures were measured once a day in the morning, at least twice to a
152 maximum of 25 times per individuals with a mean of 11.75 measurements per individual. To
153 track the progress of the moult, 7 moult stages were characterized (Fig. 1B) ranging from a
154 uniform old-plumage (Fig. 1B; M1) to a uniform new-plumage (Fig. 1B; M7) and assigned by
155 the same observer (A.L) during data collection. The intermediate stages were "pop-corn"
156 during which individuals carried two feather layers giving them a puffy appearance (Fig. 1B;
157 M2). The "first fall" stage corresponds to the advanced pop-corn stage with the first fall of old
158 feathers visible (Fig. 1B; M3). The "25%" stage corresponds to the acceleration of old feather
159 fall, with at least 25% of the trunk having lost its old plumage and thus presenting a new,
160 immature plumage (Fig. 1B; M4). The "50%" stage corresponds to the peak of the moult, with
161 50% of the trunk showing two layers of plumage and 50% showing new immature plumage
162 (Fig. 1B; M5). At the "75%" stage (Fig. 1B; M6), individuals had lost most of their old plumage
163 and the new plumage, while not yet fully grown, visibly increased in volume.

164

165 *Thermal image collection and analysis*

166

167 One or two thermal pictures of left or/and right profiles were taken per day of measurement
168 from the same angle (Playà-Montmany and Tattersall 2021) at a distance of *ca.* 1 meter with
169 each body area being larger than ten times the spot size (Tabh et al. 2021) of 0.65 mm from
170 our FLIR E96 thermal camera (640x480 pixel). For each bird, profile pictures were defined as
171 right (ringed side) or left (non-ringed) side. We hypothesized that the ringed flipper might
172 show a higher surface temperature induced by a light inflammation linked to ring friction.
173 Emissivity was set to 0.98 (Whittow 1986; Monteih and Unsworth 1990) whereas T_a and RH
174 were set for each picture using Flir ThermaCAM Researcher Professional 2.10 software. Bill,
175 flipper and foot areas were delineated by tracing a polygon around the edge to extract the
176 mean surface temperature of each area (hereafter T_{bill} , $T_{flipper}$, T_{foot} respectively). Mean surface
177 temperature of the ground (T_{ground}) was extracted using a standard square size (877 pixel²)
178 situated just below the feet. Head was also delineated and the maximum surface temperature
179 of this area was extracted corresponding to the periorbital region (hereafter T_{eye} ; Jerem et al.
180 2018). As the loss of old plumage on the trunk was not symmetrical on both sides, we could
181 not determine a representative trunk surface temperature from the profile pictures. This is
182 why, we calculated an index of (hereafter T_{trunk}) using the old and the new plumage surface
183 temperature ($T_{old\ plumage}$ and $T_{new\ plumage}$ respectively) according to the percentage of trunk
184 recovery as following:

$$185 \quad T_{Trunk} = \text{Percent of feather lost} * T_{new\ plumage} \quad (1)$$
$$186 \quad + (1 - \text{Percent of feather lost}) * T_{old\ plumage}$$

187

188 $T_{old\ plumage}$ and $T_{new\ plumage}$ corresponded to a mean surface temperature of a standard square
189 size (438 pixel²) positioned on a uniform patch of each kind of plumage. When individuals were
190 in old plumage (M1) in pop-corn (M2) and in first fall (M3) stages, T_{trunk} corresponded to T_{old}
191 $plumage$. When individuals were in new plumage stage (M7) T_{trunk} corresponded to $T_{new\ plumage}$.
192 For others moulting stages (M4; M5 and M6), T_{trunk} was calculated using the equation (1)
193 determined from the cover of the entire trunk circumference to weight the proportion of each
194 kind of plumage.

195 *Statistical analysis*

196

197
198 The effect of plumage color (black or white) on old and new plumage surface temperatures
199 was initially investigated using an ANOVA, but dropped out of final models since as expected

200 in the absence of solar radiation, we did not find any significant difference in surface
201 temperature between black and white plumage in both old and new plumage ($P>0.80$ in both
202 cases). Similarly, we did not measure any significant effect of the ring on T_{flipper} and therefore
203 excluded this variable from our final statistical models ($P=0.99$).

204 The relationship between four temperature areas (*i.e.* bill, periorbital, flipper and trunk) and
205 the moult stages were studied using general linear mixed models (GLMM), including penguin
206 ID as a random intercept, to control for repeated measures and T_w , Group (1 or 2) and Sex
207 (male or female) as fixed effects. For the T_{foot} , T_{ground} replaced T_w in the model considering the
208 large surface of foot in contact with the ground (*i.e.* conductive heat loss). Indeed, the linear
209 relationship between T_w and T_{foot} ($R^2= 0.02$; $P=0.004$) was markedly weaker than the
210 relationship between T_{ground} and T_{foot} ($R^2=0.38$; $P<0.0001$).

211 Differences were then investigated using a Tukey's honestly significant difference (HSD) *post-*
212 *hoc test* for moult stages effect. Statistical analyses were performed using JMP® v. 13 (SAS
213 Institute Inc., Cary, North Carolina, USA) and results were reported as mean \pm standard error
214 unless specified.

215

216 Results

217

218 Body surface temperatures were positively related to T_w or T_{ground} (Table 1). The variable
219 'group' was only significant for T_{trunk} ($P<0.0001$) with lower T_{trunk} measured in the group
220 exposed to the slightly colder environment (*i.e.* Group 1). Females had a slightly higher T_{eye}
221 than males (31.02 ± 0.11 and $30.71 \pm 0.10^\circ\text{C}$ respectively; $P=0.023$). Group and sex did not
222 explain any significant variation in T_{bill} , T_{flipper} and T_{foot} (Table 1). However, variation in all body
223 surface temperatures were significantly influenced by the stage of moult (Table 1).

224 T_{eye} significantly increased from the old plumage to the pop-corn stage, and stayed elevated
225 until the 50% moult stage (Fig. 2A). T_{eye} then decreased back at 75% of the moult (at a level
226 similar to the old plumage), and ended up being the lowest at the new plumage stage (Fig.
227 2A). T_{trunk} showed an initial drop from the old plumage stage to the First fall stage (Fig. 3), and
228 then increased back to its initial level as the moult progressed further towards the new
229 plumage stage (Fig. 2A). T_{trunk} at the new plumage stage ($15.93 \pm 0.14^\circ\text{C}$) did not significantly
230 differ from the old plumage stage ($16.48 \pm 0.21^\circ\text{C}$; $P=0.15$) (Fig. 2A and 3).

231 T_{flipper} had the highest temperature at stage 25, 50 and 75% of the moult (Fig. 2B). T_{flipper} at
232 those stages were higher than at first fall and new plumage stages (all $P < 0.04$; Fig. 3), but did
233 not significantly differ from the old plumage and pop-corn stages (all $P > 0.30$). T_{flipper} was 1.77°C
234 colder at new plumage stage compared to old plumage stage ($P = 0.0002$; Fig. 3).

235 T_{bill} significantly increased from the old plumage to first fall stage, and decreased thereafter
236 (Fig. 2C) with a maximum difference of -5.20°C between the first fall and the new plumage
237 stages ($P < 0.0001$; Fig. 3). T_{bill} was also lower at the new plumage stage ($17.13 \pm 0.31^{\circ}\text{C}$) than
238 at the old plumage stage ($19.92 \pm 0.52^{\circ}\text{C}$; $P < 0.0001$).

239 T_{foot} initially increased from the old plumage until the First fall stage (Fig. 3), and remained
240 slightly elevated until the end of the monitoring (i.e. new plumage; Fig. 2D). Yet, there was no
241 significant difference in T_{foot} between new plumage ($19.29 \pm 0.53^{\circ}\text{C}$) compared to old plumage
242 stages ($17.99 \pm 0.74^{\circ}\text{C}$; $P = 0.62$).

243

244 Discussion

245

246 Our study investigated the effect of moulting in captive Gentoo penguins, a fasting
247 period during which metabolic rate increases (Baudinette et al. 1986; Cherel et al. 1994) while
248 body insulation is heavily modified in penguin species (Groscolas and Cherel 1992). Our results
249 showed that at early stages of the moult, when individuals have two feather layers (Stages M2,
250 M3 and M4; Fig. 1 and 2), plumage insulation was elevated as shown by the lowest T_{trunk} (Fig.
251 2 and 3), while the surface temperatures of thermal windows (bill, flipper and foot) and the
252 periorbital region were generally elevated at these stages (Fig. 2). This effect was maintained
253 until approximately 50% percent of the moult, after which surface temperatures of non-
254 insulated body regions started to decrease (Fig. 2 and 3), such that the mean surface
255 temperatures of new plumage stage were significantly lower (except for T_{foot}) than at old
256 plumage stage (Fig. 2).

257

258 Early moulting stages in penguins may therefore provide a thermal challenge for birds
259 to dissipate extra-heat. Moult is energetically costly (Baudinette et al. 1986; Cherel et al. 1994)
260 through maintaining a peripheral blood flow for dermal perfusion sustaining feather synthesis.
261 Simultaneously with this higher heat production, we found that the potential for heat
262 dissipation is likely to be reduced by the additional insulation resulting from the combination

263 of newly growing and old feathers, as shown by the tendency of T_{trunk} to decrease at pop-corn
264 (M2), first fall (M3) and 25% of old feathers fallen (M4) stages (Fig. 2). Correspondingly,
265 uninsulated or less insulated body areas from the bill, flipper and foot exhibited the opposite
266 pattern (Fig. 2 and 3) with an increase of surface temperature allowing greater heat loss
267 through radiation and convection to the surroundings. Within our captive experimental
268 conditions, birds were measured within their thermoneutral zone (between 8° and 15°C;
269 Taylor 1985), which theoretically enable to exclude any changes in metabolic rate associated
270 with thermoregulation. Thus, our study highlights that blood flow to thermal windows may
271 help to compensate for greater insulation and heat production associated with feather
272 synthesis, in order to help maintaining a stable core body temperature during early moulting
273 stages. Since T_{eye} is relatively well correlated to core temperature in chicken (Cândido et al.
274 2020), budgerigars (*Melopsittacus undulates*; Ikkatai and Watanabe 2015) and wild red-footed
275 boobies (*Sula sula*; Gauchet et al. 2022), our results suggest that core body temperature
276 increased during the early stage of moult (+1.61°C of T_{eye} between old plumage and 25%
277 stage). This idea is supported by an increase of *ca.* 0.8°C in core temperature during moult in
278 Yellow-eyed penguin (*Megadyptes antipodes*; Farner 1958). Yet, blood flow to the eyes,
279 impacting T_{eye} , has been also shown to play a role in reducing brain temperature in pigeons
280 (*Columba livia*; Pinshow et al. 1982), suggested as heat sink in ostriches (*Struthio camelus*;
281 Fuller et al. 2003) or to maintain/enhance visual acuity during stress (Winder et al. 2020).
282 Unfortunately, without core body temperature measurements, it is not possible here to
283 formally assess if the increased heat dissipation through thermal windows we observed was
284 sufficient to maintain core body temperature at stable levels, or if the observed increase in T_{eye}
285 could reflect the inability to maintain core body temperature at stable levels.

286
287 Interestingly, the thermal challenge to dissipate heat described here at
288 thermoneutrality seems likely to be specific to penguins, due to the accumulation of this
289 double insulation. Indeed, most studies in birds measured the opposite pattern with an
290 increase of 30 to 60% in thermal conductance during moult (Lustick 1970; Dietz et al. 1992),
291 inducing for instance a rise of the lower critical temperature in Long-eared Owl (*Asio otus*;
292 Wijnandts 1984). In seals, moult represents the renewal not only of the hair but also of the
293 skin (Ling 1968; 1972). With no accumulation of old and new skin, individuals show an increase
294 of thermoregulation cost due to higher heat loss (Paterson et al. 2012). In Antarctica Weddell

295 seals (*Leptonychotes weddellii*), Walcott et al. (2020) measured that the energetic costs of
296 thermoregulation doubled during moulting period, supported by an increase of 25% of heat
297 loss in early moulting stages. Importantly, no thermal windows were detected in this study
298 suggesting that individuals were unlikely to overheat (Walcott et al. 2020). Similar results were
299 obtained in southern elephant seals (*Mirounga leonina*) with an increase of 1.8 x resting
300 metabolic rate during moult with body surface temperature decreasing throughout the moult
301 (Paterson et al. 2022), the latter suggesting an energy-saving strategy that seems opposite to
302 the results obtained in this study in Gentoo penguins maintained within their thermoneutral
303 zone. Moreover, elephant seals also showed aggregation behavior only during moult on land
304 suggesting a strategy to reduce heat loss and minimize energy costs (Chaise et al. 2019). In
305 contrast, penguins have not been shown to exhibit specific aggregation behavior during
306 moulting to the best of our knowledge.

307 Surface temperatures of new plumage stage did not reach the initial temperature
308 measured in old plumage and they were either lower (T_{bill} , T_{eye} and T_{flipper}) or similar (T_{foot} ;
309 T_{trunk}) at the end of the moult. Moult could have started before a visible change in plumage
310 (i.e. pop-corn stage). In this case, the old plumage stage (M1) could already correspond to an
311 early stage of moult (i.e. growth of new feathers below the skin, Fig. 1), with a higher
312 metabolism, rather than a pre-moult stage as initially considered in this study. Secondly, the
313 new plumage stage (M7) corresponds here to the end of the old feather loss and potentially
314 not to the end of the new feather growth. The immature new feathers could be less insulated
315 than the full-length feathers, allowing heat loss without a specific need to maintain blood flow
316 to thermal windows. Finally, since moulting progression is also associated with the progression
317 into a more advanced fasting stage, it is possible that individuals reaching the new plumage
318 stage could use peripheral vasoconstriction as an energy-saving strategy (Kooyman et al. 1976;
319 Ponganis et al. 2001, 2003; Tattersall et al. 2016) which could also explain the decrease we
320 observed in T_{bill} , T_{eye} and T_{flipper} .

321 Our study showed that under nearly constant environmental conditions, moulting
322 Gentoo penguins increase the surface temperature of poorly insulated regions (thermal
323 windows) (Fig. 2 and 3) to dissipate extra heat. In the wild, the thermal challenge of carrying
324 two feather layers could be enhanced by the solar radiation and the increase of air
325 temperature in the current context of global warming (Ainley et al. 2010; Gorodetskaya et al.
326 2022). Further studies are needed to better understand the operative temperature (Bakken

327 1976) experienced by wild birds, especially in polar marine species showing adaptations to
328 reduce heat loss while foraging in cold water.

329

330 **Data availability statement**

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332 is not done for commercial purposes, and the original authors are credited and cited.

333 <https://figshare.com/s/c64975557480cc8709f3>

334

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336

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345

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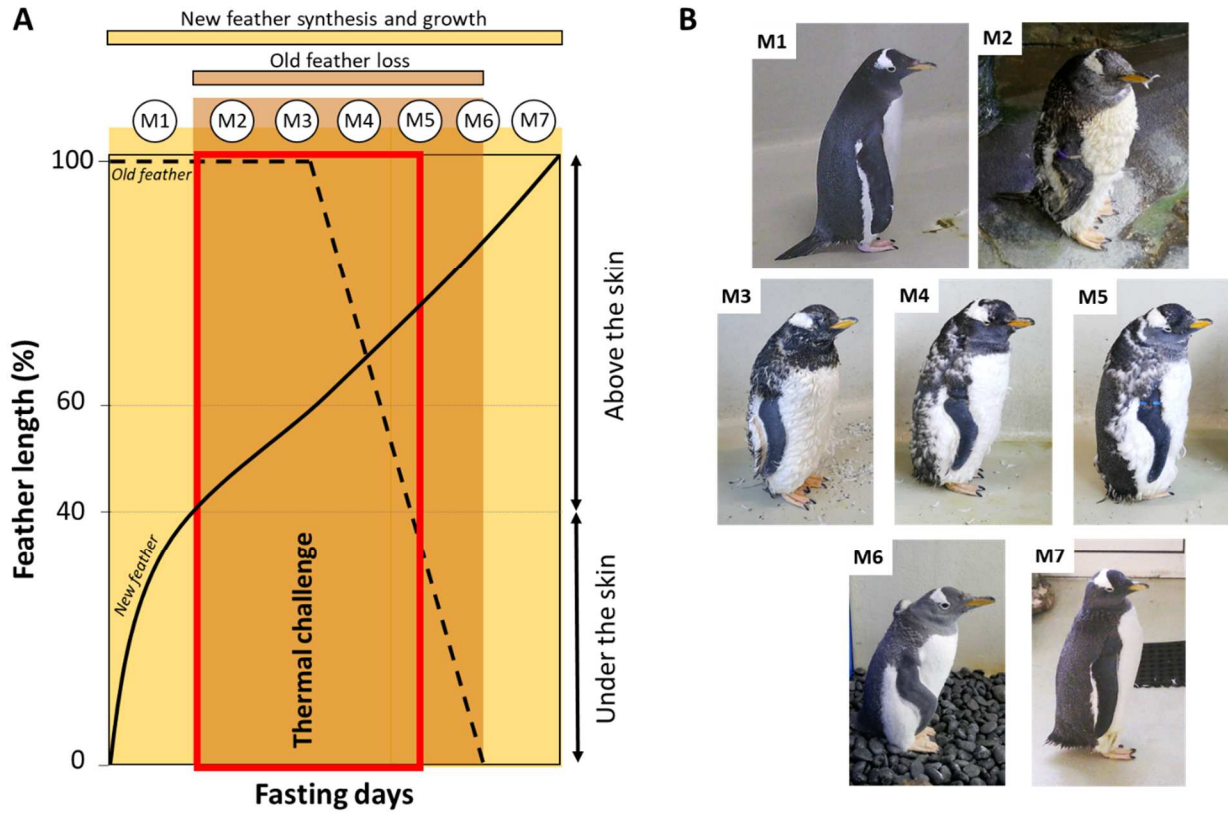
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Figures



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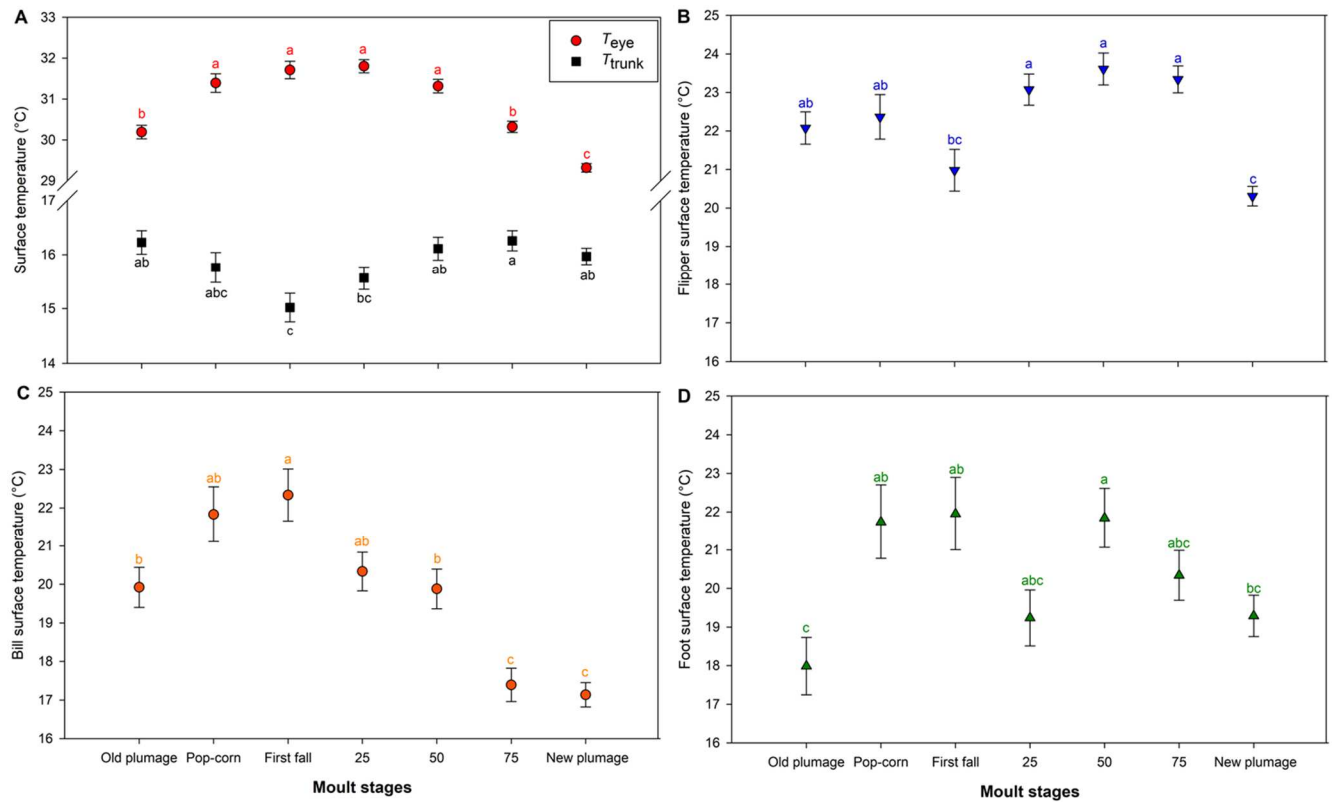
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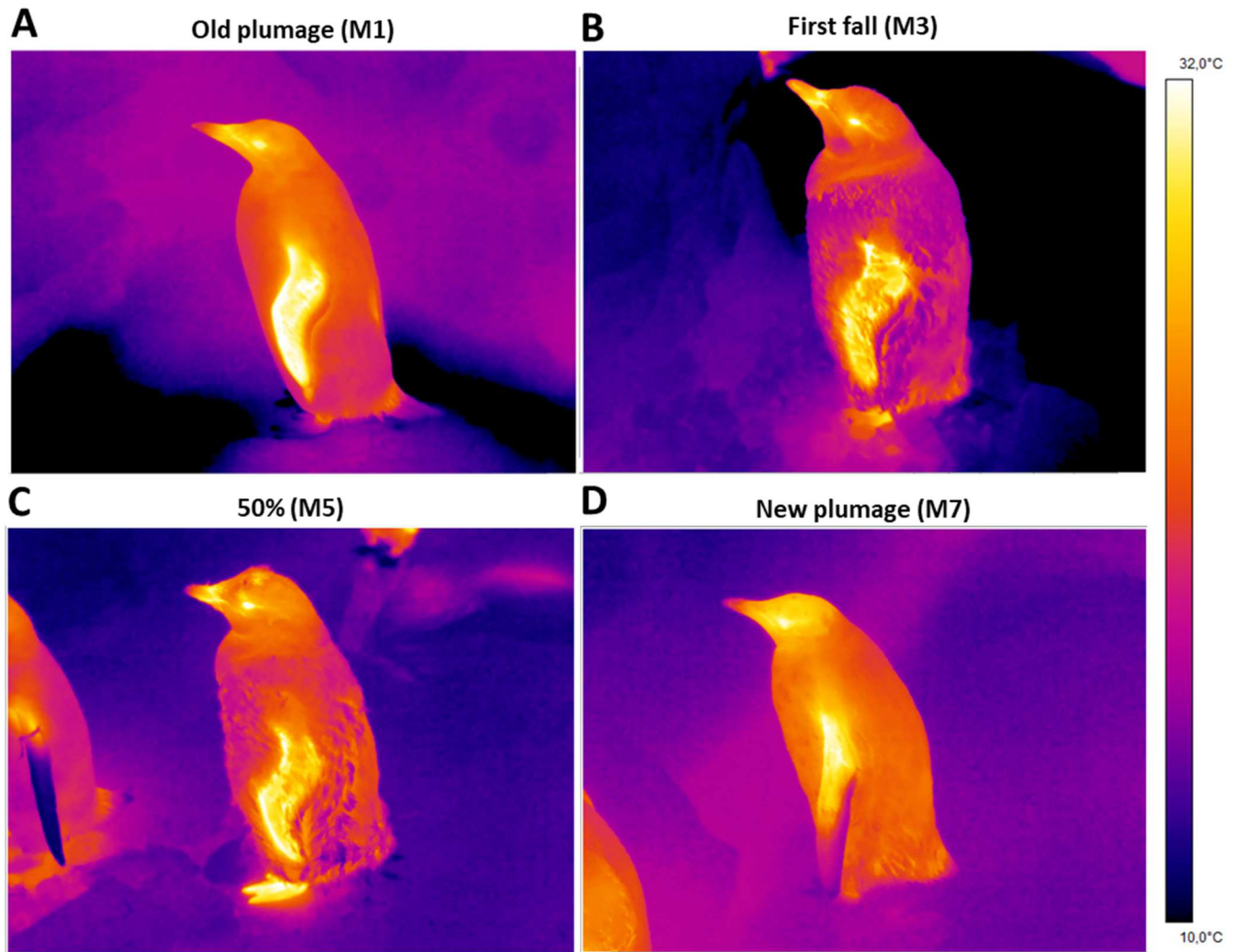
Fig. 1: Identification of the seven main moulting stages (stages M1 to M7) characterized during the Gentoo moult in captivity. The schematic representation of the penguin moult (**A**) shows the new feathers (straight-line) grow beneath the outer skin layer until 40% of their total length. Between 40 and 60% of new feather growth, penguins have a double feather layer, old (dashed line) and new. These two feather layers could lead to a thermal challenge for heat dissipation (red box). After 60% of new feather growth, the old feathers are starting to fall-off. Adapted from Groscolas and Cherel (1992). During moult, visual plumages changes can be noticed (**B**) and characterized into seven different stages: M1 = uniform old plumage, M2 = 'pop-corn' (superposition of old and new immature feathers), M3 = first fall of old plumage, M4 = 25% of old feathers fallen, M5 = 50% of old feathers fallen, M6 = 75% of old feathers fallen and M7 = uniform new plumage corresponding at the end of the monitoring. See the main text for more details ©A. Lewden

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521 **Fig. 2: Least-squared mean surface temperatures during the seven moulting stages.** Values
522 for the periorbital region (red) and the trunk (black) (A), the flipper (B), the bill (C), and the
523 foot (D) are shown. Values that do not share the same letter are significantly different from
524 each other (post-hoc Tukey's HSD test; $P < 0.05$).



525

526 **Fig. 3: Visual comparison of four Gentoo penguins measured during moult by thermal**
527 **imaging.** Individuals were measured through the moult including before moult in old plumage
528 **(A)**, at moulting stage first fall **(B)** and 50% **(C)** and in new plumage **(D)**. Images illustrate lower
529 T_{trunk} at first fall (M3), lower T_{flipper} in new plumage (M7) compared to others stages and higher,
530 higher T_{bill} at first fall (M3) than in new plumage (M7) and higher T_{foot} during moult (M3 and
531 M5) than before and at the last stage of the moult (M1 and M7).

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534 **Table:**

535 Table 1: Summary of the general linear mixed models used to investigate variation in body surface temperatures during moult in captive Gentoo
 536 penguins
 537

	T_{eye}			T_{trunk}			T_{bill}			T_{flipper}			T_{foot}		
	R ² =0.55 N= 339			R ² =0.68 N= 340			R ² = 0.36 N= 340			R ² =0.31 N= 340			R ² =0.60 N= 327		
Random effect :	<i>Variance</i>			<i>Variance</i>			<i>Variance</i>			<i>Variance</i>			<i>Variance</i>		
Bird ID	0.05			0.29			0.25			0.16			3.49		
Residual	0.91			1.18			9.38			6.05			14.03		
Fixed effect :	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Ta or Tground	1,328	6.05	0.014	1,320	42.39	<.0001	1,330	20.81	<.0001	1,330	18.66	<.0001	1,316	172.19	<.0001
Group	1,64	0.75	0.38	1,103	104.33	<.0001	1,84	0.10	0.75	1,55	1.61	0.21	1,107	2.59	0.11
Sex	1,37	5.59	0.023	1,71	1.26	0.27	1,48	3.48	0.068	1,30	1.07	0.31	1,70	1.76	0.19
Molt stages	6,323	49.67	<.0001	6,321	4.94	<.0001	6,324	16.47	<.0001	6,319	15.23	<.0001	6,309	5.29	<.0001

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