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1 **Revue des différentes stratégies de reproduction des manchots**

2 **The different breeding strategies of penguins: a review**

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14  
15 **Résumé**

16 Les 18 espèces de manchots vivent exclusivement dans l'hémisphère Sud, de  
17 l'Equateur jusqu'en Antarctique et subissent en conséquence différentes contraintes  
18 écologiques au cours de leur cycle reproducteur. Ceci se traduit par une forte  
19 variabilité dans tous les aspects de la biologie de la reproduction chez les différentes  
20 espèces. Bien que les manchots soient de prime abord adaptés à une vie marine, ils  
21 dépendent néanmoins d'une surface ferme pour se reproduire, élever leur  
22 progéniture et muer. Nous décrivons et comparons les cycles reproducteurs de  
23 toutes les espèces de manchots tout en mettant en avant les caractéristiques de  
24 chaque espèce que ce soit la durée de leur cycle reproducteur, le statut de la  
25 population et les menaces environnementales qui pèsent sur elle, la durée des

26 différentes phases du cycle reproducteur, la fidélité du couple, la masse corporelle, la  
27 taille, la durée et les dimensions des œufs. Nous nous sommes plus particulièrement  
28 étendus sur le cycle reproducteur du genre *Aptenodytes* qui diffère notablement de  
29 celui des autres espèces.

30

### 31 **Abstract**

32 The 18 penguin species are exclusively and widely distributed in the Southern  
33 hemisphere, from the Equator to the Antarctic continent, and are thus submitted to  
34 various ecological constraints in their reproductive strategy. This results in a high  
35 variability in all aspects of the breeding biology of the different species. Although  
36 penguins appear primarily adapted for a marine existence, they remain dependent on  
37 land for breeding, rearing young and moulting. Here we describe and compare the  
38 breeding cycle of all the penguin species highlighting the characteristics of each  
39 species in terms of breeding range, population status, threats induced by  
40 environmental changes, duration of the different phases of the breeding cycle, mate  
41 fidelity, body mass, body height, egg mass and duration of egg formation. We also  
42 focus on the breeding cycle of the genus *Aptenodytes* since it largely differs from the  
43 breeding cycle of most of the other penguin species.

44

45 **Keywords:** Southern hemisphere, breeding range, mate fidelity, egg formation,  
46 reproduction, vulnerability

47 **Mots clés:** hémisphère Sud, aire de reproduction, fidélité, formation de l'œuf,  
48 reproduction, vulnérabilité

49

50 **Running title:** penguin's breeding cycle – le cycle reproducteur des manchots

51

52 **Introduction**

53 Natural selection favours a breeding strategy which, in a given environment, is the  
54 most likely to ensure the production of the largest number of young which survive to  
55 breed, and the survival of parents until they breed again. The decision to breed is  
56 triggered by physiological changes set in motion by changes in the environment [1].  
57 In birds, the timing of reproduction is determined by proximate factors and is often  
58 initiated before birds return to their breeding grounds [1,2]. Among these proximate  
59 factors, the photoperiod, the temperature, and the availability and the quality of the  
60 food required for successful breeding are frequently reported [3-6].

61 The majority of birds lives in a non-uniform environment (spatially and  
62 temporarily) and must breed when the conditions are the most favourable. For  
63 instance, in temperate and Polar regions, most birds have to synchronize their  
64 breeding schedule with the time of the year that will give their offspring the best  
65 chances of survival [7]. This restricted period of time dictated by resource availability  
66 leads individuals from the same population to breed synchronously. This breeding  
67 synchrony can also be associated with different advantages such as the reduction of  
68 the impact of predators and the maximisation of chick survival, by timing fledging  
69 when prey abundance is highest [8,9], and/or when climatic conditions are most  
70 favourable [10].

71 Among seabirds, penguins are a distinctive group of flightless, long-lived  
72 pelagic seabirds. All the 18 species of penguins are grouped within a single family,  
73 the *Spheniscidae*. Within this family, there are six genera and each genus comprises  
74 one to eight species (Table 1). Several subspecies of little *Eudyptula minor* (6) and  
75 gentoo penguins *Pygoscelis papua* (2) have been identified [11,12] but for the

76 purpose of this review these penguins are considered as a single species. Some  
77 penguin species have been studied in detail, especially the Adélie penguin  
78 *Pygoscelis adeliae* (more than 400 papers, see ISI Web of Knowledge), but others,  
79 such as the Snares penguin *Eudyptes robustus* and erect-crested penguin *Eudyptes*  
80 *sclateri* have not (less than 10 publications, see ISI Web of Knowledge).  
81 Consequently, there is less information available for some species. All penguins have  
82 a similar body shape and structure. The sexes are outwardly similar in all species,  
83 though males are usually heavier, at least at the onset of the breeding season, and  
84 larger than females (Table 1). They vary considerably in height, from about 40 to  
85 130 cm, and in body mass, from 1 to 37 kg (little and emperor *Aptenodytes forsteri*  
86 penguins, respectively, Table 1). Such a range in body mass is only surpassed by  
87 another flightless family: the Struthioniformes, where the smallest species, the Little  
88 spotted kiwi *Apteryx owenii*, measures 40 cm and weighs 1.2 kg compared to the  
89 largest living ratite, the African ostrich *Struthio camelus*, that stands roughly 3 m tall  
90 and weighs 160 kg.

91 Penguins are highly adapted for marine life and some species spend as little  
92 as 20 % of the year on land (Fig. 1A). Nevertheless, this relatively short period on  
93 land represents one of the most important parts of their life cycle; during which  
94 penguins have to obtain a nest-site and mate, lay egg(s), rear chick(s), and moult.  
95 The 18 penguins' species share some breeding characteristics such as breeding  
96 synchrony (except for the Galápagos penguins *Spheniscus mendiculus*, [72]) for  
97 annual reproduction on land, and alternation of sojourns on land and at sea between  
98 partners during the chick-rearing period. An important characteristic of all penguin  
99 species is their ability to withstand prolonged period of fasting, on land or sea-ice,  
100 during breeding. With the exception of the yellow-eyed penguin *Megadyptes*

101 *antipodes*, all penguin species breed colonially [73]. In these colonies, birds often  
102 breed in high densities, for instance, 1.4 nest.m<sup>-2</sup> in Adélie penguins [74] and up to  
103 10 birds.m<sup>-2</sup> in huddling emperor penguins [16,75], which highly increases the level of  
104 social stimulations and interactions [76]. High densities of breeding birds have led to  
105 the evolution of a varied and complex repertoire of visual and vocal displays (e.g.  
106 [77]). As penguins are widely distributed in the Southern hemisphere, from the  
107 Equator to the Antarctic continent, they are submitted to various ecological  
108 constraints that will impact the timing of reproduction. For example, for a high latitude  
109 species such as the emperor penguin, two proximate factors controlling the onset of  
110 breeding are exogenous factors such as day-length [1,78] and the peak of ocean  
111 productivity preceding breeding [79]. For the equatorial Galápagos penguin, the  
112 onset of breeding is closely linked to mean sea surface temperature [70]. Therefore,  
113 because of the variety of environments where penguins live, the examination of the  
114 breeding cycle observed across the Sphenisciformes order can give some insights  
115 about how environmental conditions can shape a variety of reproductive strategies.  
116 The different aspects of the biology of penguins are relatively sparse in the literature  
117 although some books attempted to gather these data (e.g. [11,12,80,81]). Therefore,  
118 the aim of the present study is to provide researchers working on seabirds with a  
119 concise and clear overview of the breeding cycle of the 18 penguin species.

120 In this review, the breeding cycle of penguins was divided into three stages:  
121 (1) the pairing period, when breeders come ashore for courtship and mating, (2) the  
122 incubation period, when mates generally take turns to incubate the egg(s), and (3)  
123 the rearing period, from chick(s) guard to fledging. We defined the courtship period  
124 as the shortest period of time between the early arrival of both sexes on the  
125 reproductive site and the laying of the first egg because females may occasionally go

126 to sea before the full clutch is completed (e.g. gentoo penguins, [11], magellanic  
127 penguins *Spheniscus magellanicus*, [82]). The body mass of the adult birds  
128 considered was the mean body mass at the onset of the breeding period, i.e. at their  
129 arrival on the breeding site.

130

### 131 **Geographical range and population status**

132 Penguins are widely distributed in the Southern hemisphere, mainly between 45 and  
133 60°S (Fig. 2) and four penguin species are endemic to their breeding island:  
134 Fiordland (or crested) *Eudyptes pachyrhynchus*, Galápagos, royal *Eudyptes schlegeli*  
135 and Snares penguins. Penguins represent roughly 90 % of bird biomass in the  
136 Southern Ocean [12] and *Pygoscelis* species (chinstrap *P. antarctica*, Adélie and  
137 gentoo penguins) represent 70 % of Antarctic avian biomass [83]. Penguins feed in  
138 pelagic cold waters, rich in zooplankton and biomass, where they consume  
139 approximately two millions tons of carbon per year [84]. However, they occupy a wide  
140 variety of habitats while breeding on land, ranging from the burrows in the volcanic  
141 rocks of the hot Galápagos Islands (Galápagos penguin), the bushes of south  
142 Australia and New-Zealand (little penguin), to the ice of the border of the Antarctic  
143 continent (emperor, Adélie, chinstrap and gentoo penguins). This results in a high  
144 variability in all aspects of the breeding biology of the different penguins' species  
145 (Fig. 1A). While most species breed annually, some species, such as African (or  
146 jackass) and Galápagos penguins, can have no distinct annual breeding season (i.e.  
147 breeding season occurs year-round). Because of the short Antarctic summer,  
148 breeding is generally much synchronised in Antarctic species, but in temperate  
149 climates, it can be spread over a longer period of time. For example, the timing of  
150 egg-laying greatly varies between years for the little penguin [85].

151 Penguins exclusively rely on marine food sources that are spatially and  
152 temporarily unpredictable. Penguins make use of wide geographical areas in the  
153 ocean while foraging and during migrations. Penguins, which are central place  
154 foragers during the breeding season, are thus particularly sensitive to variations in  
155 ecosystem structure and processes. Of the 18 penguins' species, 13 are considered  
156 endangered or threatened (Table 1) and some species are now at their lowest  
157 recorded populations: Galápagos, yellow-eyed, and Fiordland have less than  
158 3,000 pairs; Humboldt (*Spheniscus humboldti*), Snares and African have less than  
159 30,000 pairs. Even abundant species like the macaroni (*Eudyptes chrysolophus*) and  
160 the rockhopper (*Eudyptes chrysocome* and *E. moseleyi*) are in steep decline [86]. On  
161 the contrary, the global population trend is stable for Snares and Adélie penguins [86]  
162 or is increasing for gentoo [87,88] and king penguins [86]. The status of the emperor  
163 penguin might change in the near future. Indeed, thanks to satellite images showing  
164 faecal stains on ice, Fretwell and Trathan [89] discovered 10 new emperor penguins  
165 colonies [90]. Around 80 % of the threatened species live on islands, increasing their  
166 vulnerability to threats such as introduced predators. Many penguin species face the  
167 same four key threats: global climate change, marine pollution, fisheries  
168 mismanagement, and introduced mammalian predators [91].

169

#### 170 **Relative importance of each phase of the breeding cycle: focus on pairing** 171 **period**

172 Among the 18 penguin species, the duration of the breeding season ranges from 4 to  
173 15 months (Fig. 1A). It is especially long for the two largest penguins (who need  
174 more time for their chick to grow) and particularly for the king penguin *Aptenodytes*  
175 *patagonicus*. Emperor penguins' cycle lasts 9 months including a 1.5 month pairing



176 period that is long relative to other penguin species (Fig. 1A; [79]). Indeed, while the  
177 courtship period ranges from less than 1 week in little, gentoo, Jackass or African  
178 *Spheniscus demersus* and magellanic penguins, it lasts up to 6 weeks in emperor  
179 penguins (Fig. 1A). The ratio courtship-breeding duration accounts for 16 % in  
180 emperor penguin (1.5 month vs. 9 months) whereas it accounts for only 3 % in its  
181 closest relative, the king penguin (1.5 week vs. 15 months). Considering the long  
182 duration of the total breeding cycle in emperor penguins, this ratio is, however,  
183 almost of the same magnitude (14 - 18 %) as with other species breeding in  
184 Antarctica (Adélie, chinstrap and gentoo penguins; Fig. 1B). Contrary to the emperor  
185 penguin, the king penguin does not exhibit a long courtship period but an extended  
186 chick-rearing period (84 % of the breeding cycle while it represents about 57 % in  
187 other species; Fig. 1B). In king penguins, breeding overlaps two years (Fig. 1A)  
188 which consequently results in a maximum of two chicks being reared within a three  
189 year period.

190

### 191 **Fidelity, sex ratio, and courtship**

192 All penguins are monogamous, mating with only a single partner each year. In  
193 addition, most penguin species are territorial and show a moderate to high inter-  
194 annual fidelity in breeding (59 - 89 %; Table 1), partners reuniting from year to year  
195 on their nest site. Pair bonds can therefore be long-lasting (Table 1) with many birds  
196 returning to meet their previous partners at the same breeding site each year. Two  
197 *Aptenodytes* species and especially the emperor penguin, however, show a low inter-  
198 annual fidelity (15 %; Table 1), due to the fact that they do not use a nest, and  
199 incubate their egg on their feet [92,93]. Partners cannot therefore reunite themselves  
200 from year to year on the nest site and one could hypothesize that these penguins

201 need more time than other species to find and reunite with their previous mate. King  
202 penguins, however, show a low inter-annual fidelity (29 %; Table 1) despite being  
203 highly territorial and occupying distinct nest sites. These birds could easily reunite  
204 with their partners provided they return on time but it does not seem to be the case  
205 for 70 % of them.

206 A male-biased sex ratio appears to be a characteristic of breeding populations  
207 of several penguin species such as yellow-eyed, gentoo, little, Adélie, macaroni  
208 penguins [11]. In Adélie and macaroni penguins, males return first [11] to previous  
209 year's nest-site to maximize their chances of reuniting with their mates from the  
210 previous year. This suggests that the primary "aim" of male penguins returning to the  
211 breeding colony would be to retain their old nest-sites and, only secondarily, to  
212 reunite with their previous mates. Because in many species there are more males in  
213 the population than females, male-male competition for nest-sites, rather than for  
214 mates, is an important determinant of breeding opportunity. In contrast, at least for  
215 the Pointe Géologie colony (Adélie Land, 140°E-67°S), sex ratio favours female  
216 emperor penguins that outnumber males by about 10 % [31,92-94]. This might be  
217 due to a higher mortality of male breeders after their long winter fast [95]. Because of  
218 this unbalanced sex-ratio and because mate fidelity is particularly low in this species,  
219 competition between females is high to find a male and the earlier a female returns at  
220 the onset of the breeding cycle, the higher the probability she will get a mate [31],  
221 and the lower the probability that her previous mate will already be paired with  
222 another female. Furthermore, the number of male partners available per unpaired  
223 female decreases as time passes. Consequently, an early arrival enhances the  
224 likelihood for the females to preserve their breeding status by finding an unpaired  
225 mate. Unbalanced sex ratio in emperor penguins probably also explains occurrence

226 of polygynous trios (one male with two females) but these groups are temporary, one  
227 female usually ejecting the other after a few hours [16,31].

228

### 229 **From yolk development to fledging**

230 The period of yolk development that precedes ovulation is given by the following  
231 equation for non-procellariiform seabirds:  $\log t = 0.396 + 0.283 \log \text{egg mass}$  [96]  
232 where t stands for time (day) and egg mass is expressed in grams. Once the yolk is  
233 fully developed, it is retained within the ovarian follicle for about 6 days before  
234 ovulation [97]. The albumen and shell are then added over about 24 hours, following  
235 ovulation. In species with two eggs [98-101], development of the second egg (B-egg)  
236 is initiated 4 days after the first one (A-egg). Thus, in order to calculate the time  
237 elapsed from yolk formation until egg-laying, we added 7 (6+1) and 11 days (4+6+1)  
238 for the A-egg and the B-egg, respectively (Table 1).

239 Incubation refers to the process by which birds lay their egg(s), and to the  
240 development of the embryo within the egg. The most vital factors of incubation are  
241 the temperature required for embryo development over a specific period, humidity  
242 (which could be problematic in dry environments like the Galápagos Islands or  
243 Antarctica), and egg rotation rate [102]. If the air is too dry, the egg will lose too much  
244 water, which can make hatching difficult or impossible. As incubation progresses, an  
245 avian egg becomes lighter, and the air space within the egg becomes larger owing to  
246 the evaporation from the egg. In most penguin species, incubation is divided  
247 differently between parents with the male and the female taking turns incubating the  
248 egg(s). The emperor penguin represents an exception as in this species, only the  
249 male incubates.

250 Compared with other birds, penguins lay small eggs (and small egg clutches)  
251 relative to their body weight ( $2.9 \pm 0.9 \%$ ,  $n = 16$ , mean  $\pm$  SD, Table 1), and eggs of  
252 smaller penguin species are proportionately larger (Table 1). The majority of  
253 penguins lays two white eggs (except genus *Aptenodytes* laying only one egg),  
254 weighing from 55 to 445 g (little and emperor penguins, respectively, Table 1). Within  
255 the genus *Eudyptes*, the second egg or B-egg is 20 – 78 % larger than the first one  
256 (Table 1) and consequently the first chick is smaller than the second one and  
257 generally fails to survive [11]. Erect-crested penguins are obligate brood reducers  
258 [46] and exhibit the most extreme egg-size dimorphism of any bird: the second egg is  
259 up to 100 % the size of the first and is the only one to be incubated. It remains  
260 unclear why these birds should lay two eggs but only ever rear one chick. The total  
261 time necessary for yolk deposition is proportional to female's body mass [97] but full  
262 clutch synthesis has the same duration among the 18 penguin species, ca. 3 weeks  
263 (Table 1;  $20.6 \pm 0.7$  days,  $n = 16$ , mean  $\pm$  SD). By subtracting the duration of the full  
264 clutch completion from the duration of the pairing period, we can report that egg  
265 formation begins while females are still at sea (in 13 species), while they arrive at the  
266 breeding site (in 1 species), and while they already are on the breeding site (in  
267 3 species; Fig. 3). Among the latter, emperor penguins' egg formation begins late,  
268 three weeks after their arrival on the colony. Thus, egg formation is not responsible  
269 for the long duration of the pairing period, representing only one half of the courtship  
270 duration.

271 Incubation ranges from ca. 35 to 65 days (*Eudyptes* and *Pygoscelis* species,  
272 emperor penguins, respectively, Fig. 1B). It is an energetically demanding process,  
273 especially in male emperor penguins that can lose up to 45 % of their initial body  
274 weight during this time. Some species begin incubation with the first egg, causing the

275 young to hatch asynchronously; others begin after laying the second egg, thus  
276 decreasing hatching asynchrony between siblings [103].

277 Both parents are involved in parental care. From the moment the egg is  
278 hatched, one parent cares for the newly hatched chick(s) while the other forages for  
279 food. Penguin chicks are semi-altricial, *i.e.* they need parental care (food, warmth,  
280 protection) before becoming independent. At the start of the rearing period, the  
281 chicks either sit on their parents feet (emperor and king penguins) or under their  
282 bellies, to be kept warm and dry. Young are guarded (guarding stage) by both  
283 parents for varying periods of time before forming crèches. Both parents feed the  
284 chicks by regurgitation. Nestlings beg for food by pecking adult's bill and/or by  
285 singing. Guarding stage may be affected by environmental conditions [102] and when  
286 they are not being protected by the adult, the chicks form crèches to keep warm and  
287 stay protected. As the chicks grow, their feeding requirements quickly increase,  
288 making it difficult for just one of the parents to obtain enough food. Eventually, the  
289 chicks are large enough so that both parents can go to sea to gather food for their  
290 chick simultaneously. When parental provisioning is low, alloparental feeding  
291 (feeding of offspring by adults other than their own parents) sometimes occurred in  
292 little [104], emperor [105], king [106] and Adélie penguins [74]. In most species the  
293 chicks gather together in crèches to provide protection both from predators and from  
294 the elements. In some species, such as king penguins, crèches can be large with  
295 many hundreds of chicks tightly packed together. In other species such as African  
296 penguins, the crèches are smaller (with up to 10 chicks coming together) and less  
297 dense. Age at fledging ranges from one to eleven months (Fig. 1A) and fledglings are  
298 a bit smaller and lighter than adults, except in emperor penguins for which body  
299 mass of fledglings is about half of adults' [16]. While they are still on their breeding

300 grounds, chicks have to moult to adorn themselves with a waterproof plumage, which  
301 will allow them in turn to go hunting offshore and acquire their food independently.  
302 Adults also have to moult like other birds and all penguins replace their feathers each  
303 year on their breeding grounds, except for the emperor penguins for which moulting  
304 often takes place far away from their breeding grounds [107-109]. Although other  
305 birds lose some feathers individually at a time and replace them over a few months,  
306 penguin moulting is fast, taking only two (e.g. *Pygoscelis antarctica*, [110]) to five  
307 weeks (e.g. genus *Aptenodytes*, [16,111,112]). Moulting is extremely important to  
308 penguins as they need to maintain their feathers in perfect condition at all times to  
309 insulate their body from environmental conditions at sea or on land. Adults generally  
310 moult after the breeding season. Once their chicks have moulted into their own  
311 juvenile plumage the adults return to sea for a few weeks to build up their own fat  
312 reserves and then come back ashore to moult. During the moult, penguins are no  
313 longer waterproof and cannot enter the sea, they can lose up to 50 % of their body  
314 mass, they are not well insulated and they are vulnerable to predation. Therefore,  
315 this is a critical period of time for penguins during which they have to face the  
316 elements and starve until their new set of feathers is ready.

317

### 318 **Genus *Aptenodytes***

319 Birds of the genus *Aptenodytes* (*A. forsteri* and *A. patagonicus*) are bigger and taller  
320 than other penguin species (Table 1). They do not build a nest and only lay one large  
321 egg (on average 445 and 307 g, respectively; Table 1), which is kept on the top of  
322 the incubating parents' feet at least for 54 days (Fig. 1B). As for other penguins,  
323 parents recognise their chick by voice and young also recognise parents by call [11].

324           The breeding cycle of the genus *Aptenodytes* largely differs from the breeding  
325 cycle of most of the other penguin species. In most penguin species, it takes from 8  
326 to 15 weeks to raise a chick to the juvenile stage (Fig. 1B) but it can take 10 to  
327 13 months for king penguins to fledge their chick [18]. Because of this long chick-  
328 rearing period, king penguins only produce two chicks every three years. As a result,  
329 12-month-old chicks cohabit with incubating birds in king penguin colonies. Every  
330 year, emperor penguins manage to raise their large chicks more quickly (five  
331 months), using a different strategy. Indeed the chicks moult into juvenile plumage  
332 while they are still much smaller than their parents. The juveniles then continue to  
333 grow out at sea.

334           The emperor penguin also seems to be an exception among penguins as they  
335 begin their breeding cycle when other Antarctic birds have finished theirs. Each year,  
336 from late December to March (*i.e.* late summer), emperor penguins disperse into the  
337 oceans, travelling and foraging into the waters surrounding the Antarctic continent  
338 [109,113]. In March-April, as winter approaches and fast-ice extent grows, all mature  
339 emperor penguins move south towards their colonial breeding areas at the border of  
340 the Antarctic continent. The breeding cycle of emperors stands in contrast with that of  
341 other penguin species (except for the king penguin) by its long duration and by the  
342 fact that it takes place in the midst of the severe Antarctic winter, whereas other  
343 penguins breed during the short and milder summer season. Indeed, the emperor  
344 penguin is one of the few birds for which gonadal growth is coincident with short  
345 days, when birds are still at sea. Gonadal steroids are several fold above basal level  
346 at the time of arrival on the breeding area suggesting that environmental cues,  
347 especially decreasing daylength, decreasing air temperature, and sea-ice formation,  
348 stimulate gonadal development and reproduction [1]. Before breeding, emperor

349 penguins forage far away from their breeding grounds [109,114,115]. In the Southern  
350 Ocean, a period of high productivity occurs during summer, from October to April,  
351 and is followed by a period of low productivity during winter, from May to September  
352 [116-118]. Because emperor penguins breed in winter, they have to anticipate their  
353 breeding season by accumulating body reserves during high ocean productivity in the  
354 previous summer [79]. To our knowledge, this breeding strategy is unique among  
355 animals. Furthermore, emperors breed on sea-ice in a few favourable zones that may  
356 be a hundred kilometres distant from the open sea or polynias where they exclusively  
357 feed [119]. As a consequence of the distance from the feeding grounds, and because  
358 breeding activity competes with feeding, female and male emperors fast for as long  
359 as 1.5 and 4 months, respectively [16,31]. For females, the breeding fast comprises  
360 only the courtship period, since they leave their single egg to their mate as soon as it  
361 is laid and then go back to sea for building up their reserves. For males, the period of  
362 fasting includes the courtship and the whole incubation period. To face the austral  
363 winter, emperor penguins have to exploit in an optimal way their limited body fuels in  
364 order to succeed in their breeding [16,120,121]. This is possible only thanks to their  
365 huddling behaviour, which allows them to decrease energy expenditure [120,121].

366

367 **Which environmental changes might affect the breeding cycle of the different**  
368 **penguin' species?**

369 The Earth's climate is undergoing rapid warming which is driving shifts in the  
370 distribution and phenology of many plants and animals [122,123]. Among animals,  
371 penguins are adapted to live in extreme environments (Fig. 2), but, because each  
372 species is restricted to a limited latitudinal range (Table 1), they can be highly  
373 sensitive to climate change [124]. Environmental changes are not uniform across



374 regions, with resource increasing in the subantarctic areas and decreasing in  
375 Antarctica [123]. Quantifying changes in breeding phenology is important for  
376 understanding how populations respond to these changes, especially those resulting  
377 from human activities [123].

378 **Climatic changes and resource availability:** Detecting and predicting how  
379 populations respond to environmental variability are crucial challenges in  
380 management and conservation research. This is particularly true for populations at  
381 high latitudes, many of which demonstrate changes in population dynamics  
382 associated with global warming [125]. Some seabird populations of the Southern  
383 Ocean have been responding to climate change for the last three decades and  
384 demographic models suggest that projected warming will cause dramatic population  
385 changes over the next century [114]. In the Antarctic ecosystem, population  
386 dynamics of top predators like penguins may yield important information about how  
387 the environment is changing [126]. The phenotypic plasticity of penguins may allow  
388 them to continue to exploit their transformed ecological niche and maintain their  
389 current distributional ranges. For instance, penguins may vary the timing of breeding  
390 in response to changes in environmental conditions [127]. However, paleoecological  
391 records suggest that penguins are more likely to respond by dispersal rather than  
392 adaptation [124]. Thus shift in species distribution is likely to be one of the major  
393 possible adaptations to changing environmental conditions [114]. This is exemplified  
394 by the distributional range of chinstrap [124,126,128], gentoo and Adélie penguins  
395 [124,129-130] that has shifted southwards around the Antarctic Peninsula.

396         However, as each species is limited to a specific latitudinal range, a latitudinal  
397 shift may be very limited. Thus, emperor penguins' colonies north of 70°S are  
398 projected to decrease or disappear, and limited growth might occur south of 73°S

399 [131]. These population trends are likely to be related to sea ice conditions [132]. For  
400 example, at Pointe Géologie (Adélie Land), distance to the fast ice edge and its  
401 extent are major determinants of emperor penguin breeding success [132].  
402 Therefore, the increased frequency of warm events associated with projected  
403 decreases in sea ice extent is likely to reduce population viability [133,134].

404 Other physical factors than sea-ice can also affect penguin populations. For  
405 instance, sea surface temperature consistently drives the foraging behaviour of king  
406 penguins, and, according to climate models, the projected warming of surface waters  
407 could lead to a gradual southward shift of their more profitable foraging zones [114].  
408 Such a shift would negatively affect the king penguin population, unless penguins  
409 develop alternative foraging strategies [114] as to modify their timing of breeding  
410 [127].

411 The Antarctic Peninsula is among the fastest-warming areas on the Earth, with  
412 5-6°C increases in mean winter air temperatures and associated decreases in winter  
413 sea-ice cover [135]. These perturbations have affected the ecosystem profoundly  
414 [135]. To respond to these climatic changes, varying the timing of reproduction in  
415 response to local environmental conditions is a key factor influencing reproductive  
416 success [127]. For example, clutch initiation and hatching dates of royal, Adélie and  
417 gentoo penguins occur earlier with warmer temperatures [123,127]. However, these  
418 behavioural adjustments may not be sufficient to prevent populations from declining.  
419 The “sea-ice hypothesis” proposing that ice-obligate species directly decline because  
420 of sea-ice reduction, does not appear to be sufficient to explain why populations of  
421 both ice-loving and ice-avoiding penguins have declined significantly [135]. Some  
422 researchers argue in favour of an alternative, more robust hypothesis, that attributes  
423 both increases and decreases in penguin populations to changes in the abundance

424 of their main prey, Antarctic krill [135]. Indeed, decline of chinstrap penguin  
425 populations has been suggested as being related to climate change through a  
426 reduction in sea-ice extent during winter and a consequent decline in the abundance  
427 of krill in summer during the breeding season [126].

428         Climate changes can also have more subtle consequences on the foraging  
429 behaviour of penguins. For instance, mixed water regimes resulting from storms,  
430 result in the dispersion of prey items in the water column. This lack of prey  
431 stratification has been described as resulting in reduced foraging efficiency and poor  
432 breeding success in the little penguin [136]. Mixed water regimes are currently  
433 unusual during the breeding period of little penguins, but are expected to become  
434 more frequent due to climate change and may therefore represent an important  
435 threat for this species [136].

436 **Tourism:** Antarctica now fuels one of the fastest growing tourism markets in the  
437 world with over 30,000 visitors annually travelling to the continent [137]. Increasing  
438 ecotourism activity has led to concerns about the effects of ecotourism on wildlife  
439 populations. While some species of penguins habituate to human visits, others  
440 exhibit negative effects due to disturbance [138]. Behavioural, physiological, and  
441 reproductive parameters might thereby be affected. For example, human presence at  
442 the nest site is physiologically stressful for breeding Magellanic penguins that are not  
443 accustomed to seeing humans [139]. Indeed, Magellanic penguins in visited areas  
444 have higher corticosterone stress responses than penguins in undisturbed areas  
445 [138,140]. Moreover, birds exposed to moderate levels of disturbance do not show  
446 evidence of habituation over a period of a few years [139]. However, penguins may  
447 habituate to Humans, as birds that have been exposed to very high levels of human  
448 visitation do not respond anymore to human presence as a stressor. Furthermore,

449 Magellanic chicks from tourist-visited colonies do not flee anymore when approached  
450 by humans [140], and breeding success is not affected by visitation levels in this  
451 species [138]. However, penguin species differ in their sensitivity to human presence.  
452 For instance, in contrast to Magellanic and Adélie penguins, yellow-eyed and gentoo  
453 penguins show significantly lower breeding success at sites exposed to unregulated  
454 tourism compared to areas visited infrequently [130,141]. This may be attributed to  
455 the presence of people on beaches that delays post-foraging landing by penguins  
456 provisioning their chicks, which may in turn affect the amount of food delivered to the  
457 young. Indeed, yellow-eyed chicks from nesting areas with high numbers of tourists  
458 have significantly lower fledging weights than chicks from areas with no tourist  
459 visitors [142]. Taking into account that the probability of survival is positively  
460 associated with mass at fledging, lower fledging weights may have long-term  
461 population consequences [142].

462

### 463 **Conclusion**

464 The present article shows that breeding strategies are diverse and differ between  
465 penguin species. However, breeding behaviour can also exhibit some plasticity within  
466 each penguin species and particularly when environmental conditions vary (e.g.  
467 [102]). More studies simultaneously conducted (1) in several penguin species  
468 breeding in the same location and (2) on the same species in different  
469 locations/environmental conditions would be useful to highlight how environmental  
470 conditions influence breeding strategies in penguins and how penguins can adapt to  
471 environmental perturbations.

472 Many penguin species face the same threats [91]. Marine and coastal  
473 ecosystems are undergoing unprecedented alterations in their processes and

474 structure. Penguins are sensitive species impacted by these phenomena. As top  
475 predators, they are key constituents of marine ecosystems, and are indicators of the  
476 oceanic and coastal ecosystem health. Larger scale ecosystem-based conservation  
477 planning and more focused local efforts are needed for the successful conservation  
478 of many penguin species.

479

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486

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848 **Figures and Table caption:**

849 **Figure 1.** Breeding cycle of the penguins. White, dark and dashed bars denote for  
850 fasting on land, foraging at sea and feeding, chick rearing, respectively. Lettering  
851 stands for species (see Table 1).

852 A/ Breeding cycle of the 18 penguin species and for both sexes (M stands for males  
853 and F for females).

854 B/ Relative breeding cycle of the 18 penguin species. Mean courtship period is  
855 defined as the shortest time between pair formation and the laying of the first egg.  
856 Breeding cycle is defined as the time elapsed from the arrival of the penguins on their  
857 breeding site to the fledging of the chick(s).

858 References for each species and periods:

species	pairing	incubation	chick rearing
<i>Af</i>	[31]	[16,31,35]	[31,35]
<i>Ap</i>	[17,18,59]	[17,18,35,59,63]	[17,18]
<i>Ec</i>	[11,12,20,40]	[12,20]	[12,40]
<i>Ech</i>	[32,44,60]	[32,44,60]	[32]
<i>Em</i>	[11,12,20,40]	[12,20]	[12,40]
<i>Ep</i>	[12,22]	[12,22]	[12]
<i>Er</i>	[11,12,23]	[11,12,23]	[12]
<i>Es</i>	[11,12,24,61]	[24,44,61]	[12]
<i>Esc</i>	[23,42]	[11,12,48]	[12,25]
<i>Em</i>	[62]	[11,62,64,65]	[71]
<i>Ma</i>	[11]	[27,34]	[12]
<i>Pa</i>	[12,29,52,53]	[11,12,35,50,52,66,67]	[12,35]
<i>Pan</i>	[12,29,50,53]	[12,50,53]	[12,53]
<i>Pp</i>	[29]	[11,12,54,68,69]	[69]
<i>Sd</i>	[56]	[14,56]	[56]
<i>Sh</i>	[12]	[12]	[12]
<i>Sm</i>	[30]	[30]	[12]
<i>Sme</i>	[12]	[70]	[12]

859

860 **Figure 2.** Repartition of the 18 species of breeding penguins (%) according to the  
861 Southern latitudinal gradient.

862

863 **Figure 3.** Time elapsed from arrival at the breeding site (dashed line) and onset of  
864 yolk formation for the 17 penguin species among the 18 ones. Lettering stands for  
865 penguin species (see Table 1).

866

867 **Table 1.** Some biological characteristics of the 18 penguin species.

868 Body mass is the mean body mass of birds at the onset of the breeding season.

869 Mate fidelity is from one year to the consecutive year. For egg formation values, see

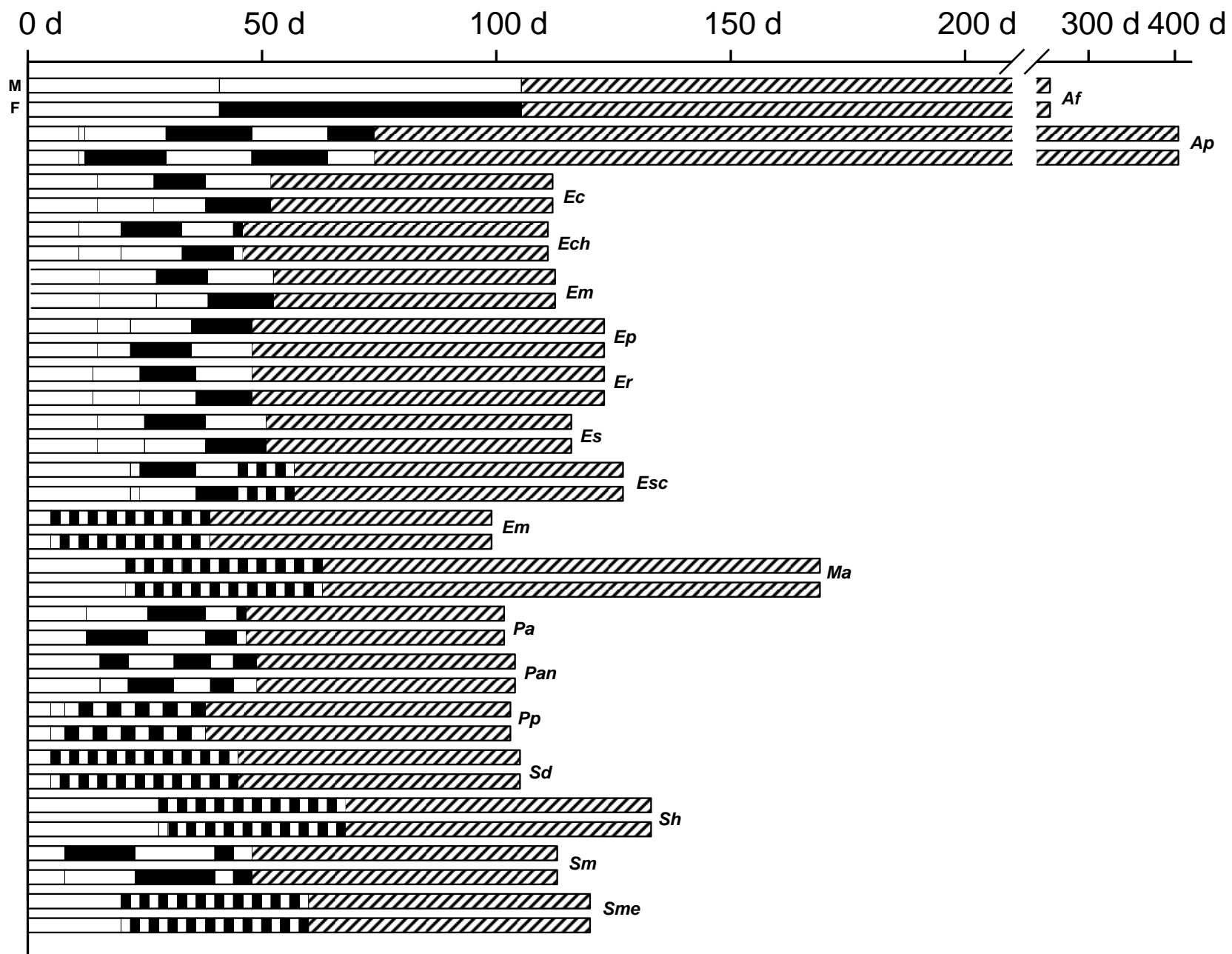
870 the Material and Methods section. The B-egg formation column represents the time

871 elapsed since the onset of the first yolk development. Abbreviations of the different

872 species are given in brackets after the scientific name of each species. Each

873 reference is indicated by a number in brackets. IUCN 2012 red list codes:

874 EN=endangered, LC=least concern, NT=near threatened, VU=vulnerable.



A

