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**Repeatability of alert and flight initiation distance in king penguins:  
effects of colony, approach speed and weather**

**Running title:** Repeatability of flight initiation distance

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20 TLH, CS, PB, VAV; writing: TLH. Revision: TLH, VAV, PB. All authors read and commented  
21 on the final manuscript.

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## 31 **CONFLICT OF INTEREST STATEMENT**

32 The authors declare that they have no conflict of interest.

33

## 34 **ABSTRACT**

35 Alert Distance (AD) and Flight Initiation Distance (FID) are popular measures used to  
36 explore the reaction of prey to approaching predators, and thus the economics that underlie  
37 optimal escape strategies. AD likely mirrors the effort invested into vigilance, while FID provides  
38 an estimate of the perceived risk of an approaching threat. Although individual variation in AD  
39 and FID is influenced by environmental factors such as variation in predation pressure and human  
40 disturbance, the repeatabilities of these traits (especially AD), and therefore their designation as a

41 personality trait, remain under investigated. Here, we studied the repeatability of AD, FID, and  
42 the decision to flee in a flightless, ground-breeding seabird, the king penguin (*Aptenodytes*  
43 *patagonicus*). A single experimenter approached three times over three consecutive days 47  
44 incubating king penguins from two different colonies with varying human disturbance levels. We  
45 explored the effects of weather, time of day, and approach speed of the experimenter on these  
46 behaviors. Weather had an effect on all three behaviors. In warm, sunny weather AD increased,  
47 while in rainy, windy weather birds were more likely to flee yet waited longer before initiating  
48 flight. Faster approach speeds between AD and FID increased FID. Weather conditions and speed  
49 of approach affected repeatability estimates, highlighting the need to consider external sources of  
50 variation when refining such estimates. FID and the decision to flee were significantly and  
51 moderately repeatable ( $r = 0.26$  and  $0.57$  respectively), while AD was not. There was no evidence  
52 of habituation or sensitization due to colony.

53 **Key words:** *Aptenodytes patagonicus*, personality, human disturbance, optimal escape decisions,  
54 predation risk,

55

## 56 INTRODUCTION

57           Understanding how wild animals react to threats - especially predators - and the  
58 economics underlying (optimal) escape decisions, is a central topic in behavioral ecology that has  
59 been widely studied by evaluating Alert (AD) and Flight Initiation (FID) Distances (Tätte et al.,  
60 2018; Blumstein, 2019; reviewed in Frid & Dill, 2002). AD and FID can be defined as the  
61 distances at which a focal animal interrupts its normal behaviour to become alert (AD) or begin to  
62 flee (FID) from an approaching predator. AD provides us with a surrogate of the amount of time,  
63 and possibly energy, invested by the focal individual into surveying its surrounding; i.e., the  
64 degree of vigilance (Fernández-Juricic and Schroeder, 2003; Beauchamp, 2015; Uchida et al.,  
65 2019; but see Tätte et al., 2019). Meanwhile, variation in FID informs us on the perceived  
66 predation-risk of the focal individual (Blumstein, 2006, 2019; Møller et al., 2008).

67           In practice, the decisions that prey undertake when approached by a predator (AD and  
68 FID) can be simulated by performing non-lethal approaches by human experimenters (Frid and  
69 Dill, 2002; Beale and Monaghan, 2004a). Animals are expected to respond in much the same  
70 way to human approach stimuli as they would to actual predators since (1) both divert time and  
71 energy that could be otherwise invested in fitness enhancing activities; and (2) animals should be  
72 selected to overestimate rather than underestimate risk due to the cost of miscalculation, *i.e.*,  
73 injury or death (Frid and Dill, 2002). While AD can be hard to observe in some species or  
74 contexts, FID has the advantage of being easily measured and quantified (Tarlow and Blumstein,  
75 2007). Both can be standardized within and across studies (Blumstein, 2006; Møller et al., 2008),  
76 and are species-specific (Blumstein et al., 2003; Møller, 2008; Carette and Tella, 2011; Piratelli et  
77 al., 2015). As a consequence, FID in particular and AD when available, have become popular  
78 measures in conservation biology used in establishing set-back distances and buffer zones to

79 minimize stress-related disturbances on wildlife (Rodgers and Schwikert, 2002; Fernández-Juricic  
80 et al., 2005).

81           Although AD and FID are species-specific, there is fast accumulating evidence that FID  
82 (and to a lesser extent AD) can vary among populations of the same species and between  
83 individuals within the same populations (Edwards et al., 2013). For instance, FID is often shorter  
84 in urban versus rural populations (Piratelli et al., 2015; Carette and Tella, 2017), suggesting either  
85 that these animals have habituated (or developed tolerance) to human disturbance (Burger and  
86 Gochfeld, 1981, 1990; Walker et al., 2006), or that less tolerant individuals have migrated away  
87 from human presence (Ellenberg et al., 2009; Carette and Tella, 2010, 2011). Further, upon  
88 repeated approaches, FID has been shown either to decrease (habituation: Carter et al., 2012;  
89 Petelle et al., 2013; Arroyo et al., 2017), or increase (sensitization: Dill, 1974; Wheeler et al.,  
90 2009), demonstrating within-individual plasticity. FID can display consistent inter-individual  
91 (repeatable) variation over time (Carette and Tella, 2010; Carter et al., 2012; van Dongen et al.,  
92 2015). The same cannot be said of AD, which remains to be explored; however, vigilance  
93 behavior has often been found to be mildly repeatable (Couchoux and Cresswell, 2012; Roche  
94 and Brown, 2013). Repeatable behavioral traits measured over time are a prerequisite for the  
95 characterization of individual personality or temperament traits (Dingemanse & Wright, 2020),  
96 and might suggest genetic or early environmental constraints shaping individual risk-taking  
97 behavior. In fact, due to its repeatability, FID is frequently used as a metric to explore boldness  
98 (Atwell et al., 2012; Petelle et al., 2013; Highcock and Carter, 2014; Young et al., 2015), one of  
99 the five main personality traits defined by Réale et al., (2007), which is associated with risk-  
100 assessment and risk-taking, particularly in the context of predation and disturbance.

101           AD and FID should be strongly selected in prey species, in a way that balances the  
102 survival benefits of escaping approaching predators with the costs of abandoning other fitness-

103 enhancing activities such as reproduction (Ydenberg and Dill, 1986). Consequently FID is known  
104 to vary with the perceived risk of predator approaches (Frid and Dill, 2002; reviewed in  
105 Stankowich and Blumstein, 2005) including the size or number of predators (Beale and  
106 Monaghan, 2004a; Geist et al., 2005), directness of approach (Smith-Castro and Rodewald, 2010;  
107 Sreekar and Quader, 2013; but see Fernández-Juricic et al., 2005), speed of approach (Bateman  
108 and Fleming, 2011; Samia et al., 2016; but see Lafferty, 2001), and predator intent (*i.e.*, predator  
109 suddenly turning towards the prey or maintaining a purposeful gaze; Cooper, 2003; Bateman and  
110 Fleming, 2011; Sreekar and Quader, 2013). FID has also been shown to vary with the time of day  
111 (Patelle et al., 2013; Piratelli et al., 2015, Ferguson et al., 2019), can be reduced when prey have  
112 low energy reserves (Beale and Monaghan, 2004b; Piratelli et al., 2015), are in a large group  
113 (dilution effect; Ydenberg and Dill, 1986; Burger and Gochfeld, 1991, Santoyo-Brito et al.,  
114 2020), or are in close proximity to refuge (Cooper and Whiting, 2007). AD has not been explored  
115 to the same extent as FID, but evidence suggests that vigilance behaviour is also modified by time  
116 of day (Edwards et al., 2013), weather conditions (Couchoux and Cresswell, 2012), conspecific  
117 interactions (Hess et al., 2016), sex and reproductive status (Burger and Gochfeld, 1994), and  
118 group size (Díaz and Asensio, 1991; Carter et al., 2009; Boujja-Miljour et al., 2018).

119         The cost-benefit fitness trade-off of fleeing a tentative predator should be particularly  
120 strong for ground-laying birds tied to vulnerable nesting sites, such as penguins. Penguins commit  
121 a high amount of time and energy to reproduction (obligate bi-parental care, long-term fasting,  
122 prolonged breeding cycle and chick development; Williams, 1995), and face a strong fitness  
123 trade-off between the survival costs of defending their brood against predators (*i.e.*, injuries and  
124 potential death for the adult) and the reproductive costs of abandoning their current reproduction  
125 but surviving to breed another year (Montgomerie and Weatherhead, 1988; Frid and Dill, 2002;  
126 Dowling and Bonier, 2018). Accordingly, penguins are usually highly territorial and defensive of

127 their brood (Viñuela et al., 1995; Amat et al., 1996; Côté, 2000), though within species there is  
128 clear variation on the degree of territoriality and aggression depending on brood value (Amat et  
129 al., 1996; Côté, 2000), the type of threat considered (Lee et al., 2017), and bird personality  
130 (Traisnel & Pichegru, 2018). Surprisingly, few studies have investigated how variable AD and  
131 FID to approaching predators are in penguins, nor the factors affecting those traits, despite their  
132 importance in shaping breeding decisions, and despite the fact that several studies have  
133 documented marked effects of disturbance (e.g. ecotourism) on penguin behavior (vigilance and  
134 locomotory behavior, time budgets; Holmes et al., 2005, 2006; Burger and Gochfeld, 2007),  
135 physiological stress (Ellenberg et al., 2006, 2012, 2013; Viblanc et al., 2012; Carroll et al., 2016),  
136 or reproduction (Giese, 1996; McClung et al., 2004; Ellenberg et al., 2006; reviewed in Bateman  
137 and Fleming, 2017).

138         Here, we investigated the variability of both AD and FID in breeding king penguins  
139 (*Aptenodytes patagonicus*). King penguins are large, ground-laying, flightless birds that form  
140 extensive colonies on the subantarctic shorelines. Breeding pairs incubate their single egg or  
141 young chick on top of their feet (Stonehouse, 1960), therefore limiting their mobility. They are  
142 subject to on-land predation mostly by giant petrels, *Macronectes halli* and *Macronectes*  
143 *giganteus*, and brown skuas, *Catharacta lonnbergi* (Hunter, 1991; Descamps et al., 2005). Giant  
144 petrels and skuas especially target eggs and chicks, but petrels are also known to prey on injured  
145 adults (Hunter, 1991). These predators will harass incubating and brooding adults sometimes  
146 causing them to flee and abandon their eggs. Breeding adults have three choices: first to stay and  
147 fight, risking potentially fatal injuries; second to flee slowly clumsily with the egg on top of  
148 their feet clustering closer to neighbouring breeders; or finally, to flee entirely, guaranteeing  
149 survival but abandoning their current reproduction.



150 We calculated individual repeatabilities for AD and FID which were measured several  
151 times on incubating adults, and assessed the potential influences of approach speed, weather  
152 conditions, and time of day on AD and FID as these may impact the levels of vigilance and  
153 responsiveness to a threat. Specifically, we expected AD and FID to vary in a quadratic function,  
154 increasing at dawn and dusk, and coinciding with highest predation risk for chicks (giant petrel  
155 activity is highest at early and late hours of the night; Le Bohec et al., 2003; Descamps et al.,  
156 2005). We further tested whether individuals sensitized or habituated to repeated approaches by a  
157 human experimenter by examining bird responses in two different colonies; one close to human  
158 settlements and one relatively unexposed to human disturbance. King penguins have been shown  
159 to express significantly lower heart rate stress responses to human approaches in disturbed areas  
160 vs. undisturbed colony areas (Viblanco et al., 2012). Thus, we expected individuals measured in  
161 the colony close to human settlements to show habituation to approaching experimenters  
162 (decreased AD and FID compared to the undisturbed colony).

163

## 164 **METHODS**

### 165 **Study sites**

166 This study was conducted in mid-to-late January during the Austral summer of 2010-  
167 2011. Birds were selected from two colonies of king penguins located on Possession Island in the  
168 Crozet Archipelago, namely the colonies “La Baie du Marin” (BDM, 46°25’S – 51°52’E) and  
169 “Jardin Japonais” (JJ, 46°21’S – 51°43’E). BDM is home to ca. 22 000 breeding pairs (Barbraud  
170 et al., 2020) and is located on the east side of Possession Island in close proximity to a  
171 permanently inhabited research station built in 1961. This colony has been exposed throughout  
172 the year for the past 50 years to the daily presence of scientists and non-scientists in or close to

173 the colony (Viblanco et al., 2012). During this time, birds in BDM have been regularly exposed to  
174 humans including tourist visits, censuses, population counts, and systematic monitoring.  
175 Meanwhile, JJ is home to ca. 39 000 breeding pairs (Barbraud et al., 2020) and is located on the  
176 north side of the island some 13 km from BDM. JJ is a relatively undisturbed colony, far from the  
177 research station and visited by scientists only a few times every year for population count and  
178 census information.

179

### 180 **Approach protocol**

181 We repeatedly approached a total of 47 incubating birds in the two colonies (23 birds  
182 from JJ and 24 birds in BDM). Each individual was approached once per day over three  
183 consecutive days between the hours of 8:00 and 19:00 (from Jan. 11 - 13 in JJ, and from Jan. 30 -  
184 Feb. 1 in BDM). It was not possible to find all birds on the subsequent days and so two birds in  
185 BDM were only approached once, and one bird each in JJ and BDM were only approached twice.  
186 Following egg-laying, king penguin partners alternate incubation duties, allowing their partner to  
187 forage at sea while they fast on land (Stonehouse, 1960). The male takes the first incubation shift,  
188 and the egg hatches some 53 days later, usually during shift four when the female has possession  
189 of the egg (Weimerskirch et al., 1992).

190 Following the STRANGE guidelines (Webster & Rutz 2020), we provide hereafter  
191 details on how incubating birds were selected and highlight potential biases related to the  
192 selection of our study subjects. Birds were selected haphazardly while incubating their eggs, and  
193 therefore we had no individual information on their sex, age, incubation shift, or previous  
194 experience with humans. Chosen individuals visually appeared in good physical condition, based  
195 on their plumage (shiny) and morphological (fat) appearance, and thus had not been fasting for

196 extended periods of time. Individuals were selected at distance, and not after being approached or  
197 captured. Therefore, we expected no strong initial sampling bias in relation to how individuals  
198 were responding to human approaches (but see discussion).

199 Selected individuals were marked from a distance (roughly 1 m) at the end of the first  
200 approach using a dot of non-permanent pressurized spray animal dye (Porcimark®, Kruuse,  
201 Lageskov; Denmark) on the belly for identification during subsequent approaches. All approaches  
202 were performed by the same observer (BG) dressed in the same clothing. Individuals were only  
203 approached if they were resting upon arrival of the observer (*i.e.*, not engaged in aggressive,  
204 preening, or sleeping behaviours). The approach started after having observed the bird resting for  
205 at least one full minute before approaching it. During this time, the experimenter hid out of line of  
206 sight. Each approach had a set starting distance of 18 m, as measured with a laser telemeter  
207 (Leica DISTO™ D5 Lasermeter, Leica Geosystems AG, Hexagon, Sweden), which we  
208 standardized due to the known influence of starting distance on FID (Blumstein, 2003, 2010;  
209 Dumont et al., 2012). We chose a starting distance of 18 m based on preliminary observations of  
210 59 king penguins, including courting (paired) and incubating birds (a sample representative of the  
211 various life-history stages in the colony, excluding moulting and chick-brooding birds), that  
212 showed the maximal distance at which birds exhibited signs of vigilance towards an experimenter  
213 was 12.45 m and the minimal distance was 3.03 m (mean  $\pm$  SD = 6.85  $\pm$  1.87 m). We used a  
214 starting distance 1.5 times greater than the maximal detection distance recorded in the preliminary  
215 study to ensure starting distance far exceeded maximum alert distance (see also Fleming and  
216 Bateman, 2017).

217 The approaching observer followed a direct trajectory toward the focal individual, in  
218 plain line of sight, always starting from outside the colony. The experimenter walked until the

219 first sign of alert was detected (the bird tilting its head or stretching its neck in the direction of the  
220 experimenter). At this distance, termed the Alert Distance (AD), the experimenter took a  
221 standardized one-minute pause to record AD and time. The time from the start of the approach  
222 until the bird became vigilant was recorded with a stopwatch and the remaining distance to the  
223 selected bird measured with a laser telemeter (closest cm). The approach was then resumed until  
224 the bird showed the first signs of fleeing (slowly walking away with its egg resting on its feet) –  
225 termed Flight Initiation Distance, FID. Some birds never showed signs of flight while being  
226 approached, right up until close (FID = 0 m) (see also Bateman and Fleming, 2011, for similar  
227 results in ibises). FID had therefore a zero-inflated distribution (see supporting information S1),  
228 suggesting this measure reflected two different processes: *i*) the decision to flee or not (0/1); and  
229 *ii*) the distance at which flight (escape) should occur if birds decide to flee. Hereafter, we  
230 analysed these two processes separately. We calculated the speed of approach (m/s) prior to the  
231 occurrence of AD and FID as the distance walked (m) divided by the duration of approach (s).  
232 The mean speed  $\pm$  SE of approach prior to AD was  $0.61 \pm 0.09$  m/s (range = 0.44 – 0.86 m/sec)  
233 and the mean  $\pm$  SE speed of approach between AD and FID was  $0.57 \pm 0.10$  m/s (range = 0.35 –  
234 0.90 m/s). Walking speed varied slightly due to topography, entering the colony, and breeder  
235 density.

236         At the start of each approach, we recorded air temperature to the nearest 1°C, and we  
237 scored wind speed, solar levels, and rain on a scale from 0 to 2, with half levels (i.e., 0.5) being  
238 allowed. A value of 0 indicated no wind or rain, or full cloud cover (no sun). A value of 2  
239 indicated heavy wind or rain or full sun. Mean temperature was 10 °C (range = 7 – 13 °C). As air  
240 temperature, wind speed, rain, and solar levels were naturally correlated, we used a Principal  
241 Components Analysis (PCA) to summarize all weather variables (package “FactoMineR”, Lê et  
242 al., 2008). This approach had the advantage of capturing climatic variation on a continuous scale

243 through two independent and orthogonal axes, and avoided strong collinearity (VIFs >30) issues  
244 if ‘raw’ meteorological variables are used in the analyses. We kept the first two principal  
245 component (PC1 and PC2) which together explained over 84% of the variation in climate data.  
246 Increasing PC1 (64.86% of variation) values were mainly associated with higher sun scores  
247 (correlation = +0.939) and higher temperature (+0.918), and to a lesser extent higher wind scores  
248 (+0.639), and lower rain scores (-0.686). In contrast, increasing PC2 (19.77% of variation) values  
249 were mainly associated with higher wind scores (+0.702), higher rain scores (+0.543), but not  
250 with sun scores (-0.010) or temperature (-0.061). Thus, increasing PC1 values described sunnier,  
251 warmer days while increasing PC2 values described windier, rainier days. On average, the  
252 climate conditions varied during our three approaches in both colonies (see supporting  
253 information S2), highlighting the need to control for climatic variation in further analyses.

254

## 255 **Statistical analyses**

256 All statistical analyses were performed in R 3.6.1. (R Development Core Team, 2020).  
257 Results are presented as means  $\pm$  SE. We investigated the sources of variation in AD (gaussian  
258 distribution), the decision to flee or not (FID: 0/1, binomial distribution), and the distance at  
259 which flight was taken for birds that did decide to flee (FID > 0; gaussian distribution) using  
260 linear mixed models (LMM) and generalized linear mixed models (GLMM) with the appropriate  
261 error distribution. In all the models, we entered individual ID as a random factor to control for  
262 repeated measures, and we included as fixed effects the time of day, weather (PC1 and PC2),  
263 approach speed, approach order (three levels: first, second, or third approach), and the colony  
264 (two levels: BDM vs JJ). To test whether birds differed in their behavior at different times of day,  
265 and whether habituation or sensitisation to human approaches occurred differently between

266 colonies, we also included second order interaction *colony x approach order* and *time of day x*  
267 *time of day* (viz.,  $\text{time}^2$ ) in our starting models. Second order interactions were dropped from the  
268 final model if not significant. Models were run using the *lmer* and *glmer* functions in the package  
269 “lme4” (Bates et al., 2015). The significance of the fixed effects was tested with the *anova*  
270 function (type 3) from the package “lmerTest” (Kuznetsova et al., 2017) using F tests with  
271 Satterthwaite estimation for the denominator degree of freedom for models with a gaussian  
272 distribution. Pseudo- $R^2$  for the models were calculated using methods developed in Nakagawa  
273 and Schielzeth (2013). Prior to analysis, time of approach was converted to decimal time, and  
274 non-zero FIDs were log-transformed (natural log) to normalize the distribution of the residuals.  
275 Independent variables were checked for collinearity using Variance Inflation Factors (VIF) (Zuur  
276 et al., 2010). A few VIFs were above 3 (see results), but those were considered acceptable as they  
277 represented different categorical levels of the same factor (e.g. approach order). All variables  
278 were scaled and centered prior to inclusion in the models to compare effect sizes (Schielzeth,  
279 2010). Where appropriate, we insured model residuals were normally distributed by visual  
280 inspection of density distributions, Q-Q plots, cumulative distribution functions, and P-P plots  
281 using the “fitdistrplus” package in R (Delignette-Muller and Dutang, 2015).

282           Repeatabilities and their confidence intervals were calculated using the functions *rpt* for  
283 AD, and FID and *rptBinary* for the decision to flee or not, from the “rptR” package in R (Stoffel  
284 et al., 2017). Repeatability was calculated as the ratio of among-individual variance in AD or FID  
285 ( $\sigma^2_a$ ) over total phenotypic variance (equal to the sum of among-individual variance and within-  
286 individual variance,  $\sigma^2_\epsilon$ ), so  $r = \sigma^2_a / \sigma^2_a + \sigma^2_\epsilon$  (Nakagawa and Schielzeth, 2010). We first  
287 calculated agreement repeatability, also called uncorrected repeatability,  $r$ , which is simply based  
288 on the among- and within-individual variance in AD or FID. Afterwards, significant effects from

289 the above models, which influenced the expression of AD and FID, were controlled for when  
290 calculating adjusted repeatability  $r_{adj}$ , (also called corrected repeatability) (Wilson, 2018).

291

## 292 **Ethics statement**

293 No animal was caught or handled over the course of this study. The research was  
294 approved by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor.  
295 Authorization to enter the colony and approach birds was obtained from Terres Australes et  
296 Antarctiques Françaises. The observations complied with the current laws of France. No eggs or  
297 chicks were abandoned during the course of this study.

298

## 299 **RESULTS**

### 300 **Alert Distance (AD)**

301 On average, focal individuals became alert when the experimenter came to a distance of  
302  $6.94 \pm 0.18$  m; (range = 1.89 – 13.14 m) (Fig. 1A and 1B). The interaction between approach x  
303 colony and time of day<sup>2</sup> did not have a significant effect influencing AD ( $F_{2,111.0}=0.22$ ,  $P=0.802$   
304 and  $F_{1,90.9}=0.02$ ,  $P=0.896$ , respectively), were sequentially removed from the model in that order  
305 (least significant term removed first). The final model with time of day, weather PC1, weather  
306 PC2, speed of approach prior to AD, approach order and colony, as fixed effects explained 13%  
307 (marginal  $R^2$ ) of the total variation, and including individual as a random effect explained 22%  
308 (conditional  $R^2$ ) of the total variation in AD (LMM, n=133 observations, N=47 individuals, 1.63  
309 < VIFs < 3.68, among-individual  $\sigma^2 = 0.37$ ; residual  $\sigma^2 = 3.63$ ). We found no evidence that AD  
310 was significantly affected by the time of day ( $F_{1,92.2}=2.00$ ,  $P=0.160$ ), speed of approach

311 ( $F_{1,120.0}=1.25$ ,  $p=0.267$ ), weather PC2 ( $F_{1,98.8}=2.90$ ,  $p=0.092$ ), colony ( $F_{1,84.0}=0.00$ ,  $P=0.982$ ), or  
312 approach order ( $F_{2,106.0}=2.14$ ,  $P=0.123$ ) (Fig 2A). However, AD was significantly influenced by  
313 weather PC1 ( $F_{1,102.1}=7.29$ ,  $P=0.008$ ) with individuals showing lower AD during warm and sunny  
314 conditions (Fig. 2B).

315 AD was not significantly repeatable when analysed on its own ( $r=0.103$ ;  $CI_{95}=[0, 0.290]$ ;  
316  $P=0.146$ ), but repeatability was close to significant after adjusting for weather (PC1) as a fixed  
317 effect ( $r_{adj}=0.145$ ;  $CI_{95}=[0, 0.313]$ ;  $P=0.062$ ). Although some individuals appeared to be  
318 repeatable, many others displayed large variability in their AD (Fig. 1A and 1B). Post-hoc power  
319 analyses (see Online Supplementary Material OSM 3) revealed that significant repeatability  
320 (power 0.8) for AD may be achieved for a sample size of 6 approaches on 47 birds – or 3  
321 approaches on 140 birds.

322

### 323 **Flight Initiation**

324 Out of the 47 selected individuals, 41 (87.2%) decided to flee (i.e., move away with their  
325 egg on their feet) during at least one of their approaches (20 birds in JJ, and 21 birds in BDM): 23  
326 individuals always fled, 12 individuals fled twice in three approaches, 6 fled once in three  
327 approaches, and 6 did not flee at all. This corresponded to 42 approaches out of a total of 135  
328 (31%) that resulted in no FID. The FID of the individuals that decided to flee at least once was  
329  $2.83 \pm 0.16$  m (range = 0.68 – 8.58 m) (Fig. 1C and 1D).

330 Time of day<sup>2</sup> and the interaction between approach x colony did not significantly  
331 influence the odds of fleeing (1) or not (0) during the approach (GLMMs; binomial,  $\chi^2=2.35$ ,  
332  $P=0.125$  and  $\chi^2=4.97$ ,  $P=0.083$ ), and were sequentially removed from the model in that order  
333 (least significant term removed first). The final model with time of day, speed of approach



334 between AD and FID, weather PC1 and weather PC2 explained 23% (marginal  $R^2$ ) of the total  
335 variation, and including individual as a random effect explained 73% (conditional  $R^2$ ) of the total  
336 variation in the odds of fleeing (GLMM,  $n=133$  observations,  $N=47$  individuals,  $1.18 < \text{VIFs} <$   
337  $5.36$ , among-individual  $\sigma^2 = 3.29$ ; residual  $\sigma^2 = 6.11$ ). The odds of fleeing were not significantly  
338 influenced by weather PC1 ( $\chi^2=0.24$ ,  $P=0.626$ ), time of day ( $\chi^2=1.19$ ,  $P=0.275$ ), speed of  
339 approach ( $\chi^2=1.86$ ,  $P=0.172$ ), approach order ( $\chi^2=4.98$ ,  $P=0.083$ ) or colony ( $\chi^2=3.09$ ,  $P=0.079$ ).  
340 (Fig. 3A). However, the probability of birds to flee increased significantly with increasing  
341 weather PC2 ( $\chi^2=4.51$ ,  $P=0.034$ ), birds being more likely to flee from the approaching  
342 experimenter in windy and rainy conditions (Fig. 3A and 3B). The decision to flee was  
343 significantly repeatable before (original-scale:  $r=0.504$ ;  $\text{CI}_{95} = [0.084, 1.724]$ ;  $P<0.001$ ) adjusting  
344 for weather, and increased slightly ( $r=0.573$ ;  $\text{CI}_{95} = [0.110, 1.686]$ ;  $P<0.001$ ) after accounting for  
345 the significant effect of weather PC2.

346 For those birds that decided to flee, time of day<sup>2</sup> and the interaction between approach x  
347 colony did not significantly influence FID during the approach (LMMs;  $F_{1,66.5}=0.15$ ,  $P=0.704$  and  
348  $F_{2,67.8}=0.48$ ,  $P=0.619$ , respectively), and were sequentially removed from the model in that order  
349 (least significant term removed first). The final model with time of day, speed of approach  
350 between AD and FID, weather PC1 and weather PC2 explained 37% (marginal  $R^2$ ) of the total  
351 variation, and including individual as a random effect explained 62% (conditional  $R^2$ ) of the total  
352 variation in FID (LMM,  $n=91$  observations,  $N=41$  individuals,  $1.19 < \text{VIFs} < 5.56$ , among-  
353 individual  $\sigma^2 = 0.13$ ; residual  $\sigma^2 = 0.09$ ). We found no evidence that FID was significantly  
354 affected by the time of day ( $F_{1,79.3}=0.122$ ,  $P=0.727$ ), weather PC1 ( $F_{1,67.5}=2.16$ ,  $p=0.146$ ), colony  
355 ( $F_{1,47.2}=0.77$ ,  $P =0.384$ ), or approach order ( $F_{2,63.8}=2.17$ ,  $P=0.123$ ) (Fig 4A). However, FID  
356 increased significantly with the speed of the approach ( $F_{1,71.8}=31.64$ ,  $P<0.001$ , Fig. 4A and 4B)  
357 and decreased significantly with increasing weather PC2 ( $F_{1,60.6}=5.17$ ,  $P=0.027$ , Fig. 4A and 4C).

358 In other words, FID decreased in windy and rainy conditions. Agreement FID repeatability was  
359 low and not significant ( $r=0.102$ ;  $CI_{95} = [0.00, 0.339]$ ;  $P=0.248$ ), but increased significantly when  
360 approach speed and weather PC2 were adjusted for in the model ( $r_{adj}=0.258$ ;  $CI_{95}=[0.010, 0.511]$ ;  
361  $P<0.022$ ).

362

## 363 **DISCUSSION**

364 Our study showed that, in king penguins, both the decision to flee and FID were  
365 significantly and moderately repeatable, whereas AD was not. Climatic conditions had marked  
366 effects on AD, FID and the probability for birds to flee, affecting repeatability estimates, and  
367 highlighting the need to consider external sources of variation in refining such estimates in the  
368 wild (discussed below).

369

### 370 **Between- and within-individual variation in flight initiation**

371 Incubating king penguins showed significant (adjusted) repeatability both in the decision to flee  
372 from an approaching observer (0.57), and in the distance at which they initiated flight (0.26). In  
373 both cases, it is important to note that repeatability values increased when accounting for weather  
374 effects on behavior, which is not surprising since birds experienced different local climate  
375 conditions when they were approached. Notwithstanding, this underlines the importance of  
376 considering heterogeneity in individual habitats and timing of measures when establishing  
377 repeatability estimates from behavioral measures in the wild. Our repeatability values are  
378 comparable, albeit slightly lower, to those reported on FID in other studies: black swans, *Cygnus*  
379 *atratus* ( $r=0.61$ , van Dongen et al., 2015), juvenile yellow-bellied marmots, *Marmota flaviventris*

380 (r=0.40, Petelle et al., 2013), Namibian rock agama, *Agama planiceps* (r=0.71, Carter et al.,  
381 2012), and burrowing owl, *Athene cunicularia* (r=0.88, Carrete and Tella, 2010), and generally  
382 moderate as would be expected for behavioral traits (Bell et al., 2009). The repeatability of both  
383 the decision to flee, and the distance at which flight was initiated, suggest that these behavioural  
384 traits could constitute good candidates for personality traits in breeding king penguins. This  
385 remains to be further explored however, since our power to detect behavioral plasticity in AD and  
386 FID occurring over longer periods was limited by the fact that birds in our study were only  
387 measured over a short period of time (3 consecutive days), and were not previously known  
388 individuals. Separating the repeatable and plastic aspects of alert and flight behavior to  
389 approaching predators in king penguins would benefit from further studies on individually  
390 monitored population where simple measures such as AD and FID are incorporated into  
391 monitoring schemes allowing to test for repeatability and plasticity over the lifetime of  
392 individuals (Dingemanse et al., 2010; Dingemanse & Wright, 2020). Logistically, this would  
393 require permanent marking of individuals in order to follow them through a longer period of time  
394 and through different contexts. In addition, FID (and AD, see below) are likely to vary according  
395 to factors such as individual age, sex, stress responsiveness, or body condition (e.g. Seltman et al.,  
396 2012; Kalb et al., 2019). Testing for such factors in future studies should allow refining  
397 repeatability estimates, with repeatability increasing as more residual variation is accounted.

398         Repeatability estimates of individual propensity to flee and FID increased as extrinsic  
399 factors were accounted for in the models. This is not surprising, but highlights contrasting climate  
400 effects acting both on the propensity to flee (1/0) and on the distance at which birds initiated  
401 flight. Interestingly, weather PC2 (wind and rain) had opposite effects on these behavioral traits.  
402 As conditions were windier and rainier, birds were more likely to flee, but those that fled had  
403 lower FID. This suggests that birds that fled waited until the last moment before they did so,

404 which could be explained by the fact that they were less likely to detect the incoming threat in  
405 windy and rainy conditions. Wind speed has been shown to have contrasting effects on animal  
406 vigilance and escape behavior, from no effect to marked effects depending on the species and  
407 taxa (e.g., no effect: birds; Clucas and Marzluff, 2011, Nordell et al., 2017, Petrelli et al., 2017;  
408 reptiles; McGowan et al., 2014; wind effects: birds; Reynolds et al., 2020; mammals; Wolf &  
409 Croft, 2010). Increased wind speed has been shown in 17 of 18 studies to decrease an animal's  
410 ability to detect an approaching predator by masking sounds, smells and visual cues (Cherry and  
411 Barton, 2017). Wind may also be a source of distraction (Chan et al., 2010; Tatte et al., 2019),  
412 leading to delayed detection of approaching predators. It has been suggested that the magnitude  
413 of FID responses should decrease under harsh weather conditions, as the energy cost of fleeing  
414 increases (Collop et al., 2016). For endotherms wind chill increases thermoregulatory costs, and a  
415 trade-off might exist between investing energy into flight and that into thermoregulation (Collop  
416 et al., 2016, but see also Reynolds et al., 2020). Because penguins rely essentially on fat stores  
417 during incubation on-land (Groscolas & Robin, 2001), and because energy-depleted birds will  
418 abandon reproduction (Groscolas et al., 2000, Gauthier-Clerc et al., 2001), any energy savings –  
419 however small – is critical. Thus, energy savings in harsh climate conditions may contribute in  
420 explaining why birds waited for the last moment to flee. FID also increased with increasing  
421 approach speed of the experimenter. Faster approach speeds after alert may be interpreted as  
422 greater threat by the targeted prey, and thus generating longer FID (Stankowich and Blumstein,  
423 2005; Cooper and Whiting, 2007; Smith-Castro and Rodewald, 2010; Bateman and Fleming,  
424 2011).

425           It is interesting to note that it was not uncommon for the incubating penguins to stay and  
426 defend their eggs aggressively instead of attempting to flee (there was an FID of 0 m in 42  
427 approaches of 135). For these birds either the perceived risk of the approaching threat (a human)

428 was not high enough to elicit a flight response, or the motivation to breed and defend the territory  
429 was stronger than that of attempting to flee. FIDs of 0 m have been observed in other ground  
430 laying birds: yellow-eyed penguins *Megadyptes antipodes* (Ellenberg et al., 2007, 2009),  
431 humboldt penguin *Spheniscus humboldti* (Ellenberg et al., 2006), magellanic penguins *Spheniscus*  
432 *magellanicus* (Fowler, 1999; Villanueva et al., 2014), and African penguins *Spheniscus demersus*  
433 (Pichegru et al., 2016). King penguins are special in that they incubate their egg on their feet in a  
434 specialized brood pouch. Thus, fleeing is at any rate limited, and essentially amounts to clustering  
435 close to neighbours in the hope to benefit from confusion, dilution or selfish herd effects. In  
436 addition, fleeing may risk damaging or losing the egg, losing the breeding territory, suffering  
437 from increased aggression by territorial neighbours (Côté, 2000), or disturbing the thermal  
438 incubation environment required for chick development and survival. For instance, exposed eggs  
439 during transitory breeding abandonment in king penguins have been found to lose heat at a rate of  
440 0.19 °C per minute (Groscolas et al., 2000).

441

#### 442 **Between- and within-individual variation in AD**

443 In contrast to FID, the repeatability of AD was low (0.10) and not significant, but  
444 improved slightly (0.15) and was close to significant ( $P = 0.062$ ) when accounting for the effects  
445 of climate (Weather PC1). As far as we are aware, there is no report of the repeatability of AD in  
446 the literature. Rather, researchers have considered vigilance behaviour when aiming to understand  
447 how animals respond to threats. More vigilant individuals are expected to detect predators earlier  
448 and thus become alert at longer distances (Fernández-Juricic and Schroeder, 2003; Beauchamp,  
449 2015; Uchida et al. 2019; but see Tätte et al., 2019). Studies that measured repeatability in  
450 vigilance behaviours also reported low, but significant, repeatability: eastern grey kangaroos,

451 *Macropus giganteus*, ( $r=0.07-0.14$ , Edwards et al., 2013); redshanks, *Tringa totanus*, ( $r=0.21$ ,  
452 Couchoux and Cresswell, 2012); house sparrows, *Passer domesticus*, ( $r=0.13-0.22$ , Boujja-  
453 Miljour et al., 2018); cliff swallows, *Petrochelidon pyrrhonota*, ( $r=0.089$ , Roche and Brown,  
454 2013). As mentioned above, repeatability estimates are likely to increase as some residual  
455 variation is accounted for by including potential factors such as age, sex, or condition, that were  
456 unfortunately not available in this study as individuals were not followed or handled. Dingemanse  
457 and Dochtermann (2013) determined that for lower repeatabilities,  $>4$  samples per individual  
458 were required if the total number of individuals is  $<100$ . Similarly, Wolak et al. (2012) found  
459 fewer samples per individual were required for higher  $r$  values (3 samples per individual for an  $r$   
460 of 0.8), but for an  $r$  of 0.2, the precision of the estimate continues to increase until up to 10  
461 samples per individual. Because of time and field constraints we were only able to repeatedly  
462 approach 45 individuals 3 times. Yet, post-hoc power analyses revealed that doubling our sample  
463 size to 6 repeated measures per bird would have been sufficient to detect significant repeatability.  
464 At any rate, repeatability was low, indicating that individuals were more flexible in this  
465 behavioral trait than in their decision to flee. Similarly, vigilance levels (and presumably AD)  
466 have been found to be highly flexible (Couchoux and Cresswell, 2012; Edwards et al., 2013) and  
467 sensitive to numerous biological factors such as group position and group size, distance to cover,  
468 predation pressure, season, weather, and time of day (reviewed in Elgar, 1989). In our study, AD  
469 was significantly lower in warm and sunny conditions, suggesting that birds were less vigilant in  
470 good weather conditions.

471

472 **Colony disturbance, predation pressure and STRANGE animals**

473 We expected AD and FID to vary depending on colony and with changes in predation  
474 pressure throughout the day. However, our analyses suggests that neither were major factors  
475 influencing escape decisions in the king penguin. First, on-land predation in king penguin  
476 colonies is highest at dawn and dusk (Le Bohec et al., 2003; Descamps et al., 2005), whereas  
477 most of our measures were done between 8 AM and 6 PM. Extending measurements to early  
478 morning and late evening when predators are most active may allow to better capture potential  
479 effects of predation pressure on penguin behavior. Second, given that the two colonies surveyed  
480 in this study differ markedly in their exposure to human presence throughout the year (BDM is  
481 located next to a research station and breeders have seen humans almost every day for the past 50  
482 years, whereas birds in JJ are rarely exposed to human visitors), we had expected birds in the  
483 BDM (vs. JJ) colony to habituate to approaching humans. However, the lack of difference in  
484 behavioral responses between the colonies is perhaps not so surprising. Previous findings indicate  
485 that birds breeding in more disturbed areas of the BDM colony show lower heart rate stress  
486 responses to an experimenter approaching to 10 m distance than birds in less disturbed areas –  
487 suggesting a potential for habituation to the presence of humans in chronically disturbed areas  
488 (Viblanco et al., 2012). Yet, heart rate responses were similar between the disturbed and  
489 undisturbed areas when birds were approached up to contact and captured (Viblanco et al., 2012).  
490 Although birds were not captured in the present study, they were approached up close (to a few  
491 cm), and the risk assessed was presumably more comparable to a capture than to an observer  
492 standing some 10 m distant.

493 Previous studies in similar seabirds have shown contrasted responses to human  
494 approaches. For instance, whereas Magellanic (*Spheniscus magellanicus*), African (*S. demersus*),  
495 and Gentoo penguins (*Pygoscelis papua*) show reduced behavioural and/or physiological  
496 responses (heart rate or corticosterone concentrations) to human visitation in high disturbance

497 areas (van Heezik and Seddon, 1990; Fowler, 1999; Walker et al., 2005, 2006; Holmes et al.,  
498 2006; Villanueva et al., 2012; Pichegru et al., 2016), yellow-eyed penguins (*Megadyptes*  
499 *antipodes*) appear to sensitize to human exposure through higher stress responses (Ellenberg et  
500 al., 2007). Taken together, these results highlight two important points: (1) behavioural and  
501 physiological responses to approaching predators (or humans) may tell seemingly different  
502 stories. A proper understanding of prey responses to approaching predators requires the  
503 integrative assessment of both physiological stress responses and behavioural reactions. (2) both  
504 behavioural and physiological responses are fine-tuned mechanisms integrating risk assessment  
505 into optimal escape decisions.

506 Finally, we must consider how STRANGE were the animals in our study (Webster &  
507 Rutz 2020). We selected birds in the colonies haphazardly, with no knowledge of their sex, age or  
508 past experience. Nonetheless we did not capture and measure bird morphometrics in our study,  
509 but visually targeted birds that appeared in overall good physical condition in order to minimize  
510 the risk of breeding abandonment for energy-depleted birds (Groscolas et al., 2000, Gauthier-  
511 Clerc et al., 2001) in this protected species. Our measures on individual birds were done over a  
512 few days during which changes in body condition were likely relatively minor. However, we  
513 might not have captured the full range of behavioral expression of AD and FID, particularly for  
514 birds of low body condition. This is important to consider since individuals in poor body  
515 condition may have enhanced stress and FID responses to approaching experimenters (Seltmann  
516 et al., 2012), and emphasizes the importance of controlling for body condition – where feasible –  
517 in performing repeated measures on wild animals.

518 As this study only tested the response to repeated approaches in two colonies, which will  
519 have obvious differences in colony size, density, and topography, replicating this study over  
520 additional colonies would help in a better characterisation of the factors shaping escape decisions



521 in penguins. In addition to landscape and social differences between colonies, there are also  
522 possible differences in predation pressure and genetic differentiation. Furthermore, the sampling  
523 in the two colonies took place 20 days apart, allowing for possible differences in the reproductive  
524 cycle to manifest. Lastly, sampling only occurred over a span of three days. Further studies  
525 should investigate these factors in more depth, as well as test repeated approaches over a longer  
526 time period – and over the lifetime of individual birds. In particular, these would help in capturing  
527 a greater range of weather conditions, and better understanding the extent of repeatability and  
528 plasticity of these behavioral traits (Dingemanse & Wright, 2020).

529         The response of a wild population to human disturbance creates special considerations in  
530 a world that is increasingly accessible to humans. Ecotourism and wildlife tourism, or travel to  
531 natural areas to engage in shared experiences with wildlife and whose aim is to conserve the  
532 environment through education and local spending, are increasingly common activities. As a  
533 charismatic anthropomorphic animal, penguins have garnered much attention. In many species,  
534 habituation occurs in response to disturbances caused by tourists (van Heezik and Seddon, 1990;  
535 Fowler, 1999, Holmes et al., 2006; Villanueva et al., 2014). However, even in species that have  
536 habituated to disturbance, human presence can impact natural behaviours, time budgets, heart  
537 rates and stress levels (Holmes et al., 2005; Walker et al., 2005, 2006; Burger and Gochfeld,  
538 2007; Viblanc et al. 2012; Villanueva et al., 2012; Pichegru et al., 2016). For species that cannot  
539 habituate or which have sensitized to disturbance, individuals may experience negative impacts  
540 on their reproductive success ultimately endangering the population as a whole (Giese, 1996;  
541 McClung et al., 2004; Ellenberg et al., 2006, 2007, 2012, 2013; Carroll et al., 2016). Knowledge  
542 of AD and FID may help inform policy makers when deciding appropriate viewing guidelines for  
543 tourists (Ellenberg et al., 2006, French et al., 2019).

544

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