



HAL
open science

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

Tracey L Hammer, Pierre Bize, Claire Saraux, Benoit Gineste, Jean-Patrice Robin, René Groscolas, Vincent A Viblanc

► To cite this version:

Tracey L Hammer, Pierre Bize, Claire Saraux, Benoit Gineste, Jean-Patrice Robin, et al.. Repeatability of alert and flight initiation distance in king penguins: effects of colony, approach speed and weather. *Ethology*, 2022, 128 (4), pp.303-316. 10.1111/eth.13264 . hal-03538580

HAL Id: hal-03538580

<https://hal.science/hal-03538580>

Submitted on 21 Jan 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Published in "Ethology"

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

Running title: Repeatability of flight initiation distance

Tracey L Hammer¹, Pierre Bize², Claire Sarau¹, Benoit Gineste^{1,3}, Jean-Patrice Robin¹, René
Groscolas¹ and Vincent A Viblanc¹

¹University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000
Strasbourg, France

²School of Biological Sciences, University of Aberdeen, AB24 2TZ, UK

³IPEV – Institut Polaire Français Paul Émile Victor, 29280 Plouzané, France

Author for correspondence:

Tracey L Hammer, tracey.hammer@iphc.cnrs.fr

19 Author contributions: Conception and design: RG, VAV; data acquisition: BG; data analysis:
20 TLH, CS, PB, VAV; writing: TLH. Revision: TLH, VAV, PB. All authors read and commented
21 on the final manuscript.

22 **ACKNOWLEDGEMENTS**

23 We thank Trish Fleming and an anonymous reviewer for their thorough and helpful
24 comments on a previous version of the manuscript. This work was supported by the French Polar
25 Institute (IPEV) through the IPEV 119 ECONERGY polar program, and by the French National
26 Center for Scientific Research (CNRS). TLH was supported by a PhD scholarship from the
27 Initiative d'excellence (IdEX), Investissements d'Avenir, Ministère de l'Enseignement Supérieur,
28 de la Recherche et de l'Innovation. We are grateful to the Terres Australes et Antarctiques
29 Françaises (TAAF) for providing logistic support in the field, and to the field personnel and field
30 assistants for providing help and support along the way.

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 cumbersomely 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 ± 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 ± 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., 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 (σ^2_a) over total phenotypic variance (equal to the sum of among-individual variance and within-
286 individual variance, σ^2_ϵ), 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 ± 0.18 m; (range = 1.89 – 13.14 m) (Fig. 1A and 1B). The interaction between approach x
303 colony and time of day² 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 ± 0.16 m (range = 0.68 – 8.58 m) (Fig. 1C and 1D).

330 Time of day² 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 day² 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

545 **REFERENCES**

- 546 Amat, J. A., Carrascal, L. M., & Moreno, J. (1996). Nest defence by chinstrap penguins
547 *Pygoscelis antarctica* in relation to offspring number and age. *Journal of Avian Biology*, 27(2),
548 177-179. doi:10.2307/3677150.
- 549 Arroyo, B., Mougeot, F., & Bretagnolle, V. (2017). Individual variation in behavioural
550 responsiveness to humans leads to differences in breeding success and long-term population
551 phenotypic changes. *Ecology Letters*, 20, 317–325. doi:10.1111/ele.12729.
- 552 Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., &
553 Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment
554 suggest rapid correlated evolutionary adaptation. *Behavioural Ecology*, 23, 960–969.
555 doi:10.1093/beheco/ars059.
- 556 Barbraud, C., Delord, K., Bost, C. A., Chaigne, A., Marteau, C., & Weimerskirch, H. (2020).
557 Population trends of penguins in the French Southern Territories. *Polar Biology*, 43, 835–850.
558 doi:10.1007/s00300-020-02691-6.
- 559 Bateman, P. W. & Fleming, P. A. (2011). Who are you looking at? Haded ibises use direction of
560 gaze, head orientation and approach speed in their risk assessment of a potential predator. *Journal*
561 *of Zoology*, 285, 316-323. doi:10.1111/j.1469-7998.2011.00846.x.
- 562 Bateman, P. W. & Fleming, P. A. (2017). Are negative effects of ecotourism over-reported? A
563 review of assessment methods and empirical results. *Biological Conservation*, 211, 10-19. doi:
564 10.1016/j.biocon.2017.05.003.
- 565 Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects
566 models using lme4. *Journal of Statistical Software*, 67, 1–48. doi:10.18637/jss.v067.i01.

567 Beale, C. M., & Monaghan, P. (2004a). Human disturbance: People as predation-free predators?
568 *Journal of Applied Ecology*, 41, 335–343. doi:10.1111/j.0021-8901.2004.00900.x.

569 Beale, C. M., & Monaghan, P. (2004b). Behavioural responses to human disturbance: A matter of
570 choice? *Animal Behaviour*, 68, 1065–1069. doi:10.1016/j.anbehav.2004.07.002.

571 Beauchamp, G. (2015). Vigilance, alarm calling, pursuit deterrence, and predator inspection. In
572 W. E. Cooper Jr. & D. T. Blumstein (Eds.), *Escaping from predators: an integrative view of*
573 *escape decisions* (pp. 265-286). Cambridge, U.K: Cambridge University Press.

574 Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-
575 analysis. *Animal behaviour*, 77(4), 771-783. doi:10.1016/j.anbehav.2008.12.022

576 Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting
577 distance. *Journal of Wildlife Management*, 67, 852–857. doi:10.2307/3802692.

578 Blumstein, D. T., Anthony, L. L., Harcourt, R., & Ross, G. (2003). Testing a key assumption of
579 wildlife buffer zones: Is flight initiation distance a species-specific trait? *Biological*
580 *Conservation*, 110, 97–100. doi:10.1016/S0006-3207(02)00180-5.

581 Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and
582 natural history traits affect disturbance tolerance in birds. *Animal Behavior*, 71, 389–399.
583 doi:10.1016/j.anbehav.2005.05.010.

584 Blumstein, D. T. (2010). Flush early and avoid the rush: A general rule of antipredator behavior?
585 *Behavioral Ecology*, 21, 440–442. doi:10.1093/beheco/arq030.

586 Blumstein, D. T. (2019). What chasing birds can teach us about predation risk effects: past
587 insights and future directions. *Journal of Ornithology*, 160, 587-592. doi:10.1007/s10336-019-
588 01634-1.

589 Boujja-Miljour, H., Leighton, P. A., & Beauchamp, G. (2018). Individual vigilance profiles in
590 flocks of House Sparrows (*Passer domesticus*). *Canadian Journal of Zoology*, 96, 1016-1023.
591 doi:10.1139/ciz-2017-0301.

592 Burger, J., & Gochfeld, M. (1981). Discrimination of the threat of direct versus tangential
593 approach to the nest by incubating herring and great black-backed gulls. *Journal of Comparative*
594 *and Physiological Psychology*, 95, 676–684. doi:10.1037/h0077811.

595 Burger, J., & Gochfeld M. (1990). Risk discrimination of direct versus tangential approach by
596 basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. *Journal of*
597 *Comparative and Physiological Psychology*, 104, 388–394. doi:10.1037/0735-7036.104.4.388.

598 Burger, J., & Gochfeld, M. (1991). Human distance and birds: tolerance and response distances of
599 resident and migrant species in India. *Environmental Conservation*, 18, 158-165.
600 doi:10.1017/S0376892900021743.

601 Burger, J., & Gochfeld, M. (1994). Vigilance in African mammals: differences among mothers,
602 other females, and males. *Behaviour*, 131, 153–169. doi:10.1163/156853994X00415.

603 Burger, J. & Gochfeld, M. (2007). Responses of Emperor Penguins (*Aptenodytes forsteri*) to
604 encounters with ecotourists while commuting to and from their breeding colony. *Polar Biology*,
605 30, 1303-1313. doi:10.1007/s00300-007-0291-1.

606 Carrete, M., & Tella, J. L. (2010). Individual consistency in flight initiation distances in
607 burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters*, 6,
608 167-170. doi:10.1098/rsbl.2009.0739.

609 Carrete, M., & Tella J, L. (2011). Inter-individual variability in fear of humans and relative brain
610 size of the species are related to contemporary urban invasion in birds. *PLoS One*, 6, e18859.
611 doi:10.1371/journal.pone.0018859.

612 Carrete, M., & Tella, J. L. (2017). Behavioral correlations associated with fear of humans differ
613 between rural and urban burrowing owls. *Frontiers in Ecology and Evolution*, 5, 54.
614 doi:10.3389/fevo.2017.00054.

615 Carroll, G., Turner, E., Dann, P., & Harcourt, R. (2016). Prior exposure to capture heightens the
616 corticosterone and behavioural responses of little penguins (*Eudyptula minor*) to acute stress.
617 *Conservation Physiology*, 4, cov061. doi:10.1093/conphys/cov061.

618 Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and
619 sampling bias in wild lizards. *Animal Behavior*, 83, 1051–1058.
620 doi:10.1016/j.anbehav.2012.01.033.

621 Carter, A. J., Pays, O., & Goldizen, A. W. (2009). Individual variation in the relationship between
622 vigilance and group size in eastern grey kangaroos. *Behavioral Ecology and Sociobiology*, 64,
623 237–245. doi:10.1007/s00265-009-0840-4.

624 Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise
625 affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters*, 6, 458–461.
626 doi:10.1098/rsbl.2009.1081.

627 Cherry, M. J., & Barton, B. T. (2017). Effects of wind on predator-prey interactions. *Food Webs*.
628 13, 92–97. doi:10.1016/j.fooweb.2017.02.005.

629 Clucas, B., & Marzluff, J. M. (2011). Attitudes and actions toward birds in urban areas: Human
630 cultural differences influence bird behavior. *The Auk*, 129(1), 1-9. doi:10.1525/auk.2011.11121.

631 Collop, C., Stillman, R. A., Garbutt, A., Yates, M. G., Rispin, E., & Yates, T. (2016). Variability
632 in the area, energy and time costs of wintering waders responding to disturbance. *IBIS*, 158(4),
633 711-725. doi:10.1111/ibi.12399.

634 Cooper, W. E. (2003). Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus*
635 *dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a
636 predator, and temperature. *Canadian Journal of Zoology*, 81, 979–984. doi:10.1139/z03-079.

637 Cooper, W. E., & Whiting MJ. (2007). Universal optimization of flight initiation distance and
638 habitat-driven variation in escape tactics in a Namibian lizard assemblage, *Ethology*. 113, 661–
639 672. doi:10.1111/j.1439-0310.2007.01363.x.

640 Côté, S. D. (2000). Aggressiveness in king penguins in relation to reproductive status and
641 territory location. *Animal Behavior*, 59, 813–821. doi:10.1006/anbe.1999.1384.

642 Couchoux, C., & Cresswell, W. (2012). Personality constraints versus flexible antipredation
643 behaviors: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging
644 in a natural system? *Behavioral Ecology*, 23, 290–301. doi:10.1093/beheco/arr185.

645 Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R package for fitting distributions.
646 *Journal of Statistical Software*, 64, 1–34. doi:10.18637/jss.v064.i04.

647 Descamps, S., Gauthier-Clerc, M., Le Bohec, C., Gendner, J. P., & Le Maho, Y. (2005). Impact
648 of predation on king penguin *Aptenodytes patagonicus* in Crozet Archipelago. *Polar Biology*, 28,
649 303–310. doi:10.1007/s00300-004-0684-3.

650 Díaz, J. A., & Asensio, B. (1991). Effects of group size and distance to protective cover on the
651 vigilance behaviour of black-billed magpies *Pica pica*. *Bird Study*. 38, 38–41.
652 doi:10.1080/00063659109477064.

653 Dill, L. M. (1974). The escape response of the zebra danio (*Brachydanio rerio*) II. The effect of
654 experience. *Animal Behavior*, 22, 723–730. doi:10.1016/S0003-3472(74)80023-0.

655 Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms:
656 animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81-89.
657 doi:10.1016/j.tree.2009.07.013

658 Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour:
659 mixed-effect modelling approaches. *Journal of Animal Ecology*, 82, 39–54. doi:10.1111/1365-
660 2656.12013.

661 Dingemanse, N. J., & Wright, J. (2020). Criteria for acceptable studies of animal personality and
662 behavioural syndromes. *Ethology*, 126(9), 865-869. doi:10.1111/eth.13082.

663 Dowling, L., & Bonier, F. (2018). Should I stay, or should I go: modeling optimal flight initiation
664 distance in nesting birds. *PLoS One*, 13, e0208210. doi:10.1371/journal.pone.0208210.

665 Dumont, F., Pasquaretta, C., Réale, D., Bogliani, G., & von Hardenberg, A. (2012). Flight
666 initiation distance and starting distance: biological effect or mathematical artefact? *Ethology*, 118,
667 1051–1062. doi:10.1111/eth.12006.

668 Edwards, A. M., Best, E. C., Blomberg, S. P., & Goldizen, A. W. (2013). Individual traits
669 influence vigilance in wild female eastern grey kangaroos. *Australian Journal of Zoology*, 61,
670 332–341. doi:10.1071/ZO13025.

671 Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of
672 the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, 64, 13–33.
673 doi:10.1111/j.1469-185X.1989.tb00636.x.

674 Ellenberg, U., Mattern, T., Seddon, P. J. & Jorquera, G. L. (2006). Physiological and reproductive
675 consequences of human disturbance in Humboldt penguins: the need for species-specific visitor
676 management. *Biological Conservation*, 133, 95-106. doi:10.1016/j.biocon.2006.05.019.

677 Ellenberg, U., Setiawan, A. N., Cree, A., Houston, D. M., & Seddon, P. J. (2007). Elevated
678 hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to
679 unregulated tourism. *General and Comparative Endocrinology*, 152, 54–63.
680 doi:10.1016/j.ygcen.2007.02.022.

681 Ellenberg, U., Mattern, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins
682 depends on sex, character and previous experience with humans. *Animal Behavior*, 77, 289–296.
683 doi:10.1016/j.anbehav.2008.09.021.

684 Ellenberg, U., Mattern, T., Houston, D. M., Davis, L. S. & Seddon, P. J. (2012). Previous
685 experiences with humans affect responses of Snares Penguins to experimental disturbance.
686 *Journal of Ornithology*, 153, 621-631. doi:10.1007/s10336-011-0780-4.

687 Ellenberg, U., Mattern, T., & Seddon, P. J. (2013). Heart rate responses provide an objective
688 evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology*. 1: cot013.
689 doi:10.1093/conphys/cot013.

690 Ferguson, S. M., Gilson, L. N. & Bateman, P. W. (2019). Look at the time: diel variation in the
691 flight initiation distance of a nectarivorous bird. *Behavioral Ecology and Sociobiology*, 73, 147.
692 doi:10.1007/s00265-019-2757-x.

693 Fernández-Juricic, E., & Schroeder, N. (2003). Do variations in scanning behavior affect
694 tolerance to human disturbance? *Applied Animal Behavior Science*, 84, 219–234.
695 doi:10.1016/j.applanim.2003.08.004.

696 Fernández-Juricic, E., Venier, M. P., Renison, D., & Blumstein, D. T. (2005). Sensitivity of
697 wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum
698 approaching distances and buffer areas for grassland birds. *Biological Conservation*, 125, 225–
699 235. doi:10.1016/j.biocon.2005.03.020.

700 Fleming, P. A. & Bateman, P. W. (2017). Scavenging opportunities modulate escape responses
701 over a small geographic scale. *Ethology*, 123, 205-212. doi:10.1111/eth.12587

702 Fowler, G. S. (1999). Behavioral and hormonal-responses of Magellanic penguins (*Spheniscus*
703 *magellanicus*) to tourism and nest site visitation. *Biological Conservation*, 90, 143–149.
704 doi:10.1016/S0006-3207(99)00026-9.

705 French, R. K., Muller, C. G., Chilvers, B. L., and Battley, P. F. (2019). Behavioural consequences
706 of human disturbance on subantarctic Yellow-eyed penguins *Megadyptes antipodes*. *Bird*
707 *Conservation International*, 29, 277-290. doi:10.1017/S0959270918000096.

708 Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk.
709 *Conservation Ecology*, 6, 11. doi:10.1016/S0723-2020(86)80016-9.

710 Gauthier-Clerc, M., Le Maho, Y., Gendner, J. P., Durant, J., & Handrich, Y. (2001). State-
711 dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during
712 courtship and incubation. *Animal Behaviour*, 62(4), 661-669. doi:10.1006/anbe.2001.1803.

713 Giese, M. (1996). Effects of human activity on Adelie penguin *Pygoscelis adeliae* breeding
714 success. *Biological Conservation*, 75, 157-164. doi:10.1016/0006-3207(95)00060-7.

715 Geist, C., Liao, J., Libby, S., & Blumstein, D. T. (2005). Does intruder group size and orientation
716 affect flight initiation distance in birds. *Animal Biodiversity and Conservation*, 28, 69–73.

717 Groscolas, R., Decrock, F., Thil, M. A., Fayolle, C., Boissery, C., & Robin, J. P. (2000).
718 Refeeding signal in fasting-incubating king penguins: changes in behavior and egg temperature.
719 *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 279(6),
720 R2104-R2112. doi:10.1152/ajpregu.2000.279.6.R2104.

721 Groscolas, R., & Robin, J. P. (2001). Long-term fasting and re-feeding in penguins. *Comparative*
722 *Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 128(3), 643-653.
723 doi:10.1016/S1095-6433(00)00341-X

724 Hess, S., Fischer, S., & Taborsky B. (2016). Territorial aggression reduces vigilance but increases
725 aggression towards predators in a cooperatively breeding fish. *Animal Behavior*, 113, 229–235.
726 doi:10.1016/j.anbehav.2016.01.008.

727 Highcock, L., & Carter, A. J. (2014). Intraindividual variability of boldness is repeatable across
728 contexts in a wild lizard. *PLoS One*, 9, e95179. doi:10.1371/journal.pone.0095179.

729 Holmes, N., Giese, M., & Kriwoken, L. K. (2005). Testing the minimum approach distance
730 guidelines for incubating royal penguins *Eudyptes schlegeli*. *Biological Conservation*, 126(3),
731 339-350. doi:10.1016/j.biocon.2005.06.009.

732 Holmes, N. D., Giese, M., Achurch, H., Robinson, S., & Kriwoken, L. K. (2006). Behaviour and
733 breeding success of gentoo penguins *Pygoscelis papua* in areas of low and high human activity.
734 *Polar Biology*, 29, 399–412. doi:10.1007/s00300-005-0070-9.

735 Hunter, S. (1991). The impact of avian predator scavengers on king penguin *Aptenodytes*
736 *patagonicus* chicks at Marion Island. *Ibis*, 133, 343–350. doi:10.1111/j.1474-
737 919X.1991.tb04581.x.

738 Kalb, N., Anger, F., & Randler, C. (2019). Flight initiation distance and escape behavior in the
739 black redstart (*Phoenicurus ochruros*). *Ethology*, 125, 430-438. doi:10.1111/eth.12867.

740 Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in
741 Linear Mixed Effects Models. *Journal of Statistical Software*, 82, 1–26.
742 doi:10.18637/jss.v082.i13.

743 Lafferty, K. D. (2001). Disturbance to wintering western snowy plovers. *Biological*
744 *Conservation*, 101, 315–325. doi:10.1016/S0006-3207(01)00075-1.

745 Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis.
746 *Journal of Statistical Software*, 25, 1–18. doi:10.18637/jss.v025.i01.

747 Le Bohec, C., Gauthier-Clerc, M., Gendner, J. P., Chatelain, N., & Le Maho, Y. (2003).
748 Nocturnal predation of king penguins by giant petrels on the Crozet Islands. *Polar Biology*, 26,
749 587–590. doi:10.1007/s00300-003-0523-y.

750 Lee, W. Y., Jung, J. W., Choi, H. G., Chung, H., Han, Y. D., Cho, S. R., & Kim, J. H. (2017).
751 Behavioral responses of chinstrap and gentoo penguins to a stuffed skua and human nest
752 intruders. *Polar Biology*, 40(3), 615-624. doi:10.1007/s00300-016-1984-0.

753 McClung, M. R., Seddon, P. J., Massaro, M. & Setiawan, A. (2004). Nature-based tourism
754 impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect
755 fledging weight and juvenile survival? *Biological Conservation*, 119, 279-285.
756 doi:10.1016/j.biocon.2003.11.012.

757 McGowan, M. M., Patel, P. D., Stroh, J. D., & Blumstein, D. T. (2014). The effect of human
758 presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology*,
759 120(11), 1081-1089. doi:10.1111/eth.12281.

760 Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life.
761 *Behavioral Ecology and Sociobiology*, 63, 63–75. doi:10.1007/s00265-008-0636-y.

762 Møller, A. P., Nielsen, J. T., & Garamzegi, L. Z. (2008). Risk taking by singing males.
763 *Behavioral Ecology*, 19, 41–53. doi:10.1093/beheco/arm098.

764 Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent
765 birds. *The Quarterly Review of Biology*, 63, 167–187.

766 Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A
767 practical guide for biologists. *Biological Reviews*, 85, 935–956. doi:10.1111/j.1469-
768 185X.2010.00141.x.

769 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from
770 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
771 doi:10.1111/j.2041-210x.2012.00261.x.

772 Nordell, C. J., Wellicome, T. I., & Bayne, E. M. (2017). Flight initiation by Ferruginous Hawks
773 depends on disturbance type, experience, and the anthropogenic landscape. *PLoS ONE*, 12(5),
774 e0177584. doi:10.1371/journal.pone.0177584.

775 Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013).
776 Development of boldness and docility in yellow-bellied marmots. *Animal Behavior*, 86, 1147–
777 1154. doi:10.1016/j.anbehav.2013.09.016

778 Petrelli, A. R., Levenhagen, M. J., Wardle, R., Barber, J. R., & Francis, C. D. (2017). First to
779 flush: The effects of ambient noise on songbird flight initiation distances and implications for
780 human experiences with nature. *Frontiers in Ecology and Evolution*, 5, 67.
781 doi:10.3389/fevo.2017.00067.

782 Pichegru, L., Edwards, T. B., Dilley, B. J., Flower, T.P., & Ryan, P.G. (2016). African Penguin
783 tolerance to humans depends on historical exposure at colony level. *Bird Conservation*
784 *International*, 26, 307–322. doi:10.1017/S0959270915000313.

785 Piratelli, A. J., Favoretto, G. R., & de Almeida Maximiano, M. F. (2015). Factors affecting
786 escape distance in birds. *Zoologia*, 32, 438–444. doi:10.1590/S1984-46702015000600002.

787 Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating
788 animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318.
789 doi:10.1111/j.1469-185X.2007.00010.x.

790 Reynolds, C., Henry, D. A. W., Tye, D. R. C., & Tye, N. D. (2020). Defining separation zones for
791 coastal birds at a wetland of global importance. *Wildlife Research*, 48(2), 134-141.
792 doi:10.1071/WR20098.

793 R Development Core Team. (2020). R: A language and environment for statistical computing. R
794 Foundation for Statistical Computing, Vienna, Austria.

795 Roche, E. A., & Brown, C. R. (2013). Among-individual variation in vigilance at the nest in
796 colonial Cliff Swallows. *Wilson Journal of Ornithology*, 125, 685–695. doi:10.1676/12-196.1.

797 Rodgers, J. A., & Schwikert, S. T. (2002). Buffer-Zone Distances to Protect Foraging and
798 Loafing Waterbirds from Disturbance by Personal Watercraft and Outboard-Powered Boats.
799 *Conservation Biology*, 16, 216–224. doi:10.1046/j.1523-1739.2002.00316.x.

800 Samia, D. S. M., Blumstein, D. T., Stankowich, T., & Cooper, W. E. (2016). Fifty years of
801 chasing lizards: new insights advance optimal escape theory. *Biological Reviews*, 91(2), 349-366.
802 doi:10.1111/brv.12173.

803 Santoyo-Brito, E., Núñez, H., Cooper, W. E., & Fox, S. F. (2020). Comparison of escape
804 behavior between solitary and grouped *Liolaemus leopardinus* lizards from the central Chilean
805 Andes. *Herpetologica*, 76(3), 285-289. doi:10.1655/Herpetologica-D-19-00057.1.

806 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
807 *Methods in Ecology and Evolution*, 1, 103–113. doi:10.1111/j.2041-210x.2010.00012.x.

808 Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., & Hollmén, T. (2012).
809 Stress responsiveness, age and body condition interactively affect flight initiation distance in
810 breeding female eiders. *Animal Behaviour*, 84, 889-896. doi:10.1016/j.anbehav.2012.07.012.

811 Smith- Castro, J. R. & Rodewald, A. D. (2010). Behavioral responses of nesting birds to human
812 disturbance along recreational trails. *Journal of Field Ornithology*, 81(2), 130-138.
813 doi:10.1111/j.1557-9263.2010.00270.x.

814 Sreekar, R., & Quader, S. (2013). Influence of gaze and directness of approach on the escape
815 responses of the Indian rock lizard, *Psammophilus dorsalis* (Gray, 1831). *Journal of Biosciences*,
816 38, 829–833. <https://doi.org/10.1007/s12038-013-9378-8>.

817 Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk
818 assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2627–2634.
819 doi:10.1098/rspb.2005.3251.

820 Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance
821 decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8,
822 1639-1644. doi:10.1111/2041-210X.12797

823 Stonehouse, B. (1960). The king penguin *Aptenodytes patagonica* of South Georgia. *Scientific*
824 *Reports Falkland Islands Dependencies Survey*, 23, 1–96.

825 Tarlow, E. M., & Blumstein, D. T. (2007). Evaluating methods to quantify anthropogenic
826 stressors on wild animals. *Applied Animal Behaviour Science*, 102, 429–451.
827 doi:10.1016/j.applanim.2006.05.040.

828 Tätte, K., Møller, A. P., & Mänd, R. (2018). Towards an integrated view of escape decisions in
829 birds: relation between flight initiation distance and distance fled. *Animal Behaviour*, 136, 75-86.
830 doi:10.1016/j.anbehav.2017.12.008.

831 Tätte, K., Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator
832 function of vigilance re-examined: vigilant birds delay escape. *Animal Behavior*, 156, 97–110.
833 doi:10.1016/j.anbehav.2019.08.010.

834 Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one's nest? A case study in
835 African penguin. *Ethology*, 124(1), 74-83. doi:10.1111/eth.12704.

836 Uchida, K., Suzuki, K. K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2019). Decreased
837 vigilance or habituation to humans? Mechanisms on increased boldness in urban animals.
838 *Behavioral Ecology*, 30, 1583–1590. doi:10.1093/beheco/arz117.

839 van Dongen, W. F. D., Robinson, R. W., Weston, M. A., Mulder, R. A., & Guay, P. J. (2015).
840 Variation at the DRD4 locus is associated with wariness and local site selection in urban black
841 swans. *BMC Evolutionary Biology*, 15, 253. doi:10.1186/s12862-015-0533-8.

842 van Heezik, Y., & Seddon, P. J. (1990). Effect of human disturbance on beach groups of jackass
843 penguins. *South African Journal of Wildlife Research*, 20, 89–93.

844 Viblanc, V. A., Smith, A. D., Gineste, B., & Groscolas, R. (2012). Coping with continuous
845 human disturbance in the wild: Insights from penguin heart rate response to various stressors.
846 *BMC Ecology*, 12, 1–11. doi:10.1186/1472-6785-12-10.

847 Villanueva, C., Walker, B. G., & Bertellotti, M. (2012). A matter of history: Effects of tourism on
848 physiology, behaviour and breeding parameters in Magellanic Penguins (*Spheniscus*
849 *magellanicus*) at two colonies in Argentina. *Journal of Ornithology*, 153, 219–228.
850 doi:10.1007/s10336-011-0730-1.9

851 Villanueva, C., Walker, B. G., and Bertellotti, M. (2014). Seasonal variation in the physiological
852 and behavioural responses to tourist visitation in Magellanic penguins. *The Journal of Wildlife*
853 *Management*, 78(8), 1466-1476. doi:10.1002/jwmg.791

854 Viñuela, J., Amat, J. A., & Ferrer, M. (1995). Nest defence of nesting chinstrap penguins
855 (*Pygoscelis antarctica*) against intruders. *Ethology*, 99(4), 323-331. doi:10.1111/j.1439-
856 0310.1995.tb00906.x.

857 Walker, B. G., Dee Boersma, P., & Wingfield, J. C. (2005). Physiological and behavioral
858 differences in Magellanic Penguin chicks in undisturbed and tourist-visited locations of a colony.
859 *Conservation Biology*, 19, 1571–1577. doi:10.1111/j.1523-1739.2005.00104.x.

860 Walker, B. G., Dee Boersma, P., & Wingfield, J. C. (2006). Habituation of adult Magellanic
861 Penguins to human visitation as expressed through behavior and corticosterone secretion.
862 *Conservation Biology*, 20, 146–154. doi:10.1111/j.1523-1739.2005.00271.x.

863 Webster, M.M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, 582, 337–
864 340. doi:10.1038/d41586-020-01751-5.

865 Weimerskirch, H., Stahl, J. C., & Jouventin, P. (1992). The breeding biology and population
866 dynamics of King Penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis*. 134, 107–117.
867 doi:10.1111/j.1474-919X.1992.tb08387.x.

868 Wheeler, M., De Villiers, M. S., & Majiedt, P. A. (2009). The effect of frequency and nature of
869 pedestrian approaches on the behaviour of wandering albatrosses at sub-Antarctic Marion Island.
870 *Polar Biology*, 32, 197–205. doi:10.1007/s00300-008-0520-2.

871 Williams, T. D. (1995). The penguins. Perrins, C. M., Bock, W. J., & Kikkawa, J. (Eds.), Oxford
872 University Press, New York. pp 295.

873 Wilson, A. J. (2018). How should we interpret estimates of individual repeatability? *Evolution*
874 *Letters*, 2-1, 4-8. doi:10.1002/evl3.40.

875 Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating repeatability.
876 *Methods in Ecology and Evolution*, 3, 129-137. doi:10.1111/j.2041-210X.2011.00125.x.

877 Wolf, I. D., & Croft, D. B. (2010). Minimizing disturbance to wildlife by tourists approaching on
878 foot or in a car: A study of kangaroos in the Australian rangelands. *Applied Animal Behaviour*
879 *Science*, 126(1-2), 75-84. doi:10.1016/j.applanim.2010.06.001.

880 Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. *Advances in*
881 *the Study of Behavior*, 16, 229–249. doi:10.1016/S0065-3454(08)60192-8.

882 Young, J. K., Mahe, M., & Breck, S. (2015). Evaluating behavioral syndromes in coyotes (*Canis*
883 *latrans*). *Journal of Ethology*, 33, 137–144. doi:10.1007/s10164-015-0422-z.

884 Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid
885 common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. doi:10.1111/j.2041-
886 210x.2009.00001.x.

887