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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29   **CONFLICT OF INTEREST STATEMENT**

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

31

32   **ABSTRACT**

33   Alert Distance (AD) and Flight Initiation Distance (FID) are popular measures used to

34   explore the reaction of prey to approaching predators, and thus the economics that underlie optimal

35   escape strategies. AD likely mirrors the effort invested into vigilance, while FID provides an

36   estimate of the perceived risk of an approaching threat. Although individual variation in AD and

37   FID is influenced by environmental factors such as variation in predation pressure and human

38   disturbance, the repeatabilities of these traits (especially AD), and therefore their designation as a

39   personality trait, remain under investigated. Here, we studied the repeatability of AD, FID, and the

40   decision to flee in a flightless, ground-breeding seabird, the king penguin (*Aptenodytes*

41   *patagonicus*). A single experimenter approached three times over three consecutive days 47

42   incubating king penguins from two different colonies with varying human disturbance levels. We

43   explored the effects of weather, time of day, and approach speed of the experimenter on these

44 behaviors. Weather had an effect on all three behaviors. In warm, sunny weather AD increased,

45 while in rainy, windy weather birds were more likely to flee yet waited longer before initiating

46 flight. Faster approach speeds between AD and FID increased FID. Weather conditions and speed

47 of approach affected repeatability estimates, highlighting the need to consider external sources of

48 variation when refining such estimates. FID and the decision to flee were significantly and

49 moderately repeatable ($r = 0.26$ and 0.57 respectively), while AD was not. There was no evidence

50 of habituation or sensitization due to colony.

53

INTRODUCTION

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

In practice, the decisions that prey undertake when approached by a predator (AD and FID) can be simulated by performing non-lethal approaches by human experimenters (Frid and Dill, 2002; Beale and Monaghan, 2004a). Animals are expected to respond in much the same way to human approach stimuli as they would to actual predators since (1) both divert time and energy that could be otherwise invested in fitness enhancing activities; and (2) animals should be selected to overestimate rather than underestimate risk due to the cost of miscalculation, *i.e.*, injury or death (Frid and Dill, 2002). While AD can be hard to observe in some species or contexts, FID has the advantage of being easily measured and quantified (Tarlow and Blumstein, 2007). Both can be standardized within and across studies (Blumstein, 2006; Møller et al., 2008), and are species-specific (Blumstein et al., 2003; Møller, 2008; Carette and Tella, 2011; Piratelli et al., 2015). As a consequence, FID in particular and AD when available, have become popular measures in conservation biology used in establishing set-back distances and buffer zones to minimize stress-related disturbances on wildlife (Rodgers and Schwikert, 2002; Fernández-Juricic et al., 2005).

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

AD and FID should be strongly selected in prey species, in a way that balances the survival benefits of escaping approaching predators with the costs of abandonning other fitness-enhancing activities such as reproduction (Ydenberg and Dill, 1986). Consequently FID is known to vary with the perceived risk of predator approaches (Frid and Dill, 2002; reviewed in Stankowich and

102 Blumstein, 2005) including the size or number of predators (Beale and Monaghan, 2004a; Geist et

103 al., 2005), directness of approach (Smith-Castro and Rodewald, 2010; Sreekar and Quader, 2013;

104 but see Fernández-Juricic et al., 2005), speed of approach (Bateman and Fleming, 2011; Samia et

105 al., 2016; but see Lafferty, 2001), and predator intent (*i.e.*, predator suddenly turning towards the

106 prey or maintaining a purposeful gaze; Cooper, 2003; Bateman and Fleming, 2011; Sreekar and

107 Quader, 2013). FID has also been shown to vary with the time of day (Patelle et al., 2013; Piratelli

108 et al., 2015, Ferguson et al., 2019), can be reduced when prey have low energy reserves (Beale and

109 Monaghan, 2004b; Piratelli et al., 2015), are in a large group (dilution effect; Ydenberg and Dill,

110 1986; Burger and Gochfeld, 1991, Santoyo-Brito et al., 2020), or are in close proximity to refuge

111 (Cooper and Whiting, 2007). AD has not been explored to the same extent as FID, but evidence

112 suggests that vigilance behaviour is also modified by time of day (Edwards et al., 2013), weather

113 conditions (Couchoux and Cresswell, 2012), conspecific interactions (Hess et al., 2016), sex and

114 reproductive status (Burger and Gochfeld, 1994), and group size (Díaz and Asensio, 1991; Carter

115 et al., 2009; Boujja-Miljour et al., 2018).

116   The cost-benefit fitness trade-off of fleeing a tentative predator should be particularly

117 strong for ground-laying birds tied to vulnerable nesting sites, such as penguins. Penguins commit

118 a high amount of time and energy to reproduction (obligate bi-parental care, long-term fasting,

119 prolonged breeding cycle and chick development; Williams, 1995), and face a strong fitness trade-

120 off between the survival costs of defending their brood against predators (*i.e.,* injuries and potential

121 death for the adult) and the reproductive costs of abandoning their current reproduction but

122 surviving to breed another year (Montgomerie and Weatherhead, 1988; Frid and Dill, 2002;

123 Dowling and Bonier, 2018). Accordingly, penguins are usually highly territorial and defensive of

124 their brood (Viñuela et al., 1995; Amat et al., 1996; Côté, 2000), though within species there is

125 clear variation on the degree of territoriality and aggression depending on brood value (Amat et al.,

126   1996; Côté, 2000), the type of threat considered (Lee et al., 2017), and bird personality (Traisnel &

127   Pichegru, 2018). Surprisingly, few studies have investigated how variable AD and FID to

128   approaching predators are in penguins, nor the factors affecting those traits, despite their

129   importance in shaping breeding decisions, and despite the fact that several studies have documented

130   marked effects of disturbance (e.g. ecotourism) on penguin behavior (vigilance and locomotory

131   behavior, time budgets; Holmes et al., 2005, 2006; Burger and Gochfeld, 2007), physiological

132   stress (Ellenberg et al., 2006, 2012, 2013; Viblanc et al., 2012; Carroll et al., 2016), or reproduction

133   (Giese, 1996; McClung et al., 2004; Ellenberg et al., 2006; reviewed in Bateman and Fleming,

134   2017).

135   Here, we investigated the variability of both AD and FID in breeding king penguins

136   (*Aptenodytes patagonicus*). King penguins are large, ground-laying, flightless birds that form

137   extensive colonies on the subantarctic shorelines. Breeding pairs incubate their single egg or young

138   chick on top of their feet (Stonehouse, 1960), therefore limiting their mobility. They are subject to

139   on-land predation mostly by giant petrels, *Macronectes halli* and *Macronectes giganteus*, and

140   brown skuas, *Catharacta lonnbergi* (Hunter, 1991; Descamps et al., 2005). Giant petrels and skuas

141   especially target eggs and chicks, but petrels are also known to prey on injured adults (Hunter,

142   1991). These predators will harass incubating and brooding adults sometimes causing them to flee

143   and abandon their eggs. Breeding adults have three choices: first to stay and fight, risking

144   potentially fatal injuries; second to flee slowly cumbersomely with the egg on top of their feet

145   clustering closer to neighbouring breeders; or finally, to flee entirely, guaranteeing survival but

146   abandoning their current reproduction.

147   We calculated individual repeatabilities for AD and FID which were measured several

148   times on incubating adults, and assessed the potential influences of approach speed, weather

149   conditions, and time of day on AD and FID as these may impact the levels of vigilance and

150   responsiveness to a threat. Specifically, we expected AD and FID to vary in a quadratic function,

151   increasing at dawn and dusk, and coinciding with highest predation risk for chicks (giant petrel

152   activity is highest at early and late hours of the night; Le Bohec et al., 2003; Descamps et al., 2005).

153   We further tested whether individuals sensitized or habituated to repeated approaches by a human

154   experimenter by examining bird responses in two different colonies; one close to human settlements

155   and one relatively unexposed to human disturbance. King penguins have been shown to express

156   significantly lower heart rate stress responses to human approaches in disturbed areas vs.

157   undisturbed colony areas (Viblanc et al., 2012). Thus, we expected individuals measured in the

158   colony close to human settlements to show habituation to approaching experimenters (decreased

159   AD and FID compared to the undisturbed colony).

160

161   **METHODS**

162   **Study sites**

163   This study was conducted in mid-to-late January during the Austral summer of 2010-2011.

164   Birds were selected from two colonies of king penguins located on Possession Island in the Crozet

165   Archipelago, namely the colonies "La Baie du Marin" (BDM, 46°25'S – 51°52'E) and "Jardin

166   Japonais" (JJ, 46°21'S – 51°43'E). BDM is home to ca. 22 000 breeding pairs (Barbraud et al.,

167   2020) and is located on the east side of Possession Island in close proximity to a permanently

168   inhabited research station built in 1961. This colony has been exposed throughout the year for the

169   past 50 years to the daily presence of scientists and non-scientists in or close to the colony (Viblanc

170   et al., 2012). During this time, birds in BDM have been regularly exposed to humans including

171   tourist visits, censuses, population counts, and systematic monitoring. Meanwhile, JJ is home to ca.

172   39 000 breeding pairs (Barbraud et al., 2020) and is located on the north side of the island some 13

173   km from BDM. JJ is a relatively undisturbed colony, far from the research station and visited by

174   scientists only a few times every year for population count and census information.

175

176   **Approach protocol**

177   We repeatedly approached a total of 47 incubating birds in the two colonies (23 birds from

178   JJ and 24 birds in BDM). Each individual was approached once per day over three consecutive

179   days between the hours of 8:00 and 19:00 (from Jan. 11 - 13 in JJ, and from Jan. 30 - Feb. 1 in

180   BDM). It was not possible to find all birds on the subsequent days and so two birds in BDM were

181   only approached once, and one bird each in JJ and BDM were only approached twice. Following

182   egg-laying, king penguin partners alternate incubation duties, allowing their partner to forage at sea

183   while they fast on land (Stonehouse, 1960). The male takes the first incubation shift, and the egg

184   hatches some 53 days later, usually during shift four when the female has possession of the egg

185   (Weimerskirch et al., 1992).

186   Following the STRANGE guidelines (Webster & Rutz 2020), we provide hereafter details

187   on how incubating birds were selected and highlight potential biases related to the selection of our

188   study subjects. Birds were selected haphazardly while incubating their eggs, and therefore we had

189   no individual information on their sex, age, incubation shift, or previous experience with humans.

190   Chosen individuals visually appeared in good physical condition, based on their plumage (shiny)

191   and morphological (fat) appearance, and thus had not been fasting for extended periods of time.

192   Individuals were selected at distance, and not after being approached or captured. Therefore, we

193   expected no strong initial sampling bias in relation to how individuals were responding to human

194   approaches (but see discussion).

195   Selected individuals were marked from a distance (roughly 1 m) at the end of the first

196   approach using a dot of non-permanent pressurized spray animal dye (Porcimark®, Kruuse,

197   Lageskov; Denmark) on the belly for identification during subsequent approaches. All approaches

198   were performed by the same observer (BG) dressed in the same clothing. Individuals were only

199   approached if they were resting upon arrival of the observer (*i.e.*, not engaged in aggressive,

200   preening, or sleeping behaviours). The approach started after having observed the bird resting for

201   at least one full minute before approaching it. During this time, the experimenter hid out of line of

202   sight. Each approach had a set starting distance of 18 m, as measured with a laser telemeter (Leica

203   DISTO^{TM} D5 Lasermeter, Leica Geosystems AG, Hexagon, Sweden), which we standardized due

204   to the known influence of starting distance on FID (Blumstein, 2003, 2010; Dumont et al., 2012).

205   We chose a starting distance of 18 m based on preliminary observations of 59 king penguins,

206   including courting (paired) and incubating birds (a sample representative of the various life-history

207   stages in the colony, excluding moulting and chick-brooding birds), that showed the maximal

208   distance at which birds exhibited signs of vigilance towards an experimenter was 12.45 m and the

209   minimal distance was 3.03 m (mean $\pm$ SD = 6.85 $\pm$ 1.87 m). We used a starting distance 1.5 times

210   greater than the maximal detection distance recorded in the preliminary study to ensure starting

211   distance far exceeded maximum alert distance (see also Fleming and Bateman, 2017).

212   The approaching observer followed a direct trajectory toward the focal individual, in plain

213   line of sight, always starting from outside the colony. The experimenter walked until the first sign

214   of alert was detected (the bird tilting its head or stretching its neck in the direction of the

215   experimenter). At this distance, termed the Alert Distance (AD), the experimenter took a

216   standardized one-minute pause to record AD and time. The time from the start of the approach until

217   the bird became vigilant was recorded with a stopwatch and the remaining distance to the selected

218   bird measured with a laser telemeter (closest cm). The approach was then resumed until the bird

219   showed the first signs of fleeing (slowly walking away with its egg resting on its feet) – termed

220   Flight Initiation Distance, FID. Some birds never showed signs of flight while being approached,

221   right up until close (FID = 0 m) (see also Bateman and Fleming, 2011, for similar results in ibises).

222   FID had therefore a zero-inflated distribution (see supporting information S1), suggesting this

223   measure reflected two different processes: *i*) the decision to flee or not (0/1); and *ii*) the distance at

224   which flight (escape) should occur if birds decide to flee. Hereafter, we analysed these two

225   processes separately. We calculated the speed of approach (m/s) prior to the occurrence of AD and

226   FID as the distance walked (m) divided by the duration of approach (s). The mean speed ± SE of

227   approach prior to AD was 0.61 ± 0.09 m/s (range = $0.44 – 0.86$ m/sec) and the mean ± SE speed of

228   approach between AD and FID was 0.57 ± 0.10 m/s (range = $0.35 – 0.90$ m/s). Walking speed

229   varied slightly due to topography, entering the colony, and breeder density.

230   At the start of each approach, we recorded air temperature to the nearest $1°C$, and we scored

231   wind speed, solar levels, and rain on a scale from 0 to 2, with half levels (i.e., 0.5) being allowed.

232   A value of 0 indicated no wind or rain, or full cloud cover (no sun). A value of 2 indicated heavy

233   wind or rain or full sun. Mean temperature was $10 °C$ (range = $7 – 13 °C$). As air temperature, wind

234   speed, rain, and solar levels were naturally correlated, we used a Principal Components Analysis

235   (PCA) to summarize all weather variables (package "FactoMineR", Lê et al., 2008). This approach

236   had the advantage of capturing climatic variation on a continuous scale through two independent

237   and orthogonal axes, and avoided strong collinearity (VIFs >30) issues if 'raw' meteorological

238   variables are used in the analyses. We kept the first two principal component (PC1 and PC2) which

239   together explained over 84% of the variation in climate data. Increasing PC1 (64.86% of variation)

240   values were mainly associated with higher sun scores (correlation = +0.939) and higher temperature

241   (+0.918), and to a lesser extent higher wind scores (+0.639), and lower rain scores (-0.686). In

242   contrast, increasing PC2 (19.77% of variation) values were mainly associated with higher wind

243 scores (+0.702), higher rain scores (+0.543), but not with sun scores (-0.010) or temperature (-

244 0.061). Thus, increasing PC1 values described sunnier, warmer days while increasing PC2 values

245 described windier, rainier days. On average, the climate conditions varied during our three

246 approaches in both colonies (see supporting information S2), highlighting the need to control for

247 climatic variation in further analyses.

248

249 **Statistical analyses**

250   All statistical analyses were performed in R 3.6.1. (R Development Core Team, 2020).

251 Results are presented as means ± SE. We investigated the sources of variation in AD (gaussian

252 distribution), the decision to flee or not (FID: 0/1, binomial distribution), and the distance at which

253 flight was taken for birds that did decide to flee (FID > 0; gaussian distribution) using linear mixed

254 models (LMM) and generalized linear mixed models (GLMM) with the appropriate error

255 distribution. In all the models, we entered individual ID as a random factor to control for repeated

256 measures, and we included as fixed effects the time of day, weather (PC1 and PC2), approach

257 speed, approach order (three levels: first, second, or third approach), and the colony (two levels:

258 BDM vs JJ). To test whether birds differed in their behavior at different times of day, and whether

259 habituation or sensitisation to human approaches occurred differently between colonies, we also

260 included second order interaction *colony* x *approach order* and *time of day x time of day* (viz.,

261 time^2) in our starting models. Second order interactions were dropped from the final model if not

262 significant. Models were run using the *lmer* and *glmer* functions in the package "lme4" (Bates et

263 al., 2015). The significance of the fixed effects was tested with the *anova* function (type 3) from

264 the package "lmerTest" (Kuznetsova et al., 2017) using F tests with Satterthwaite estimation for

265 the denominator degree of freedom for models with a gaussian distribution. Pseudo-R^2 for the

266   models were calculated using methods developed in Nakagawa and Schielzeth (2013). Prior to

267   analysis, time of approach was converted to decimal time, and non-zero FIDs were log-transformed

268   (natural log) to normalize the distribution of the residuals. Independent variables were checked for

269   collinearity using Variance Inflation Factors (VIF) (Zuur et al., 2010). A few VIFs were above 3

270   (see results), but those were considered acceptable as they represented different categorical levels

271   of the same factor (*e.g.* approach order). All variables were scaled and centered prior to inclusion

272   in the models to compare effect sizes (Schielzeth, 2010). Where appropriate, we insured model

273   residuals were normally distributed by visual inspection of density distributions, Q-Q plots,

274   cumulative distribution functions, and P-P plots using the "fitdistrplus" package in R (Delignette-

275   Muller and Dutang, 2015).

276   Repeatabilities and their confidence intervals were calculated using the functions *rpt* for

277   AD, and FID and *rptBinary* for the decision to flee or not, from the "rptR" package in R (Stoffel et

278   al., 2017). Repeatability was calculated as the ratio of among-individual variance in AD or FID

279   (σ^2_α) over total phenotypic variance (equal to the sum of among-individual variance and within-

280   individual variance, σ^2_ε), so $r = \sigma^2_\alpha / \sigma^2_\alpha + \sigma^2_\varepsilon$ (Nakagawa and Schielzeth, 2010). We first calculated

281   agreement repeatability, also called uncorrected repeatability, *r*, which is simply based on the

282   among- and within-individual variance in AD or FID. Afterwards, significant effects from the

283   above models, which influenced the expression of AD and FID, were controlled for when

284   calculating adjusted repeatability r_{adj}, (also called corrected repeatability) (Wilson, 2018).

285

286   **Ethics statement**

287   No animal was caught or handled over the course of this study. The research was approved

288   by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor. Authorization to

289 enter the colony and approach birds was obtained from Terres Australes et Antarctiques Françaises.

290 The observations complied with the current laws of France. No eggs or chicks were abandoned

291 during the course of this study.

292

293 **RESULTS**

294 **Alert Distance (AD)**

295 On average, focal individuals became alert when the experimenter came to a distance of

296 6.94 ± 0.18 m; (range = $1.89 - 13.14$ m) (Fig. 1A and 1B). The interaction between approach x

297 colony and time of day^2 did not have a significant effect influencing AD ($F_{2,111.0}=0.22$, $P=0.802$

298 and $F_{1,90.9}=0.02$, $P=0.896$, respectively), were sequentially removed from the model in that order

299 (least significant term removed first). The final model with time of day, weather PC1, weather PC2,

300 speed of approach prior to AD, approach order and colony, as fixed effects explained 13%

301 (marginal R^2) of the total variation, and including individual as a random effect explained 22%

302 (conditional R^2) of the total variation in AD (LMM, n=133 observations, N=47 individuals, $1.63 <$

303 VIFs < 3.68, among-individual $\sigma^2 = 0.37$; residual $\sigma^2 = 3.63$). We found no evidence that AD was

304 significantly affected by the time of day ($F_{1,92.2}=2.00$, $P=0.160$), speed of approach ($F_{1,120.0}=1.25$,

305 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 approach order

306 ($F_{2,106.0}=2.14$, $P=0.123$) (Fig 2A). However, AD was significantly influenced by weather PC1

307 ($F_{1,102.1}=7.29$, $P=0.008$) with individuals showing lower AD during warm and sunny conditions

308 (Fig. 2B).

309 AD was not significantly repeatable when analysed on its own ($r=0.103$; $CI_{95}=[0, 0.290]$;

310 $P=0.146$), but repeatability was close to significant after adjusting for weather (PC1) as a fixed

311 effect ($r_{adj}=0.145$; $CI_{95}=[0, 0.313]$; $P=0.062$). Although some individuals appeared to be repeatable,

312   many others displayed large variability in their AD (Fig. 1A and 1B). Post-hoc power analyses (see

313   Online Supplementary Material OSM 3) revealed that significant repeatability (power 0.8) for AD

314   may be achieved for a sample size of 6 approaches on 47 birds – or 3 approaches on 140 birds.

315

316   **Flight Initiation**

317   Out of the 47 selected individuals, 41 (87.2%) decided to flee (i.e., move away with their

318   egg on their feet) during at least one of their approaches (20 birds in JJ, and 21 birds in BDM): 23

319   individuals always fled, 12 individuals fled twice in three approaches, 6 fled once in three

320   approaches, and 6 did not flee at all. This corresponded to 42 approaches out of a total of 135 (31%)

321   that resulted in no FID. The FID of the individuals that decided to flee at least once was 2.83 ± 0.16

322   m (range = 0.68 – 8.58 m) (Fig. 1C and 1D).

323   Time of day^2 and the interaction between approach x colony did not significantly influence

324   the odds of fleeing (1) or not (0) during the approach (GLMMs; binomial, χ^2=2.35, P=0.125 and

325   χ^2=4.97, P=0.083), and were sequentially removed from the model in that order (least significant

326   term removed first). The final model with time of day, speed of approach between AD and FID,

327   weather PC1 and weather PC2 explained 23% (marginal R^2) of the total variation, and including

328   individual as a random effect explained 73% (conditional R^2) of the total variation in the odds of

329   fleeing (GLMM, n=133 observations, N=47 individuals, 1.18 < VIFs < 5.36, among-individual σ^2

330   = 3.29; residual σ^2 = 6.11). The odds of fleeing were not significantly influenced by weather PC1

331   (χ^2=0.24, P=0.626), time of day (χ^2=1.19, P=0.275), speed of approach (χ^2=1.86, P=0.172),

332   approach order (χ^2=4.98, P=0.083) or colony (χ^2=3.09, P=0.079). (Fig. 3A). However, the

333   probability of birds to flee increased significantly with increasing weather PC2 (χ^2=4.51, P=0.034),

334   birds being more likely to flee from the approaching experimenter in windy and rainy conditions

335 (Fig. 3A and 3B). The decision to flee was significantly repeatable before (original-scale: r=0.504;

336 CI$_{95}$= [0.084, 1.724]; P<0.001) adjusting for weather, and increased slightly (r=0.573; CI$_{95}$= [0.110,

337 1.686]; P<0.001) after accounting for the significant effect of weather PC2.

338   For those birds that decided to flee, time of day^2 and the interaction between approach x

339 colony did not significantly influence FID during the approach (LMMs; $F_{1,66.5}$=0.15, P=0.704 and

340 $F_{2,67.8}$=0.48, P=0.619, respectively), and were sequentially removed from the model in that order

341 (least significant term removed first). The final model with time of day, speed of approach between

342 AD and FID, weather PC1 and weather PC2 explained 37% (marginal R^2) of the total variation,

343 and including individual as a random effect explained 62% (conditional R^2) of the total variation

344 in FID (LMM, n=91 observations, N=41 individuals, 1.19 < VIFs < 5.56, among-individual σ^2 =

345 0.13; residual σ^2 = 0.09). We found no evidence that FID was significantly affected by the time of

346 day ($F_{1,79.3}$=0.122, P=0.727), weather PC1 ($F_{1,67.5}$=2.16, p=0.146), colony ($F_{1,47.2}$=0.77, P =0.384),

347 or approach order ($F_{2,63.8}$=2.17, P=0.123) (Fig 4A). However, FID increased significantly with the

348 speed of the approach ($F_{1,71.8}$=31.64, P<0.001, Fig. 4A and 4B) and decreased significantly with

349 increasing weather PC2 ($F_{1,60.6}$=5.17, P=0.027, Fig. 4A and 4C). In other words, FID decreased in

350 windy and rainy conditions. Agreement FID repeatability was low and not significant (r=0.102;

351 CI$_{95}$ = [0.00, 0.339]; P=0.248), but increased significantly when approach speed and weather PC2

352 were adjusted for in the model (r_{adj}=0.258; CI$_{95}$=[0.010, 0.511]; P<0.022).

353

354 **DISCUSSION**

355   Our study showed that, in king penguins, both the decision to flee and FID were

356 significantly and moderately repeatable, whereas AD was not. Climatic conditions had marked

357 effects on AD, FID and the probability for birds to flee, affecting repeatability estimates, and

358 highlighting the need to consider external sources of variation in refining such estimates in the wild

359 (discussed below).

360

361 **Between- and within-individual variation in flight initiation**

362 Incubating king penguins showed significant (adjusted) repeatability both in the decision to flee

363 from an approaching observer (0.57), and in the distance at which they initiated flight (0.26). In

364 both cases, it is important to note that repeatability values increased when accounting for weather

365 effects on behavior, which is not surprising since birds experienced different local climate

366 conditions when they were approached. Notwithstanding, this underlines the importance of

367 considering heterogeneity in individual habitats and timing of measures when establishing

368 repeatability estimates from behavioral measures in the wild. Our repeatability values are

369 comparable, albeit slightly lower, to those reported on FID in other studies: black swans, *Cygnus*

370 *atratus* (r=0.61, van Dongen et al., 2015), juvenile yellow-bellied marmots, *Marmota flaviventris*

371 (r=0.40, Petelle et al., 2013), Namibian rock agama, *Agama planiceps* (r=0.71, Carter et al., 2012),

372 and burrowing owl, *Athene cunicularia* (r=0.88, Carrete and Tella, 2010), and generally moderate

373 as would be expected for behavioral traits (Bell et al., 2009). The repeatability of both the decision

374 to flee, and the distance at which flight was initiated, suggest that these behavioural traits could

375 constitute good candidates for personality traits in breeding king penguins. This remains to be

376 further explored however, since our power to detect behavioral plasticity in AD and FID occurring

377 over longer periods was limited by the fact that birds in our study were only measured over a short

378 period of time (3 consecutive days), and were not previously known individuals. Separating the

379 repeatable and plastic aspects of alert and flight behavior to approaching predators in king penguins

380 would benefit from further studies on individually monitored population where simple measures

such as AD and FID are incorporated into monitoring schemes allowing to test for repeatability and plasticity over the lifetime of individuals (Dingemanse et al., 2010; Dingemanse & Wright, 2020). Logistically, this would require permanent marking of individuals in order to follow them through a longer period of time and through different contexts. In addition, FID (and AD, see below) are likely to vary according to factors such as individual age, sex, stress responsiveness, or body condition (e.g. Seltman et al., 2012; Kalb et al., 2019). Testing for such factors in future studies should allow refining repeatability estimates, with repeatability increasing as more residual variation is accounted.

Repeatability estimates of individual propensity to flee and FID increased as extrinsic factors were accounted for in the models. This is not surprising, but highlights contrasting climate effects acting both on the propensity to flee (1/0) and on the distance at which birds initiated flight. Interestingly, weather PC2 (wind and rain) had opposite effects on these behavioral traits. As conditions were windier and rainier, birds were more likely to flee, but those that fled had lower FID. This suggests that birds that fled waited until the last moment before they did so, which could be explained by the fact that they were less likely to detect the incoming threat in windy and rainy conditions. Wind speed has been shown to have contrasting effects on animal vigilance and escape behavior, from no effect to marked effects depending on the species and taxa (e.g., no effect: birds; Clucas and Marzluff, 2011, Nordell et al., 2017, Petrelli et al., 2017; reptiles; McGowan et al., 2014; wind effects: birds; Reynolds et al., 2020; mammals; Wolf & Croft, 2010). Increased wind speed has been shown in 17 of 18 studies to decrease an animal's ability to detect an approaching predator by masking sounds, smells and visual cues (Cherry and Barton, 2017). Wind may also be a source of distraction (Chan et al., 2010; Tätte et al., 2019), leading to delayed detection of approaching predators. It has been suggested that the magnitude of FID responses should decrease under harsh weather conditions, as the energy cost of fleeing increases (Collop et al., 2016). For

405   endotherms wind chill increases thermoregulatory costs, and a trade-off might exist between

406   investing energy into flight and that into thermoregulation (Collop et al., 2016, but see also

407   Reynolds et al., 2020). Because penguins rely essentially on fat stores during incubation on-land

408   (Groscolas & Robin, 2001), and because energy-depleted birds will abandon reproduction

409   (Groscolas et al., 2000, Gauthier-Clerc et al., 2001), any energy savings – however small – is

410   critical. Thus, energy savings in harsh climate conditions may contribute in explaining why birds

411   waited for the last moment to flee. FID also increased with increasing approach speed of the

412   experimenter. Faster approach speeds after alert may be interpreted as greater threat by the targeted

413   prey, and thus generating longer FID (Stankowich and Blumstein, 2005; Cooper and Whiting,

414   2007; Smith-Castro and Rodewald, 2010; Bateman and Fleming, 2011).

415   It is interesting to note that it was not uncommon for the incubating penguins to stay and

416   defend their eggs aggressively instead of attempting to flee (there was an FID of 0 m in 42

417   approaches of 135). For these birds either the perceived risk of the approaching threat (a human)

418   was not high enough to elicit a flight response, or the motivation to breed and defend the territory

419   was stronger than that of attempting to flee. FIDs of 0 m have been observed in other ground laying

420   birds: yellow-eyed penguins *Megadyptes antipodes* (Ellenberg et al., 2007, 2009), humboldt

421   penguin *Spheniscus humboldti* (Ellenberg et al., 2006), magellanic penguins *Spheniscus*

422   *magellanicus* (Fowler, 1999; Villanueva et al., 2014), and African penguins *Spheniscus demersus*

423   (Pichegru et al., 2016). King penguins are special in that they incubate their egg on their feet in a

424   specialized brood pouch. Thus, fleeing is at any rate limited, and essentially amounts to clustering

425   close to neighbours in the hope to benefit from confusion, dilution or selfish herd effects. In

426   addition, fleeing may risk damaging or losing the egg, losing the breeding territory, suffering from

427   increased aggression by territorial neighbours (Côté, 2000), or disturbing the thermal incubation

428   environment required for chick development and survival. For instance, exposed eggs during

429   transitory breeding abandonment in king penguins have been found to lose heat at a rate of 0.19 °C

430   per minute (Groscolas et al., 2000).

431

432   **Between- and within-individual variation in AD**

433   In contrast to FID, the repeatability of AD was low (0.10) and not significant, but improved

434   slightly (0.15) and was close to significant ($P = 0.062$) when accounting for the effects of climate

435   (Weather PC1). As far as we are aware, there is no report of the repeatability of AD in the literature.

436   Rather, researchers have considered vigilance behaviour when aiming to understand how animals

437   respond to threats. More vigilant individuals are expected to detect predators earlier and thus

438   become alert at longer distances (Fernández-Juricic and Schroeder, 2003; Beauchamp, 2015;

439   Uchida et al. 2019; but see Tätte et al., 2019). Studies that measured repeatability in vigilance

440   behaviours also reported low, but significant, repeatability: eastern grey kangaroos, *Macropus*

441   *giganteus*, (r=0.07-0.14, Edwards et al., 2013); redshanks, *Tringa totanus*, (r=0.21, Couchoux and

442   Cresswell, 2012); house sparrows, *Passer domesticus*, (r=0.13-0.22, Boujja-Miljour et al., 2018);

443   cliff swallows, *Petrocheldion pyrrhonota*, (r=0.089, Roche and Brown, 2013). As mentioned

444   above, repeatability estimates are likely to increase as some residual variation is accounted for by

445   including potential factors such as age, sex, or condition, that were unfortunately not available in

446   this study as individuals were not followed or handled. Dingemanse and Dochtermannn (2013)

447   determined that for lower repeatabilities, >4 samples per individual were required if the total

448   number of individuals is <100. Similarly, Wolak et al. (2012) found fewer samples per individual

449   were required for higher r values (3 samples per individual for an r of 0.8), but for an r of 0.2, the

450   precision of the estimate continues to increase until up to 10 samples per individual. Because of

451   time and field constraints we were only able to repeatedly approach 45 individuals 3 times. Yet,

452   post-hoc power analyses revealed that doubling our sample size to 6 repeated measures per bird

453   would have been sufficient to detect significant repeatability. At any rate, repeatability was low,

454   indicating that individuals were more flexible in this behavioral trait than in their decision to flee.

455   Similarly, vigilance levels (and presumably AD) have been found to be highly flexible (Couchoux

456   and Cresswell, 2012; Edwards et al., 2013) and sensitive to numerous biological factors such as

457   group position and group size, distance to cover, predation pressure, season, weather, and time of

458   day (reviewed in Elgar, 1989). In our study, AD was significantly lower in warm and sunny

459   conditions, suggesting that birds were less vigilant in good weather conditions.

460

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

462   We expected AD and FID to vary depending on colony and with changes in predation

463   pressure throughout the day. However, our analyses suggests that neither were major factors

464   influencing escape decisions in the king penguin. First, on-land predation in king penguin colonies

465   is highest at dawn and dusk (Le Bohec et al., 2003; Descamps et al., 2005), whereas most of our

466   measures were done between 8 AM and 6 PM. Extending measurements to early morning and late

467   evening when predators are most active may allow to better capture potential effects of predation

468   pressure on penguin behavior. Second, given that the two colonies surveyed in this study differ

469   markedly in their exposure to human presence throughout the year (BDM is located next to a

470   research station and breeders have seen humans almost every day for the past 50 years, whereas

471   birds in JJ are rarely exposed to human visitors), we had expected birds in the BDM (vs. JJ) colony

472   to habituate to approaching humans. However, the lack of difference in behavioral responses

473   between the colonies is perhaps not so surprising. Previous findings indicate that birds breeding in

474   more disturbed areas of the BDM colony show lower heart rate stress responses to an experimenter

475   approaching to 10 m distance than birds in less disturbed areas – suggesting a potential for

476   habituation to the presence of humans in chronically disturbed areas (Viblanc et al., 2012). Yet,

477   heart rate responses were similar between the disturbed and undisturbed areas when birds were

478   approached up to contact and captured (Viblanc et al., 2012). Although birds were not captured in

479   the present study, they were approached up close (to a few cm), and the risk assessed was

480   presumably more comparable to a capture than to an observer standing some 10 m distant.

481   Previous studies in similar seabirds have shown contrasted responses to human approaches.

482   For instance, whereas Magellanic (*Spheniscus magellanicus*), African (*S. demersus*), and Gentoo

483   penguins (*Pygoscelis papua)* show reduced behavioural and/or physiological responses (heart rate

484   or corticosterone concentrations) to human visitation in high disturbance areas (van Heezik and

485   Seddon, 1990; Fowler, 1999; Walker et al., 2005, 2006; Holmes et al., 2006; Villanueva et al.,

486   2012; Pichegru et al., 2016), yellow-eyed penguins (*Megadyptes antipodes*) appear to sensitize to

487   human exposure through higher stress responses (Ellenberg et al., 2007). Taken together, these

488   results highlight two important points: (1) behavioural and physiological responses to approaching

489   predators (or humans) may tell seemingly different stories. A proper understanding of prey

490   responses to approaching predators requires the integrative assessment of both physiological stress

491   responses and behavioural reactions. (2) both behavioural and physiological responses are fine-

492   tuned mechanisms integrating risk assessment into optimal escape decisions.

493   Finally, we must consider how STRANGE were the animals in our study (Webster & Rutz

494   2020). We selected birds in the colonies haphazardly, with no knowledge of their sex, age or past

495   experience. Nonetheless we did not capture and measure bird morphometrics in our study, but

496   visually targeted birds that appeared in overall good physical condition in order to minimize the

497   risk of breeding abandonment for energy-depleted birds (Groscolas et al., 2000, Gauthier-Clerc et

498   al., 2001) in this protected species. Our measures on individual birds were done over a few days

499   during which changes in body condition were likely relatively minor. However, we might not have

500   captured the full range of behavioral expression of AD and FID, particularly for birds of low body

501   condition. This is important to consider since individuals in poor body condition may have

502   enhanced stress and FID responses to approaching experimenters (Seltmann et al., 2012), and

503   emphasizes the importance of controlling for body condition – where feasible – in performing

504   repeated measures on wild animals.

505   As this study only tested the response to repeated approaches in two colonies, which will

506   have obvious differences in colony size, density, and topography, replicating this study over

507   additional colonies would help in a better characterisation of the factors shaping escape decisions

508   in penguins. In addition to landscape and social differences between colonies, there are also

509   possible differences in predation pressure and genetic differentiation. Furthermore, the sampling in

510   the two colonies took place 20 days apart, allowing for possible differences in the reproductive

511   cycle to manifest. Lastly, sampling only occurred over a span of three days. Further studies should

512   investigate these factors in more depth, as well as test repeated approaches over a longer time period

513   – and over the lifetime of individual birds. In particular, these would help in capturing a greater

514   range of weather conditions, and better understanding the extent of repeatability and plasticity of

515   these behavioral traits (Dingemanse & Wright, 2020).

516   The response of a wild population to human disturbance creates special considerations in

517   a world that is increasingly accessible to humans. Ecotourism and wildlife tourism, or travel to

518   natural areas to engage in shared experiences with wildlife and whose aim is to conserve the

519   environment through education and local spending, are increasingly common activities. As a

520   charismatic anthropomorphic animal, penguins have garnered much attention. In many species,

521   habituation occurs in response to disturbances caused by tourists (van Heezik and Seddon, 1990;

522   Fowler, 1999, Holmes et al., 2006; Villanueva et al., 2014). However, even in species that have

523 habituated to disturbance, human presence can impact natural behaviours, time budgets, heart rates

524 and stress levels (Holmes et al., 2005; Walker et al., 2005, 2006; Burger and Gochfeld, 2007;

525 Viblanc et al. 2012; Villanueva et al., 2012; Pichegru et al., 2016). For species that cannot habituate

526 or which have sensitized to disturbance, individuals may experience negative impacts on their

527 reproductive success ultimately endangering the population as a whole (Giese, 1996; McClung et

528 al., 2004; Ellenberg et al., 2006, 2007, 2012, 2013; Carroll et al., 2016). Knowledge of AD and FID

529 may help inform policy makers when deciding appropriate viewing guidelines for tourists

530 (Ellenberg et al., 2006, French et al., 2019).

531

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FIGURE LEGENDS

Figure 1. Scatter plots (generated from three observations per individual incubating king penguin, *Aptenodytes patagonicus*) of: A) Alert Distance (AD) in the Jardin Japonais colony (JJ; N = 23 individuals; circles); B) AD in the Baie du Marin colony (BDM; N = 24 individuals, triangles); C) Flight Initiation Distance (FID) in the JJ colony (N = 23 individuals); and D) FID in the BDM colony (N = 24 individuals), on Possession Island in the Crozet Archipelago. Individuals are ranked from lowest to highest mean scores of AD and FID per colony to allow for the visualisation of within versus among individual variability.

Figure 2. Variables affecting Alert Distance (AD) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervals for the effects of time of day (z-time), weather (PC1 and PC2), speed of approach prior to AD (z-speed), colony of origin (Baie du Marin, BDM, or Jardon Japonais, JJ), and approach number. n = 133 observations, N = 47 individuals. B) The significant predicted effect of weather PC1 on AD is depicted. Dots represent the raw AD values (BDM = circles, JJ = triangles); shading represents a 95% confidence interval predicted from the model while holding other variables in the model constant. A high weather PC1 value is associated with less rain, higher temperature, more sun, and more wind.

Figure 3. Variables affecting the decision to flee (binomial; 0 = no flight initiated, 1 = flight initiated) in incubating king penguins (*Aptenodytes patagonicus*). A) Odds ratios and 95% confidence intervals for time of day (z-time), weather (PC1 and PC2), speed of approach between AD and FID (z-speed), colony of origin (Baie du Marin, BDM, versus Jardin Japonais, JJ), and approach number. n = 133 observations, N = 47 individuals. The odds ratio can be interpreted for a given predictor in terms of increasing (>1) or decreasing (<1) the likelihood to flee for a one-unit increase in that predictor, holding all other variables constant. B) The significant predicted effect of weather PC2 on flight probability is depicted along with its 95% confidence interval (shading). Dots represent raw values separated by colony (BDM = circles, JJ = triangles). High weather PC2 is associated with increased rain and wind.

Figure 4. Variables affecting Flight Initiation Distance (FID) in incubating king penguins (*Aptenodytes patagonicus*). A) Standardized linear mixed model estimates (z-scores) and 95% confidence intervales (CI) for the effects of time of day (z-time), weather (PC1 and PC2), speed of approach between AD and FID (z-speed), colony of origin (Baie du Marin, BDM, or Jardin Japonais, JJ), and approach number. n = 91 observations, N = 41 individuals. B) The significant predicted effect of approach speed on FID is depicted along with its 95% CI. Dots represent raw FID values separated by colony, circles = BDM, triangles = JJ. C) The significant predicted effect of weather PC2 on FID is depicted along with its 95% CI. Dots represent raw FID values separated by colony, circles = BDM, triangles = JJ.
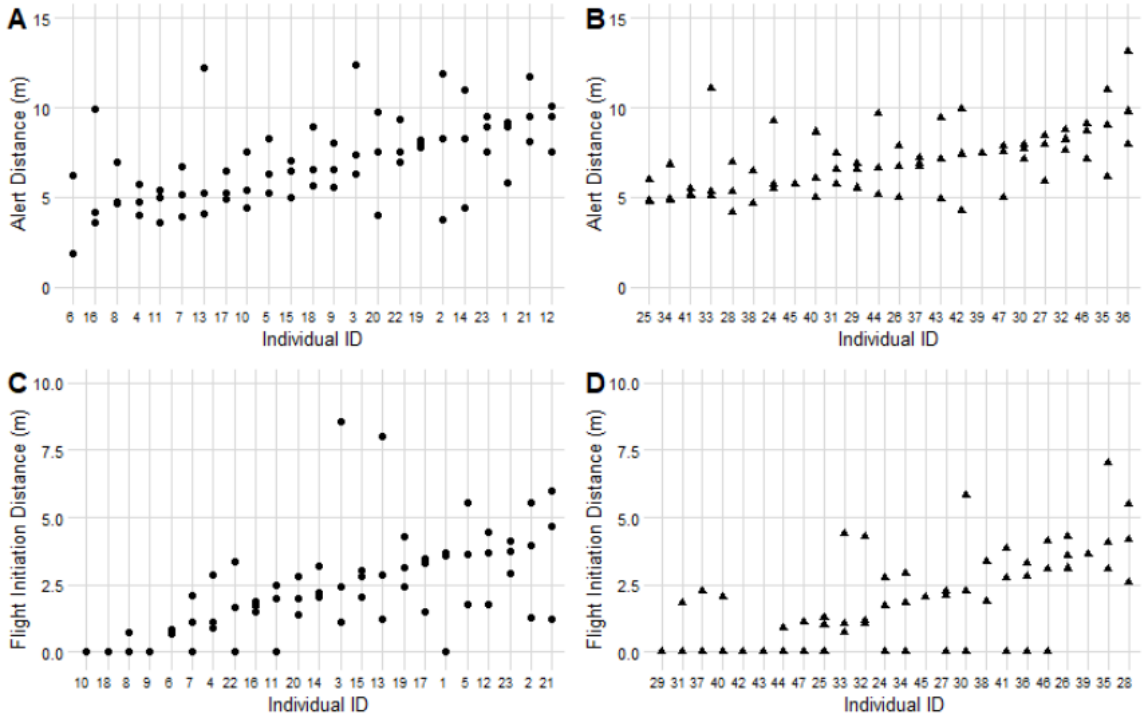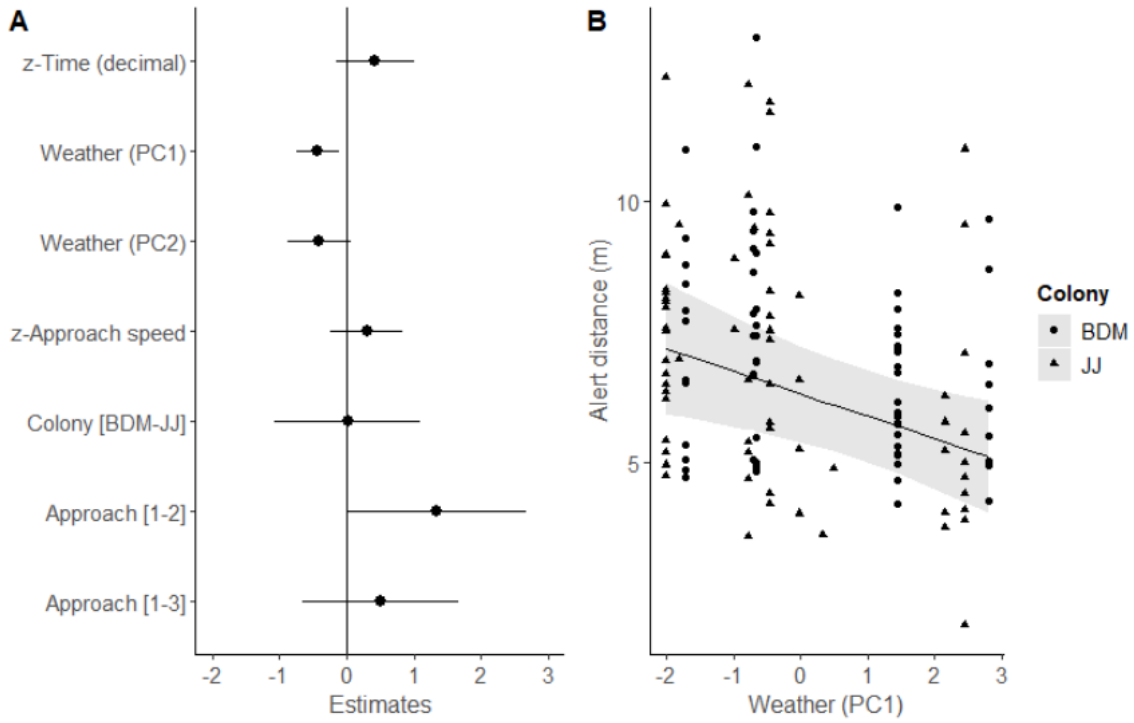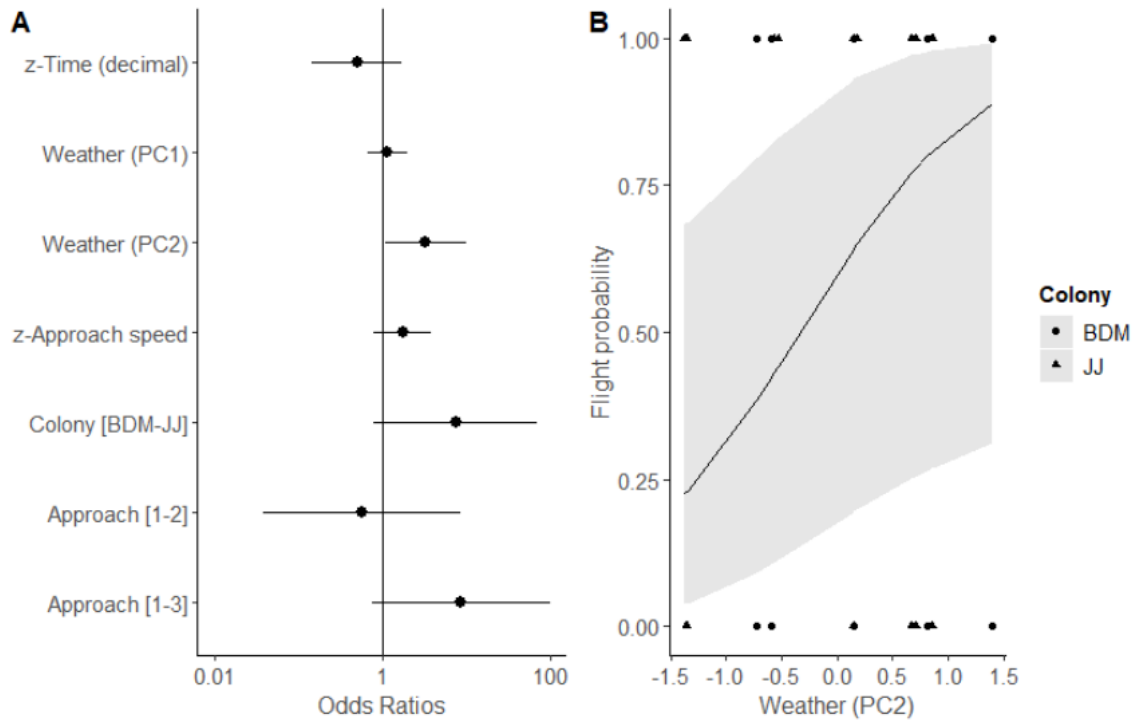
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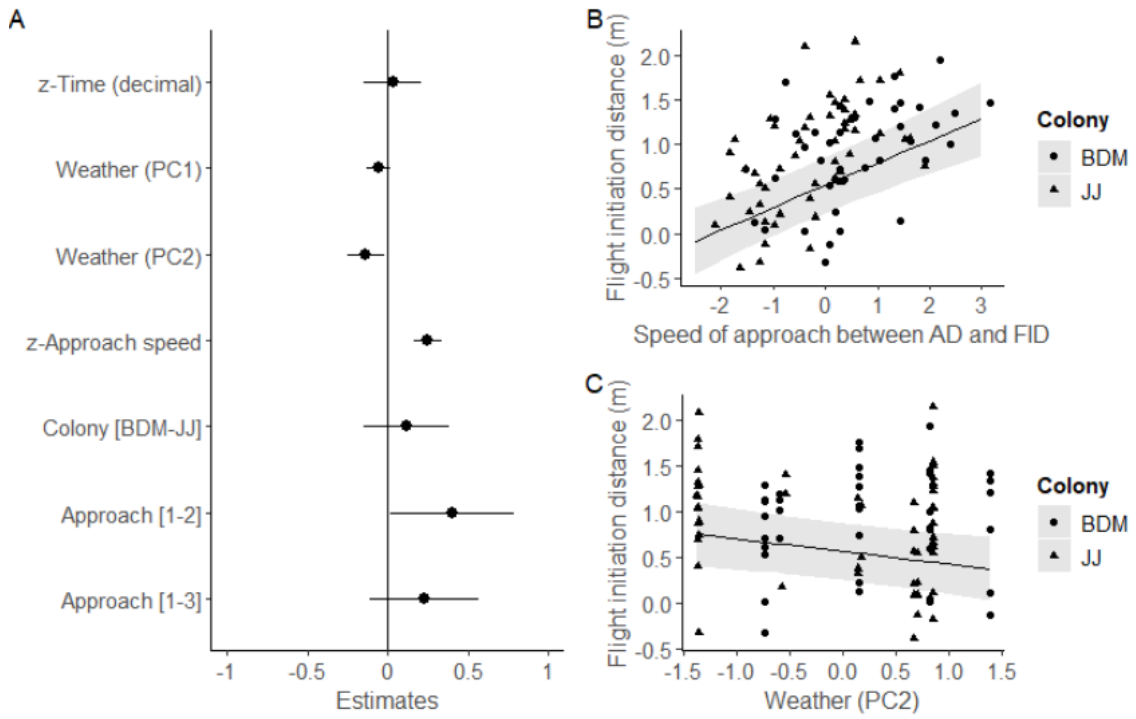
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