



HAL
open science

Disentangling the “many-eyes”, “dilution effect”, “selfish herd”, and “distracted prey” hypotheses in shaping alert and flight initiation distance in a colonial seabird

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

► To cite this version:

Tracey L Hammer, Pierre Bize, Benoit Gineste, Jean-Patrice Robin, René Groscolas, et al.. Disentangling the “many-eyes”, “dilution effect”, “selfish herd”, and “distracted prey” hypotheses in shaping alert and flight initiation distance in a colonial seabird. *Behavioural Processes*, 2023, 210, pp.104919. 10.1016/j.beproc.2023.104919 . hal-04265783

HAL Id: hal-04265783

<https://hal.science/hal-04265783v1>

Submitted on 31 Oct 2023

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.

18 **ABSTRACT**

19 Group living is thought to have important antipredator benefits for animals, owing to the
20 mechanisms of shared vigilance (“many-eyes” hypothesis), risk dilution (“dilution effect”
21 hypothesis), and relative safety in the center of the group (“selfish herd” hypothesis). However, it
22 can also incur costs since social stimuli, such as conspecific aggression, may distract individuals
23 from anti-predator behavior (“distracted prey” hypothesis). We simultaneously evaluated how
24 these four different hypotheses shape anti-predator behaviors of breeding king penguins
25 (*Aptenodytes patagonicus*), which aggregate into large colonies, experience frequent aggressive
26 social interactions, and are regularly exposed to predation by giant petrels (*Macronectes sp.*) and
27 brown skuas (*Catharacta loonbergi*) when breeding on land. We approached 200 incubating
28 penguins at four different periods of the breeding season across a range of overall increasing
29 colony densities. We measured the distance at which focal birds detected the approaching threat
30 (alert distance: AD), whether birds decided to flee or not, and the distance of flight initiation
31 (flight initiation distance: FID, *viz.* the bird attempting to walk away with its egg on its feet). We
32 quantified relative local neighbor density, centrality within the colony (rank), and the number of
33 aggressions the focal bird emitted towards neighbors during the approach. We found that birds
34 engaged in aggressive conflicts with neighbors were less likely to flee, and that increasing
35 relative local neighbor density at low and medium overall colony density resulted in a decrease
36 in bird AD, both supporting the “distracted prey” hypothesis. However, at maximal overall
37 colony density, increasing relative local neighbor density resulted in longer AD, supporting the
38 “many-eyes” hypothesis. We found no support for the “dilution effect” and “selfish herd”
39 hypotheses, and no effects of any hypothesis on FID.

40 **Keywords:** antipredator behaviour, escape flight distance, optimal escape decisions, predation
41 risk, predator-prey decision, risk taking

42 INTRODUCTION

43 Predation can be an important source of mortality in wild animals (Roos et al. 2018).
44 Aggregating into large social groups is often viewed as a solution to decrease predation risk for
45 the individual and its offspring (Alexander 1974; Hoogland 1981). At least four non-mutually
46 exclusive hypotheses have been proposed to explain how group size and social interactions may
47 influence predator-prey interactions (for a review of the relationship between group size and
48 flight initiation distance, see Ydenberg and Dill 1986; Stankowich and Blumstein 2005).

49 Firstly, one important mechanism identified in decreasing predation risk with increasing
50 group size is that of shared vigilance by group members towards potential threats (Caraco et al.
51 1980; Lima and Dill 1990; Quenette 1990). Since larger groups have more individuals scanning
52 for predators at any given time, the presence of “many eyes” in a group allows for the earlier
53 detection of predators than would be possible for single individuals (the “many-eyes hypothesis”;
54 Pulliam 1973; Lima and Dill 1990). Information on the presence of a predator can disseminate
55 rapidly through the group, most often through the use of alarm calls, allowing individuals to
56 assess the risk and decide to flee sooner than is possible alone (Burger and Gochfeld 1991;
57 Mayer et al. 2019). Thus, larger groups are often more rapid in detecting a predator than single
58 individuals, and more likely to raise alarm of an approaching predator sooner than smaller
59 groups (Hoogland 1981; van Heezik and Seddon 1990; Cresswell 1994), though vigilance
60 behavior may also be affected by other environmental characteristics such as species
61 gregariousness, diet or habitat (Morelli et al. 2019).

62 Secondly, large groups also provide the advantage of diluting individual predation risk
63 (Ydenberg and Dill 1986). Most predatory species can only capture a single prey at a time, and
64 thus the chance that each individual prey will be the target of predation reduces with increasing
65 group size (Dehn 1990; Roberts 1996; Bednekoff and Lima 1998). According to the “dilution
66 effect hypothesis” individuals in larger groups may tolerate the closer approach of predators
67 before initiating flight (enabling a longer amount of time to be spent on tasks such as foraging),
68 since the risk of predation is diluted with each additional conspecific nearby (Cresswell 1994;
69 Boland 2003; Fernández-Juricic and Schroeder 2003). The dilution effect is not only limited to
70 larger group sizes, but also to denser groupings of individual prey, regardless of overall group
71 size (Roberts 1996; Hebblewhite and Pletscher 2002; Frommen et al. 2009). For example, many
72 bird species that migrate in flocks or cluster together on breeding grounds may benefit from the
73 dilution effect by reducing individual predation risk while foraging or breeding (Wiklund and
74 Andersson 1994; Harts et al. 2016; Duca et al. 2019), though in some groups individual risk-
75 taking may vary with life-history stage (*e.g.*, in long-distance migratory waders,
76 Charadriiformes, risk-taking is lowest during reproduction and highest during migration; Mikula
77 et al. 2018).

78 Thirdly, individual spatial positioning within the group may provide dissimilar anti-
79 predator benefits. The “selfish herd” hypothesis (Hamilton 1971) suggests that animals located
80 more centrally in a group should be less vulnerable to attacks from predators than those on the
81 periphery as predators come from outside the group and target the closest available prey
82 (Hamilton 1971). In other words, maintaining conspecifics between a predator and oneself will
83 reduce individual predation risk. Prey animals should therefore select higher value central
84 positions when joining a group, which is indeed seen in minnows, *Phoxinus phoxinus* (Krause

85 1993), sheep, *Ovis aries* (King et al. 2012), and fiddler crabs, *Uca pugilator* (Viscido and
86 Wethey 2002). If selfish herd effects are important, there should be evidence of divergent
87 predation rate, pressure or risk between the center and the periphery of a group (Morton et al.
88 1994; Viscido et al. 2001). When redshanks, *Tringa totanus*, were targeted by sparrowhawks,
89 *Accipiter nisus*, birds that were more peripheral and further from neighbors were at the highest
90 risk of predation (Quinn and Cresswell 2006). In colonial web-building spiders, *Meteperira*
91 *incrassata*, predatory attacks occur most often on the periphery (Rayor and Uetz 1990). There
92 may also be evidence of different levels of investment by prey into anti-predator monitoring
93 between central and peripheral animals. Increased vigilance by peripheral animals has been
94 observed in black-tail prairie dogs, *Cynomys ludovicianus* (Hoogland 1981), African mammals
95 (Burger and Gochfeld 1994), including springboks, *Antidorcas marsupialis*, (Bednekoff and
96 Ritter 1994), and scaled doves, *Columbina squammata* (Dias 2006).

97 Finally, although larger groups provide the benefit of shared vigilance and predation risk
98 dilution, individuals in such groups have to process a noteworthy amount of social information
99 from their conspecifics (Treves 2000). As a consequence, the time spent processing social cues
100 and interacting with conspecifics, noise and conflicts from and between conspecifics may detract
101 from the time and energy investments usually placed into scanning for predators (Mooring and
102 Hart 1995; Yee et al. 2013). This is known as the “distracted prey hypothesis” which proposes
103 that external stimuli – such as sounds – are capable of hijacking finite resources, thus impairing
104 the prey’s ability to detect and react to approaching predators (Chan et al. 2010; Petrelli et al.
105 2017). Social distractions (such as aggressive interactions between conspecifics) may also
106 distract prey from predator detection and delay behavioral responses such as the initiation of
107 flight. This is, for instance, the case in a cichlid fish species (*Neolamprologus pulcher*), where

108 individuals respond significantly later to predator images during territorial contests than when
109 they are alone, illustrating the trade-off between time and energy investments into aggressive
110 social behaviors and vigilance towards predators (Hess et al. 2016).

111 Here, we investigated the relative importance of the (1) “many-eyes”, (2) “dilution
112 effect”, (3) “selfish herd” and (4) “distracted prey” hypotheses on prey anti-predator behaviors of
113 breeding king penguins (*Aptenodytes patagonicus*). These four hypotheses are not mutually-
114 exclusive, and thus can be investigated simultaneously. For instance, individuals in larger groups
115 may benefit from risk-dilution, shared vigilance, and selfish herd effects, all while paying
116 potential costs of social distractions. King penguins are an ideal model system to test these non-
117 mutually exclusive alternatives. This seabird species forms extensive, densely packed colonies
118 when breeding on land (over tens of thousands of birds strong, Barbraud et al. 2020). Breeding
119 birds incubate/raise a single egg/chick on their feet and aggressively defend their small breeding
120 territory against both predators and conspecifics (Stonehouse 1960; Weimerskirch et al. 1992).
121 Aggressive social interactions are particularly high and can average 100 interactions per hour
122 (Côté 2000). Of particular interest is the finding that king penguins are highly sensitive to social
123 aggression, even when they are not directly involved in social conflicts (as demonstrated by
124 elevated by-stander heart rate responses when witnessing aggressive neighbors fighting; Viblanc
125 et al. 2012). In addition, higher stress hormones and heart rates are detected in more densely
126 packed colony areas (Viblanc et al. 2014a; Viblanc et al. 2014b). Thus, frequent social
127 aggression in these birds may interfere with antipredator behaviors, such as vigilance and flight.
128 King penguins are subject to on-land predation by giant petrels, *Macronectes giganteus* and
129 *Macronectes halli*, and brown skuas, *Catharacta loonbergi*, especially known to predate on eggs
130 and young chicks, but occasionally targeting adults as well (Hunter 1991; Descamps et al. 2005).

131 These predators will harass incubating and brooding adults sometimes causing them to flee and
132 abandon their eggs. Breeding birds then face three choices: to stay and fight, risking injuries that
133 could be fatal; to flee clumsily by waking with their egg or offspring on the top of their
134 feet and to cluster closer to neighbors; or to abandon reproduction and flee entirely by walking
135 rapidly (often includes tripping and flipper beating against the ground; RG, VAV, JPR, BG, PB,
136 TH; personal observations). Yet, how shared vigilance (1. “many-eyes” hypothesis), safety in
137 large numbers (2. “dilution effect” hypothesis), safety in a central location (3. “selfish herd”),
138 and acute social interactions (4. “distracted prey” hypothesis) (Table 1) interact in shaping prey
139 antipredator behavioral responses is unknown.

140 We used Alert Distance (AD), or the distance at which the targeted bird detects an
141 approaching threat (in this case, an experimenter), and Flight Initiation Distance (FID), or the
142 distance at which the targeted bird begins to flee from the approaching threat to simultaneously
143 investigate the “many-eyes”, “dilution effect”, “selfish herd” and “distracted prey” hypotheses.
144 AD and FID are popular measures used in the literature to study the reactions of prey to
145 approaching danger and optimal escape strategies. The great advantage of these measures is that
146 they can be collected through non-lethal approaches by a human experimenter using standardized
147 approach protocols (see Hammer et al. 2022 for an example in king penguins). From an
148 evolutionary perspective, prey are expected to react in much the same way to a human approach
149 as to an approach by a true predator, as behavioral responses should be selected to over-estimate
150 rather than under-estimate risk (Frid and Dill 2002; Beale and Monaghan 2004). AD and FID are
151 therefore promising behavioral responses that can be used to better understand how group size
152 and social interactions may shape predator-prey interactions.

153 We evaluated AD and FID in response to standardized human approaches in relation to
154 both overall colony density (low, med, high, maximal) that increased as the breeding season
155 progressed, relative local neighbor density (number of neighbors around a focal bird centered
156 around the mean overall colony density at any given stage of the season), relative colony rank
157 (rank centered with each colony density stage), and the number of aggressive interactions (i.e.,
158 social distractions) exchanged between the focal bird and its neighboring conspecifics during the
159 approach. Whereas the “many eyes” hypothesis predicts that AD should occur earlier in larger
160 groupings as there are more vigilant individuals present at any given point in time, the
161 “distracted prey” hypothesis predicts that AD and/or FID will be delayed in denser groups due to
162 increased social stimuli, such as aggression with neighbors, that hinders predator detection and
163 flight. The “selfish herd” hypothesis predicts that peripheral individuals in the colony (those of
164 low colony rank as counted from the periphery to the center of the colony) where predation risk
165 is highest, will have higher AD and FID than individuals in less risky central positions. Finally,
166 the “dilution effect” predicts that FID will be delayed at high local social density due to reduced
167 predation risk on the individual, but should be unrelated to social interactions (social aggression,
168 in our case). Predators may be allowed to approach even closer in aggressive groupings of prey
169 than the dilution effect predicts alone, as is the case in king penguins, as larger groups may allow
170 for group defense from predators (i.e., mobbing).

171

172 **METHODS**

173 *Study site and animals*

174 During the 2011-2012 breeding season, 200 king penguins were randomly chosen and
175 approached in “La Baie du Marin” colony (Possession Island, Crozet Archipelago, 46°25’S –
176 51°52’E), home to approximately 22 000 breeding pairs (Barbraud et al. 2020). According to
177 STRANGE guidelines (Webster and Rutz 2020), study subjects were selected to reduce potential
178 biases (and were hence not blindly selected), nevertheless we highlight some of the potential
179 biases here. All birds were incubating and therefore of similar breeding status (but see
180 discussion) and appeared in physically good overall condition; but we did not have any
181 information on bird age, sex, laying date, or previous exposure to humans. Individuals were
182 chosen from a distance and not after being approached or captured, therefore we expect no strong
183 initial sampling bias. Between successive approaches, birds were at least 50 meters apart. The
184 individuals were divided into four groups of 50 birds, measured approximately 15 days apart
185 from mid-November 2011 to mid-January 2012. As colony density increases over the breeding
186 season (see Viblanc et al. 2014b for colony dynamics), our objective was to sample birds in
187 natural conditions of increasing social density. Thus, we defined four groups corresponding to
188 periods of increasing overall colony density with: low density (mean \pm SE birds/m²: 4.05 \pm 0.11,
189 19-22 Nov. 2011), medium density (4.48 \pm 0.14, 3-5 Dec. 2011), high density (5.04 \pm 0.11, 22-
190 23 Dec 2011), and maximal density (5.47 \pm 0.11, 13-16 Jan 2012).

191

192 ***Approach protocol***

193 Approaches (always the same experimenter, BG, dressed in the same clothing) were started at a
194 standardized start distance of 18 m when the focal individual was awake. A distance of 18 m
195 corresponded to a distance 1.5 times greater than maximal detection distance recorded in a
196 preliminary study to ensure starting distance far exceeded maximum alert distance (Hammer et
197 al. 2022, see also Fleming and Bateman 2017). Start distance was standardized due to its known
198 effect on AD and FID (Blumstein 2003; Blumstein 2010; Dumont et al. 2012). Distances were
199 measured to the nearest cm using a laser telemeter (Leica DISTO™ D5 Lasermeter, Leica
200 Geosystems AG, Hexagon, Sweden). The experimenter, while walking at a regular speed,
201 followed a direct trajectory towards the focal individual. Both when the first sign of detection
202 was observed (AD; focal animal tilting its head or stretching its neck in the direction of the
203 experimenter), and when flight was initiated (FID; focal animal attempting to walk away with its
204 egg on its feet), the experimenter took a standardized one-minute pause to record the distance
205 between his position and the bird. Several focal birds did not flee up until contact. Thus, FID was
206 divided into two separate analyses: *i*) the decision to flee or not, and *ii*) the flight initiation
207 distance for birds that decided to flee. During the approach, the number of aggressive
208 interactions initiated by the focal bird towards its neighbors was counted by the approaching
209 experimenter and recorded as a proxy of social distraction. Aggressive interactions included: bill
210 gaping (non-physical-threats displays, the focal bird extending its head with bill open wide,
211 vocalizing towards a neighbor); bill pecking (the birds extending its neck and physically pecking
212 a neighbour) and flipper blows (the bird striking a neighbor with an extended flipper) (see Côté
213 2000, Viera et al. 2011). The number of aggressive interactions initiated by the focal bird was
214 then weighted to account for known differences in energetics: aggressions with physical contact

215 (bill pecking, flipper blows) weighed more heavily than non-physical threats (bill gaping);
216 according to Viera et al. (2011), contact aggressions are 3.2 times more energy costly than
217 threats (mean \pm SE = 0.69 ± 1.00 , range = 0.0 – 5.2).

218 Two speeds of approach (prior to AD and prior to FID) were calculated using the
219 distance walked (m) and the duration of approach (s). The mean \pm SE speed of approach prior to
220 AD was 0.51 ± 0.07 m/s (range = 0.28 – 0.76 m/s), and between AD and FID was 0.42 ± 0.05
221 m/s (range = 0.24 – 0.54 m/s). Weather conditions were recorded prior to each approach and
222 used as control variables in the analyses (Hammer et al. 2022). Air temperature was recorded to
223 the nearest 1°C, and wind and rain levels were scored between 0 (none) and 2 (strong or heavy),
224 intermediate levels (0.5) being allowed.

225 Before approaching the birds, we counted the number of neighbors surrounding each
226 focal individual, defined as the first circle of animals that were direct neighbors (mean \pm SE =
227 7.49 ± 1.93 ; range = 4 - 14) and recorded the mean distance of the neighbors to the focal
228 individual (mean \pm SE = 0.81 ± 0.14 ; range = 0.53 – 1.22 m). The distance between the birds
229 was initially visually estimated from a distance and subsequently corrected to the closest 10 cm
230 during the approach. Local density (number of birds/m²) was then calculated as the number of
231 neighbors surrounding a focal bird divided by the area of a circle (πr^2) with the mean distance
232 between the focal bird and its neighbors acting as the radius. Local bird density increased with
233 overall colony density ($F_{3,192}=28.0$, $P<0.001$) (Fig. 1). As local neighbor density naturally
234 increased together with increasing colony density (i.e., low, medium, high, maximal) as the
235 breeding season advanced, we centered local neighbor density within each colony density stage
236 to obtain an index of local neighbor density which was independent of overall colony density.

237 Thus, relative local neighbor density was calculated as $d - \mu\bar{d}$, with d being the local neighbor
238 density of a focal bird, and $\mu\bar{d}$ being the mean neighbor density over all birds measured at a
239 given stage (i.e., within low, medium, high, and maximal colony density stages). A bird with
240 relative local neighbor density >0 (or <0) thus experienced a “local” social environment that was
241 relatively more or less crowded than the average at a given stage.

242

243 *Statistical analyses*

244 All statistical analyses were performed in R 1.4.1106 (R Development Core Team 2021). Results
245 are presented as means \pm SE. Effects were considered statistically significant for $P < 0.05$. We
246 investigated the “many eyes”, “dilution effect”, “selfish herd”, and “distracted prey” hypotheses
247 by considering the joint effects of overall colony density, relative local neighbor density, relative
248 colony rank (see below), and number of aggressive interactions of the focal individual to their
249 neighbor (all independent variables) on focal bird AD, FID, and decision to flee or not (all
250 dependent variables in separate models). The number of aggressions displayed against
251 neighboring individuals during the entire approach was used to quantify the amount of social
252 distraction to which the focal birds were subject. Similar to relative local neighbor density, we
253 calculated relative colony rank (or the relative centrality of the focal bird within the colony) by
254 centering bird rank within each overall colony density stage (low, medium, high, maximal) in the
255 manner of $r - \mu\bar{r}$, with r being the rank of a focal bird, and $\mu\bar{r}$ being the mean rank over all
256 measured birds at a given stage. Thus, a bird with a relative colony rank >0 (or <0) was
257 relatively more (or less) central in the colony than the average at a given stage. General linear
258 mixed models with appropriate error distributions were used to investigate sources of variation in

259 AD (gaussian distribution), the decision to flee or not (binomial distribution), and FID (gaussian
260 distribution after log transformation). Models were run using the package “lme4” functions *lmer*
261 and *glmer* (Bates et al. 2015). Models were checked for the normality of their residuals using
262 “fitdistrplus” (Delignette-Muller and Dutang 2015). For models with a gaussian distribution, the
263 significance of fixed effects were tested with “lmerTest” *anova* (Kuznetsova et al. 2017) using F
264 tests with Satterthwaite estimation for the denominator degree of freedom. Wald chi-square tests
265 were used for models with a binomial distribution (*Anova*). We further tested if behavioral
266 decisions (AD, FID, and the decision to flee or not) were affected by the interaction between
267 relative local neighbor density and overall colony density (low, medium, high, maximal); this
268 interaction was dropped from the models if it was non-significant. The area of the colony in
269 which we approached the bird was initially included as a random factor in all our models to
270 control for unmeasured differences in landscape, chronic and spatially variable amounts of
271 human disturbance, etc., and the fact that several birds were measured in similar areas. However,
272 this random effect was removed from the binomial model as no variation in the decision to flee
273 could be attributed, and the model could not converge. In all models we initially controlled for
274 time of day (linear and quadratic effects, decimal), weather (temperature, wind and rain levels),
275 and speed of approach to account for tentative effects on AD, FID, and the decision to flee
276 (Hammer et al. 2022), but removed them from the final models if they were non-significant (all P
277 > 0.097). All independent variables were tested for collinearity using Variance Inflation Factors
278 (VIF) according to the suggestions by Zuur et al. (2010) and all variables were scaled and
279 centered prior to inclusion (Schielzeth 2010). Temperature was, in any case, removed from all
280 the models due to collinearity issues with colony density as temperature generally increased as
281 the summer season progressed and the breeding season advanced.

282

283 ***Ethics statement***

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

289

290 **RESULTS**

291 Over the entire season, individuals (N = 194) became alert on average at 7.31 ± 1.91 m; (range =
292 3.41 – 12.3 m). The interaction between relative local neighbor density and overall colony
293 density was significant (LMM, $F_{3,173.3} = 2.84$, $P = 0.039$) (Fig. 2). AD decreased with increasing
294 relative local neighbor density at low (slope = -0.48, 95% CI [-1.02, 0.06]) (Fig. 3). However, at
295 medium (slope = -0.46, 95% CI [-0.95, 0.04]) and high (slope = -0.12, 95% CI [-0.71, 0.47])
296 overall colony density, there was no relationship between AD and relative local neighbor
297 density. Finally, at maximal colony density AD increased with increasing relative local neighbor
298 density (slope = 0.64, 95% CI [0.02, 1.26]). AD was not significantly affected by the number of
299 aggressive interactions between the focal individual and their neighbors ($F_{1,172.7} < 1$), nor by
300 relative colony rank ($F_{1,175.0} < 1$).

301 Of the 200 individuals approached, 50% did not flee. Focal birds that were more
302 aggressive towards their neighbors during approach were significantly less likely to flee ($X^2 =$

303 4.16, $P = 0.041$). The decision to flee (GLM, $N = 193$ with complete information), was not
304 explained by relative colony rank, relative local neighbor density, or overall colony density (all
305 $X^2 < 1.6$) (Fig. 4).

306 Of the individuals that decided to flee (LMM, $N = 93$), the mean FID was at 3.00 ± 1.57
307 m; (range = 0.54 – 8.46 m). Birds showed greater FID when approached at faster speeds between
308 AD and FID ($F_{1,79.8} = 20.1$, $P < 0.001$) (Fig. 5). Variation in FID was not explained by aggression
309 with neighbors ($F_{1,78.5} = 2.45$, $P = 0.122$), relative colony rank ($F_{1,72.0} < 1$), relative local neighbor
310 density ($F_{1,80.0} < 1$), or overall colony density ($F_{3,78.7} = 1.02$, $P = 0.390$).

311

312 **DISCUSSION**

313 This study examined the contribution of the “many-eyes”, “dilution effect”, “selfish
314 herd”, and “distracted prey” hypotheses in shaping prey anti-predator behavior in colonial king
315 penguins. Our results show that at low and medium overall colony density, increasing relative
316 local neighbor density resulted in a decrease in bird alert distance (AD) to an approaching
317 experimenter, while at maximum overall colony density, increasing relative local neighbor
318 density resulted in longer AD. These results provide support for the “distracted prey” hypothesis
319 at low colony densities and the “many-eyes” hypothesis at maximum colony density. In addition,
320 birds who engaged in aggressive behaviors with their neighbors during the approach were less
321 likely to initiate flight, supporting the “distracted prey” hypothesis. In contrast, bird flight
322 initiation distance (FID) did not appear to vary depending on overall or relative local bird
323 density, nor was it affected by bird aggression or relative colony rank. Our results provide
324 limited evidence in support of a selfish herd effect or risk dilution effect in flightless colonial

325 penguins typically exposed to both land-based (giant petrels stalking the outskirts of the colony)
326 and airborne (brown skuas) predators.

327 To the best of our knowledge, no study has so far investigated all four of these
328 hypotheses simultaneously, especially not in incubating birds, although the “many-eyes” and
329 “dilution effect” hypotheses have been simultaneously studied using both mathematical models
330 (Fairbanks and Dobson 2007; Rieucou and Martin 2008; Beauchamp 2017) and field studies
331 (Boland 2003; Schmitt et al. 2014). For instance, in bighorn sheep (*Ovis canadensis*) foraging
332 ewes were found in predictive models to benefit from both the “many-eyes” and “dilution effect”
333 hypotheses as group size increased (Rieucou and Martin 2008). Similarly, emus (*Dromaius*
334 *novaehollandiae*) spent less time in vigilance in larger groups, detected approaching threats
335 sooner, and waited longer before initiating flight, supporting both the many-eyes and dilution
336 effect hypotheses (Boland 2003). In Columbian ground squirrels (*Urocitellus columbianus*) a
337 predator detection model was better supported than a dilution model (Fairbanks and Dobson
338 2007), and in plains zebras (*Equus quagga*), predator detection benefits were found to be more
339 influential in mixed-species groupings than dilution effects (Schmitt et al. 2014). Over 53
340 published studies, Beauchamp (2017) found the many-eyes and dilution effect hypothesis acted
341 together to reduce predation risk most often in species that form groupings. These studies serve
342 to emphasize the point that hypotheses in relation to group size on prey reactions to approaching
343 predators and other environmental (social) stimuli are not mutually exclusive and may frequently
344 work in concert (Roberts 1996). Yet, whereas the “many-eyes” and “dilution effect” hypotheses
345 have been considered together in past studies, the inclusion of the “distracted prey” or “selfish
346 herd” hypotheses in understanding prey reactions remains an open question. Although these
347 hypotheses have not been considered conjointly, all but the “distracted prey” hypothesis have

348 been tested individual in starlings, *Sturnus vulgaris* (Zoratto et al. 2009). They have been shown
349 in larger groups to decrease individual vigilance yet respond faster to the approach of a model
350 predator (“many-eyes”, Powell 1974), form larger flocks when predation risk is high (“dilution
351 effect”, Carere et al. 2009), and individuals show higher rates of vigilance and decreased
352 foraging rate when on the periphery of the group (“selfish herd”, Jennings and Evans 1980).
353 When considered alone, the “selfish herd” hypothesis has mixed support in the field (for
354 mathematical support see: Reluga and Viscido 2005; Morrell et al. 2011), with some studies
355 supporting individual risk minimization by selfish attraction to other members when under attack
356 (sheep, King et al. 2012; fish, Krause 1993; crabs, Viscido and Wetthey 2002), and other failing
357 to detect such effects (fish, Parrish 1989; birds, Sankey et al. 2021).

358 Of the four hypotheses (“many-eyes”, “dilution effect”, “selfish herd”, and “distracted
359 prey”), only the “many-eyes”, “selfish herd”, and “distracted prey” hypotheses imply changes in
360 vigilance effort. In the “many-eyes” hypothesis, larger and/or denser groupings contain more
361 individuals that can contribute to group-vigilance at any point in time, leading to an increase in
362 AD. Indeed, AD is expected to be longer when the focal individual is investing more into
363 vigilance behavior, surveying its surroundings, thus being able to detect approaching threats
364 sooner (Fernández-Juricic and Schroeder 2003; Beauchamp 2015; Uchida et al. 2019; Morelli et
365 al. 2019; but see Tätte et al. 2019). According to the “selfish herd” hypothesis, individuals in the
366 periphery who are less protected by conspecifics face the highest predation risk and should
367 therefore have the highest vigilance (hence highest AD). In contrast, the “distracted prey”
368 hypothesis predicts that external stimuli may distract from vigilance behavior, leading to shorter
369 AD. At low and medium colony densities, we observed that incubating adult king penguins show
370 a decrease in AD as relative local neighbor density increased supporting the “distracted prey”

371 hypothesis. However, at maximal colony density AD increased with relative local neighbor
372 density, consistent with the “many-eyes” hypothesis. Earlier in the breeding season (at low
373 colony density) king penguin breeding pairs establish their territories within the colony
374 (Stonehouse 1960; Weimerskirch et al. 1992). The social aggression that occurs during territory
375 establishment (Côté 2000) and the resulting colony instability at that time (Viblanç et al. 2014b)
376 may distract individual birds from surveying for predators. These results are consistent with
377 reports from other species. For instance, in a study that surveyed both a South American cichlid
378 fish, *Nannacara anomala*, and the willow warbler, *Phylloscopus trochilus*, male-male conflicts
379 reduced vigilance behavior and resulted in a delay of predator detection when shown the image
380 of a predator (Jakobsson et al. 1995) A similar result was found in another cichlid species,
381 *Neolamprologus pulcher* (Hess et al. 2016). Similarly, European robins, *Erithacus rubecula*,
382 were significantly slower to react to a stuffed sparrowhawk, *Accipiter nisus*, when engaged in
383 territorial defense (Dunn et al. 2004). Later in the breeding season (at maximum colony density),
384 king penguins are already settled into their territories and colony density is relatively stable
385 (Viblanç et al. 2014). At high density, the information about disturbances may disseminate
386 rapidly from neighbor to neighbor and may aid in searching for and detecting predators (a ripple
387 of disturbance is caused by entering the colony, which alerts neighboring individuals of
388 approaching threats, TLH, VAV, PB *pers. obs.*) (see also Hernández-Matías et al. 2003). Hence,
389 at low colony densities, the distraction hypothesis appears supported, but at high colony densities
390 the many eyes hypothesis is supported. Furthermore, those results may be amplified in concert
391 with predation pressure on the eggs of incubating king penguins which varies across the breeding
392 season. Indeed, previous studies show that predation pressure increases over the breeding season
393 (Descamps et al. 2005). With low predation pressure and low colony density at the start of the

394 breeding season, breeding king penguins may be more attentive to their social environment than
395 to predators. In contrast, with higher predation pressure later in the season when the colony is at
396 its peak density, breeders would shift their attention more towards predators and antipredator
397 responses than to their peers (Descamps et al. 2005).

398 In contrast to AD, bird flight initiation distance (FID) is expected to vary with the
399 “dilution effect”, “distracted prey” and “selfish herd” hypotheses. All hypotheses predict similar
400 responses in terms of FID. FID is the result of a decision-making process that occurs after a
401 predator is detected. On one hand, as the number of individuals within a group increases,
402 individual predation risk decreases, and therefore FID should be reduced (“dilution effect”
403 hypothesis). On the other hand, as the number of individuals increases, so does the number of
404 social distractions (e.g., aggression between neighbors), which in turn should distract the focal
405 individuals from performing the necessary decisions needed to initiate flight at an appropriate
406 time, causing FID to be delayed. In the “selfish herd” hypothesis, central positions face reduced
407 predation risk, and the colony is more densely packed, and should therefore have shorter FID.
408 Yet, FID was not impacted by relative local neighbor density, overall colony density, rank, or
409 aggression with neighbors in incubating king penguins, and therefore neither hypothesis
410 appeared to be strongly supported. One potential explanation to this result may have to do with
411 the cost of reproduction shaping optimal flight initiation distances (Cooper and Frederick 2007).
412 In king penguins, truly fleeing from an approaching predator means abandoning the egg/chick
413 and losing reproduction for the year. Most often, flight is attempted by slowly moving away with
414 the egg or young chick on top of the feet – an action that is obviously mechanically constrained.
415 In addition, even attempting to slowly move away with the egg or young chick may trigger
416 aggressive responses from neighboring conspecifics and increase the risk of injuries and damage

417 to the egg. Indeed, the commitment to reproduction is especially high in king penguins, as it
418 takes the cooperation of a breeding pair for over 14 months to raise a single chick, and successful
419 reproduction occurs at best every two years (Jiguet and Jouventin 1999). Thus, there may be
420 strong selection in this species for behaviors aimed at the early detection of approaching threats
421 and for active territory defense (Côté 2000) despite risks of injury, rather than fleeing altogether
422 from approaching predators, given the elevated fitness costs of abandoning reproduction. FID
423 may then be a relatively inflexible trait in breeding individuals of this species and therefore
424 dilution or distraction effects on this trait may be small. Our previous study found that FID and
425 the decision to flee were significantly repeatable, highlighting moderate to strong individual
426 components in incubating king penguins (Hammer et al. 2022). It is perhaps then not surprising
427 that personality traits were not significantly affected by the social environment, whereas AD, a
428 trait found to be highly flexible and lowly repeatable (Hammer et al. 2022), was.

429 We found that the decision to initiate flight in this species was significantly reduced when
430 the focal bird was engaged in social aggression with neighboring conspecifics, a result which
431 supports the “distracted prey” hypothesis. In this species, territorial defense of incubation and
432 brooding territories is high (Côté 2000), and the “distracted prey” hypothesis suggests that time
433 spent processing social cues and engaging in social interactions with conspecifics may
434 undermine the ability to perform anti-predator behaviors such as vigilance and flight (Chan et al.
435 2010). It appears that for king penguins, social aggression may be a strong distraction from the
436 ability to decide when to initiate flight. Although previous studies have not considered how
437 social aggression may affect individual responses to approaching predators, allogrooming
438 impala, *Aepyceros melampus*, had reduced vigilance rates and responded on average 4 seconds
439 later to a simulated predator than non-allogrooming individuals (Mooring and Hart 1995).

440 Anoles, *Anolis sagrei*, when presented with a conspecific tolerated closer approaches of a model
441 predator before initiating flight (Yee et al. 2013). Of particular interest is that territorial defense,
442 such is seen in king penguins, is particularly distracting for focal individuals (as discussed
443 above). For example, in a South American cichlid fish, *Nannacara anomala*, individuals engaged
444 in territorial mouth wrestling showed reduced vigilance, and chose low intensity behaviors such
445 as display and tail beating when in the presence of a model predator (Brick 1998).

446 Many studies have focused on prey behavioral responses to predators in the context of
447 foraging (Fernández et al. 2003; Randler 2005; Fairbanks and Dobson 2007; Rieucan and Martin
448 2008; Taraborelli 2008; Schmitt et al. 2014), urbanization (Chapman et al. 2012; Møller et al.
449 2015; Hall et al. 2020; Morelli et al. 2019), distance to refuges (Dill & Houtman 1989;
450 Bonenfant & Kramer 1996; Engelhardt et al. 2011; Morelli et al. 2022), or in relation to sexual
451 dimorphism (Møller et al. 2016, 2019; Kalb et al. 2019; Hensley et al. 2015; Samia et al. 2015).
452 In contrast, ours focused on the existence of a trade-off between vigilance and flight behavior
453 depending on the individual perceptions of the social and predatory environments in the context
454 of colonial breeding (Williams 1966). Colonial breeding in seabirds has mostly been suggested
455 to emerge as a consequence of the utilization of patchy and unpredictable marine food resources
456 and limited favorable breeding grounds (Clode 1993; Boulinier et al. 1996; Danchin and Wagner
457 1997; Boulinier et al. 2008). The role predation plays in its evolution, however, remains unclear
458 (Rolland et al. 1998). Several studies have reported antipredator benefits to colonial breeding, by
459 diminishing individual predation risk through dilution, predator-mobbing, or selfish herd effects
460 (Brown and Brown 1987; Picman et al. 2002; Hoogland and Sherman 2012). Our results are
461 consistent with apparent anti-predator benefits of colonial breeding which comes in the form of

462 shared vigilance and predator detectability, but that are traded-off with costs and loss of predator
463 detectability due to social distractions.

464 Although our present study provided little support for selfish herd effects in king
465 penguins, observations in the field show that birds subject to an experimental reduction in local
466 breeding density (by means of enclosure pens) cluster closer together rather than use the
467 available freed-up space (Viblanç 2011), consistent with the selfish herd notion of minimizing
468 individual predation risk. Clustering close to conspecifics combined with the high territorial and
469 aggressive behavior of king penguins (Côté 2000) results in producing a tightly woven network
470 or aggressive birds, making it hard for predators to land in the middle of the colony (TLH, PB,
471 BG, JPR, RG, VAV; personal observations). Of interest is the idea that breeding aggregations in
472 penguins result from a combination of self-organized dynamics related to predation risk (selfish
473 herd effects) and external forcing factors such as topographically limited possibilities of spatial
474 re-arrangement, for instance due to the retainment of nesting sites year after year (e.g., in Adélie
475 penguins, *Pygoscelis adeliae*, McDowall and Lynch 2019). This may result in trapping
476 individuals into suboptimal spatial arrangements, with strong edge effects (McDowall and Lynch
477 2019; Schmidt et al. 2021). King penguins incubate their single egg on their feet, hence, virtually
478 nothing is known on how closely individuals retain breeding sites year after year, nor whether
479 variation in individual's ability to maintain a breeding site may lead to a situation of entrapment
480 into suboptimal conditions. Future studies should aim at understanding how the “dilution effect”,
481 “many-eyes”, “selfish herd”, and “distracted prey” hypotheses are shaped not only by social and
482 predatory environments, but in interaction with local topography and individual quality. In
483 addition, nothing is known on how such interactions might be shaped by residual reproductive
484 value. For instance, studies in seabirds have found that older parents for which residual

485 reproductive value is low are less responsive to stressors (Heidinger et al. 2006, 2010, but see
486 Elliott et al. 2014). It would thus be of interest to understand how age and residual reproductive
487 values factor into affecting physiological stress responses in addition to behavior in shaping
488 antipredator decisions.

489 While overall colony density increases as the breeding season progresses, reproductive
490 investment of the breeding individuals also changes with advancing breeding season. Two
491 factors might affect the responses of incubating birds sampled early or late in the breeding
492 season. First, birds that entered reproduction early in the season come nearer to hatching as the
493 breeding season progresses, and hence reproductive investment should increase. It is likely that,
494 as reproductive investment increases, protecting the investment (i.e., deciding to not flee, or to
495 flee later from an approaching threat) may weigh more heavily on anti-predator behavior (Clark
496 and Ydenberg 1990). Second, birds sampled later in the season may be late breeding birds just
497 starting their incubation. Late breeders in king penguins rarely, if ever, succeed, as chicks are
498 most likely to die before or over winter (Stonehouse 1960; Weimerskirch et al. 1992; Stier et al.
499 2014). In turn, the lower value of reproduction later in the season may render individuals less
500 willing to defend their brood and more likely to flee. Unfortunately, not knowing the incubation
501 stage of birds in our study, we were unable to differentiate responses under those different
502 scenarios. Thus, future studies are needed to specifically test if anti-predator responses are linked
503 to reproductive value and breeding advancement in the king penguin as found in other species
504 (Albrecht & Klvana 2004; Osiejuk & Kuczynski 2007; see also Dowling & Bonier 2018). While
505 we did not see a change in FID or a change in the probability of initiating flight as the breeding
506 season progressed, there remains a link between reproductive success, brood investment, and risk
507 assessment in later breeding birds that needs to be explored in more depth. For instance, focusing

508 on physiological stress responses (e.g., heart rate known to vary with advancing breeding season;
509 Viblanc et al. 2015) in addition to behavioral responses to approaching predators may yield some
510 valuable information (Viblanc et al. 2015).

511 To conclude, our study found that the “many-eyes” hypothesis was supported at
512 maximum colony density, while the “distracted prey” hypothesis was supported at lower colony
513 densities in incubating king penguins. In addition, focal birds that were engaged in social
514 aggression with neighboring conspecifics were less likely to initiate flight. We found little
515 support for the “selfish herd” hypothesis based on bird centrality in the colony, and no evidence
516 that the dilution effect was strongly influential. These results show that prey behavioral decisions
517 towards approaching threats are complex, and likely explained by a mix of mutually non-
518 exclusive hypotheses. Future studies on prey reactions to predators should consider testing for
519 joint effects of environmental and social factors in understanding risk-benefit assessments in
520 wild animals.

521

522 **ACKNOWLEDGEMENTS**

523 This work was supported by the French Polar Institute (IPEV) through the IPEV 119
524 ECONERGY polar program, and by the French National Center for Scientific Research (CNRS).
525 TLH was supported by a PhD scholarship from the Initiative d’excellence (IdEX),
526 Investissements d’Avenir, Ministère de l’Enseignement Supérieur, de la Recherche et de
527 l’Innovation. We are grateful to the Terres Australes et Antarctiques Françaises (TAAF) for
528 providing logistic support in the field, and to the field personnel and field assistants for providing

529 help and support along the way. We wish to thank to anonymous reviewers for helpful
530 suggestions on a previous version of this paper.

531

532 **LITERATURE CITED**

533 Albrecht T, Klvana P. 2004. Nest crypsis, reproductive value of a clutch and escape decisions in
534 incubating female mallards *Anas platyrhynchos*. *Ethology* 110: 603–613.

535 Alexander RD. 1974. The evolution of social behaviour. *Annu Rev Ecol Syst.* 5:325–383.
536 doi:10.1111/eth.13212.

537 Barbraud C, Delord K, Bost CA, Chaigne A, Marteau C, Weimerskirch H. 2020. Population
538 trends of penguins in the French Southern Territories. *Polar Biol.* 43(7):835–850.
539 doi:10.1007/s00300-020-02691-6.

540 Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using
541 lme4. *J Stat Softw.* 67(1):1–48. doi:10.18637/jss.v067.i01.

542 Beale CM, Monaghan P. 2004. Human disturbance: People as predation-free predators? *J Appl*
543 *Ecol.* 41:335–343. doi:10.1111/j.0021-8901.2004.00900.x.

544 Beauchamp G. 2015. Vigilance, alarm calling, pursuit deterrence, and predator inspection. In:
545 Cooper WE, Blumstein DT, editors. *Escaping from predators: an integrative view of escape*
546 *decisions*. Cambridge: Cambridge University Press. p. 265–286.

547 Beauchamp G. 2017. Disentangling the various mechanisms that account for the decline in
548 vigilance with group size. *Behav Processes.* 136:59–63. doi:10.1016/j.beproc.2017.01.014.

549 Bednekoff PA, Lima SL. 1998. Re-examining safety in numbers: Interactions between risk
550 dilution and collective detection depend upon predator targeting behaviour. Proc R Soc B Biol
551 Sci. 265:2021–2026. doi:10.1098/rspb.1998.0535.

552 Bednekoff PA, Ritter R. 1994. Vigilance in Nxai Pan springbok, *Antidorcas marsupialis*.
553 Behaviour. 129(1–2):1–11.

554 Blumstein DT. 2003. Flight-initiation distance in birds is dependent on intruder starting distance.
555 J Wildl Manage. 67(4):852–857.

556 Blumstein DT. 2010. Flush early and avoid the rush: a general rule of antipredator behavior?
557 Behav Ecol. 21(3):440–442. doi:10.1093/beheco/arq030.

558 Boland CRJ. 2003. An experimental test of predator detection rates using groups of free-living
559 emus. Ethology. 109:209–222.

560 Bonenfant M, Kramer DL. 1996. The influence of distance to burrow on flight initiation distance
561 in the woodchuck, *Marmota monax*. Behav Ecol, 7(3): 299-303.

562 Boulinier T, Danchin E, Monnat J-Y, Doutrelant C, Cadiou B. 1996. Timing of prospecting and
563 the value of information in a colonial breeding bird. J Avian Biol. 27(3):252.
564 doi:10.2307/3677230.

565 Boulinier T, McCoy KD, Yoccoz NG, Gasparini J, Tveraa T. 2008. Public information affects
566 breeding dispersal in a colonial bird: Kittiwakes cue on neighbours. Biol Lett. 4:538–540.
567 doi:10.1098/rsbl.2008.0291.

568 Brick O. 1998. Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara*
569 *anomala*. Anim Behav. 56:309–317. doi:10.1006/anbe.1998.0782.

570 Brown CR, Brown MB. 1987. Group-living in cliff swallows as an advantage in avoiding
571 predators. *Behav Ecol Sociobiol.* 21(2):97–107. doi:10.1007/BF02395437.

572 Burger J, Gochfeld M. 1991. Human distance and birds: tolerance and response distances of
573 resident and migrant species in India. *Environ Conserv.* 18(2):158–165.
574 doi:10.1017/S0376892900021743.

575 Burger J, Gochfeld M. 1994. Vigilance in African mammals: differences among mothers, other
576 females, and males. *Behaviour.* 131(3–4):153–169. doi:10.1163/156853994X00415.

577 Caraco T, Martindale S, Pulliam HR. 1980. Avian flocking in the presence of a predator. *Nature.*
578 285(5):400–401.

579 Carere C, Montanino S, Moreschini F, Zoratto F, Chiarotti F, Santucci D, Alleva E. 2009. Aerial
580 flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. *Anim*
581 *Behav.* 77:101–107. doi:10.1016/j.anbehav.2008.08.034.

582 Chan AAYH, Giraldo-Perez P, Smith S, Blumstein DT. 2010. Anthropogenic noise affects risk
583 assessment and attention: The distracted prey hypothesis. *Biol Lett.* 6:458–461.
584 doi:10.1098/rsbl.2009.1081.

585 Chapman T, Rymer T, Pillay N. (2012). Behavioural correlates of urbanisation in the Cape
586 ground squirrel *Xerus inauris*. *Naturwissenschaften*, 99: 893-902.

587 Clark CW, Ydenberg RC. 1990. The risks of parenthood. I. General theory and applications.
588 *Evol Ecol.* 4:21–34. doi:10.1007/BF02270712.

589 Clode D. 1993. Colonially breeding seabirds: predators or prey? *Trends Ecol Evol.* 8(9):336–
590 338. doi:10.1016/0169-5347(93)90242-H.

591 Cooper WE, Frederick WG. 2007. Optimal flight initiation distance. *J Theor Biol.* 244:59–67.
592 doi:10.1016/j.jtbi.2006.07.011.

593 Côté SD. 2000. Aggressiveness in king penguins in relation to reproductive status and territory
594 location. *Anim Behav.* 59:813–821. doi:10.1006/anbe.1999.1384.

595 Cresswell W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*.
596 *Anim Behav.* 47:433–442. doi:10.1006/anbe.1994.1057.

597 Danchin E, Wagner RH. 1997. The evolution of coloniality: the emergence of new perspectives.
598 *Trends Ecol Evol.* 12(9):342–347. doi:10.1016/S0169-5347(97)01124-5.

599 Dehn MM. 1990. Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol.*
600 26:337–342.

601 Delignette-Muller ML, Dutang C. 2015. fitdistrplus: An R package for fitting distributions. *J Stat*
602 *Softw.* 64(4):1–34. doi:10.18637/jss.v064.i04.

603 Descamps S, Gauthier-Clerc M, Le Bohec C, Gendner JP, Le Maho Y. 2005. Impact of predation
604 on king penguin *Aptenodytes patagonicus* in Crozet Archipelago. *Polar Biol.* 28(4):303–310.
605 doi:10.1007/s00300-004-0684-3.

606 Dias RI. 2006. Effects of position and flock size on vigilance and foraging behaviour of the
607 scaled dove *Columbina squammata*. *Behav Processes.* 73:248–252.
608 doi:10.1016/j.beproc.2006.06.002.

609 Dill LM, Houtman R. 1989. The influence of distance to refuge on flight initiation distance in the
610 gray squirrel (*Sciurus carolinensis*). *Can J Zool.* 67(1): 233-235.

611 Dowling L, Bonier F. 2018. Should I stay, or should I go: Modeling optimal flight initiation
612 distance in nesting birds. *PloS one*, 13(11): e0208210

613 Duca C, Brunelli WA, Doherty PF. 2019. Predator search image and the dilution effect: when is
614 the best time to nest? *Auk*. 136:1–7. doi:10.1093/auk/ukz009.

615 Dumont F, Pasquaretta C, Réale D, Bogliani G, von Hardenberg A. 2012. Flight initiation
616 distance and starting distance: biological effect or mathematical artefact? *Ethology*. 118:1051–
617 1062. doi:10.1111/eth.12006.

618 Dunn M, Copelston M, Workman L. 2004. Trade-offs and seasonal variation in territorial
619 defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis (Lond 1859)*.
620 146:77–84. doi:10.1111/j.1474-919X.2004.00221.x.

621 Elliott KH, O'Reilly KM, Hatch SA, Gaston AJ, Hare JF, Anderson WG. 2014. The prudent
622 parent meets old age: a high stress response in very old seabirds supports the terminal restraint
623 hypothesis. *Horm Behav*. 66:828–837. doi:10.1016/j.yhbeh.2014.11.001.

624 Engelhardt SC, Weladji RB. 2011. Effects of levels of human exposure on flight initiation
625 distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can J*
626 *Zool*, 89(9): 823-830.

627 Fairbanks B, Dobson FS. 2007. Mechanisms of the group-size effect on vigilance in Columbian
628 ground squirrels: dilution versus detection. *Anim Behav*. 73:115–123.
629 doi:10.1016/j.anbehav.2006.07.002.

630 Fernández-Juricic E, Schroeder N. 2003. Do variations in scanning behavior affect tolerance to
631 human disturbance? *Appl Anim Behav Sci*. 84(3):219–234. doi:10.1016/j.applanim.2003.08.004.

632 Fernández GJ, Capurro AF, Reboreda JC. 2003. Effect of group size on individual and collective
633 vigilance in greater rheas. *Ethology*. 109:413–425. doi:10.1046/j.1439-0310.2003.00887.x.

634 Fleming PA, Bateman PW. 2017. Scavenging opportunities modulate escape responses over a
635 small geographic scale. *Ethology*. 123:205–212. doi:10.1111/eth.12587.

636 Frid A, Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv
637 Ecol*. 6(1):11. doi:10.1016/S0723-2020(86)80016-9.

638 Frommen JG, Hiermes M, Bakker TCM. 2009. Disentangling the effects of group size and
639 density on shoaling decisions of three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol
640 Sociobiol*. 63:1141–1148. doi:10.1007/s00265-009-0767-9.

641 Hall MJ, Burns AL, Martin JM, Hochuli DF. 2020. Flight initiation distance changes across
642 landscapes and habitats in a successful urban coloniser. *Urban Ecosystems*, 23: 785-791.

643 Hamilton WD. 1971. Geometry for the selfish herd. *J Theor Biol*. 31:295–311.

644 Hammer TL, Bize P, Saraux C, Gineste B, Robin J, Groscolas R, Viblanc VA. 2022.
645 Repeatability of alert and flight initiation distances in king penguins: effects of colony, approach
646 speed, and weather. *Ethology*. 00:1–14. doi:10.1111/eth.13264.

647 Harts AMF, Kristensen NP, Kokko H. 2016. Predation can select for later and more synchronous
648 arrival times in migrating species. *Oikos*. 125(10):1528–1538. doi:10.1111/oik.02973.

649 Hebblewhite M, Pletscher DH. 2002. Effects of elk group size on predation by wolves. *Can J
650 Zool*. 80:800–809. doi:10.1139/z02-059.

651 Van Heezik Y, Seddon PJ. 1990. Effect of human disturbance on beach groups of jackass
652 penguins. *South African J Wildl Res*. 20(3):89–93.

653 Heidinger BJ, Chastel O, Nisbet ICT, Ketterson ED. 2010. Mellowing with age: older parents are
654 less responsive to a stressor in a long-lived seabird. *Funct Ecol.* 24:1037–1044.
655 doi:10.1111/j.1365-2435.2010.01733.x.

656 Heidinger BJ, Nisbet ICT, Ketterson ED. 2006. Older parents are less responsive to a stressor in
657 a long-lived seabird: a mechanism for increased reproductive performance with age? *Proc R Soc*
658 *B Biol Sci.* 273(1598):2227–2231. doi:10.1098/rspb.2006.3557.

659 Hensley NM, Drury JP, Garland Jr T, Blumstein DT. 2015. Vivid birds do not initiate flight
660 sooner despite their potential conspicuousness. *Curr. Zool.*, 61(4): 773-780.

661 Hernández-Matías A, Jover L, Ruiz X. 2003. Predation on common tern eggs in relation to sub-
662 colony size, nest aggregation and breeding synchrony. *Waterbirds.* 26(3):280–289.
663 doi:10.1675/1524-4695(2003)026[0280:POCTEI]2.0.CO;2.

664 Hess S, Fischer S, Taborsky B. 2016. Territorial aggression reduces vigilance but increases
665 aggression towards predators in a cooperatively breeding fish. *Anim Behav.* 113:229–235.
666 doi:10.1016/j.anbehav.2016.01.008. <http://dx.doi.org/10.1016/j.anbehav.2016.01.008>.

667 Hoogland JL. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs
668 (Sciuridae: *Cynomys Leucurus* and *C. Ludovicianus*). *Ecology.* 62:252–272.

669 Hoogland JL, Sherman PW. 2012. Advantages and disadvantages of bank swallow (*Riparia*
670 *riparia*) coloniality. *Ecol Monogr.* 46:33–58.

671 Hunter S. 1991. The impact of avian predator scavengers on king penguin *Aptenodytes*
672 *patagonicus* chicks at Marion Island. *Ibis (Lond 1859).* 133(4):343–350.

673 Jakobsson S, Brick O, Kullberg C. 1995. Escalated fighting behaviour incurs increased predation
674 risk. *Anim Behav.* 49:235–239. doi:10.1016/0003-3472(95)80172-3.

675 Jennings T, Evans SM. 1980. Influence of position in the flock and flock size on vigilance in the
676 starling, *Sturnus vulgaris*. *Anim Behav.* 28:634–635. doi:10.1016/S0003-3472(80)80071-6.

677 Jiguet F, Jouventin P. 1999. Individual breeding decisions and long-term reproductive strategy in
678 the King Penguin *Aptenodytes patagonicus*. *Ibis (Lond 1859)*. 141:428–433. doi:10.1111/j.1474-
679 919x.1999.tb04411.x.

680 Kalb N, Anger F, Randler C. 2019. Flight initiation distance and escape behavior in the black
681 redstart (*Phoenicurus ochruros*). *Ethology*, 125(7): 430-438.

682 King AJ, Wilson AM, Wilshin SD, Lowe J, Haddadi H, Hailes S, Morton AJ. 2012. Selfish-herd
683 behaviour of sheep under threat. *Curr Biol.* 22(14):R561–R562. doi:10.1016/j.cub.2012.05.008.
684 <http://dx.doi.org/10.1016/j.cub.2012.05.008>.

685 Krause J. 1993. the effect of “Schreckstoff” on the shoaling behaviour of the minnow: a test of
686 Hamilton’s selfish herd theory. *Anim Behav.* 45:1019–1024.

687 Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest Package: Tests in Linear Mixed
688 Effects Models. *J Stat Softw.* 82(13):1–26. doi:10.18637/jss.v082.i13.

689 Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and
690 prospectus. *Can J Zool.* 68:619–640. doi:10.1139/z90-092.

691 Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Anim*
692 *Behav*, 49(1): 11-20.

693 Mayer M, Natusch D, Frank S. 2019. Water body type and group size affect the flight initiation
694 distance of European waterbirds. *PLoS One*. 14(7):e0219845.
695 doi:10.1371/journal.pone.0219845.

696 McDowall PS, Lynch HJ. 2019. When the “selfish herd” becomes the “frozen herd”: spatial
697 dynamics and population persistence in a colonial seabird. *Ecology*. 100(10):e02823.
698 doi:10.1002/ecy.2823.

699 Mikula P, Díaz M, Albrecht T, Jokimäki J, Kaisanlahti-Jokimäki M-L, Kroitero G, Møller AP,
700 Tryjanowski P, Yosef R, Hromada M. 2018. Adjusting risk-taking to the annual cycle of long-
701 distance migratory birds. *Scientific Reports* 8:13989. doi: 10.1038/s41598-018-32252-1.

702 Møller AP, Tryjanowski P, Díaz M, Kwieciński Z, Indykiewicz P, Mitrus C, Goławski A
703 Polakowski M. 2015. Urban habitats and feeders both contribute to flight initiation distance
704 reduction in birds. *Behav Ecol*, 26(3): 861-865.

705 Møller AP, Liang W, Samia, DS. 2019. Flight initiation distance, color and camouflage. *Curr*
706 *Zool*, 65(5): 535-540.

707 Møller AP, Samia DS, Weston MA, Guay PJ, Blumstein, DT. 2016. Flight initiation distances in
708 relation to sexual dichromatism and body size in birds from three continents. *Biol J Linn*
709 *Soc*, 117(4): 823-831.

710 Morelli F, Benedetti Y, Díaz M, Grim T, Ibáñez- Álamo JD, Jokimäki J, Kaisanlahti-Jokimäki
711 M-J, Tätte K, Markó G, Jiang Y, Tryjanowski P, Møller, AP. 2019. Contagious fear: Escape
712 behavior increases with flock size in European gregarious birds. *Ecology and evolution*, 9(10):
713 6096-6104. Doi:10.1002/ece3.5193

714 Morelli F, Mikula P, Blumstein DT, Díaz M, Markó G, Jokimäki J, Kaisanlahti-Jokimäki M-J,
715 Floigl K, Abou Zeid Z, Siretckaia A, Benedetti Y. (2022). Flight initiation distance and refuge
716 in urban birds. *Sci Tot Env*, 842: 156939.

717 Mooring MS, Hart BL. 1995. Costs of allogrooming in impala: distraction from vigilance. *Anim*
718 *Behav.* 49:1414–1416. doi:10.1006/anbe.1995.0175.

719 Morrell LJ, Ruxton GD, James R. 2011. Spatial positioning in the selfish herd. *Behav Ecol.*
720 22:16–22. doi:10.1093/beheco/arq157.

721 Morton TL, Haefner JW, Nugala V, Decino RD, Mendes L. 1994. The selfish herd revisited: do
722 simple movement rules reduce relative predation risk? *J Theor Biol.* 167:73–79.
723 doi:10.1006/jtbi.1994.1051.

724 Osiejuk TS, Kuczynski L. 2007. Factors affecting flushing distance in incubating female greylag
725 geese *Anser anser*. *Wildl. Biol.* 13: 11–18.

726 Parrish JK. 1989. Re-examining the selfish herd: are central fish safer? *Anim Behav.*
727 38(6):1048–1053. doi:10.1016/S0003-3472(89)80143-5.

728 Petrelli AR, Levenhagen MJ, Wardle R, Barber JR, Francis CD. 2017. First to flush: the effects
729 of ambient noise on songbird flight initiation distances and implications for human experiences
730 with nature. *Front Ecol Evol.* 5:67. doi:10.3389/fevo.2017.00067.

731 Picman J, Pribil S, Isabelle A. 2002. Antipredation value of colonial nesting in yellow-headed
732 blackbirds. *Auk.* 119(2):461–472. doi:10.2307/4089892.

733 Powell GVN. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus*
734 *vulgaris*) in relation to predation and foraging. *Anim Behav.* 22:501–505. doi:10.1016/S0003-
735 3472(74)80049-7.

736 Pulliam HR. 1973. On the advantages of flocking. *J Theor Biol.* 38:419–422. doi:10.1016/0022-
737 5193(73)90184-7.

738 Quenette PY. 1990. Functions of vigilance behaviour in mammals: a review. *Acta Oecologica.*
739 11(6):801–818.

740 Quinn JL, Cresswell W. 2006. Testing domains of danger in the selfish herd: sparrowhawks
741 target widely spaced redshanks in flocks. *Proc R Soc B Biol Sci.* 273:2521–2526.
742 doi:10.1098/rspb.2006.3612.

743 R Development Core Team. 2021. A language and environment for statistical computing. R
744 Found Stat Comput.

745 Randler C. 2005. Vigilance during preening in coots *Fulica atra*. *Ethology.* 111:169–178.
746 doi:10.1111/j.1439-0310.2004.01050.x.

747 Rayor LS, Uetz GW. 1990. Trade-offs in foraging success and predation risk with spatial
748 position in colonial spiders. *Behav Ecol Sociobiol.* 27:77–85. doi:10.1007/BF00168449.

749 Reluga TC, Viscido S. 2005. Simulated evolution of selfish herd behavior. *J Theor Biol.*
750 234(2):213–225. doi:10.1016/j.jtbi.2004.11.035.

751 Rieucan G, Martin JGA. 2008. Many eyes or many ewes: vigilance tactics in female bighorn
752 sheep *Ovis canadensis* vary according to reproductive status. *Oikos.* 117:501–506.
753 doi:10.1111/j.2007.0030-1299.16274x.

754 Roberts G. 1996. Why individual vigilance declines as group size increases. *Anim Behav.*
755 51:1077–1086. doi:10.1006/anbe.1996.0109.

756 Rolland C, Danchin E, De Fraipont M. 1998. The evolution of coloniality in birds in relation to
757 food, habitat, predation, and life-history traits: a comparative analysis. *Am Nat.* 151(6):514–529.
758 doi:10.1086/286137.

759 Roos S, Smart J, Gibbons DW, Wilson JD. 2018. A review of predation as a limiting factor for
760 bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol Rev.* 93(4):1915–
761 1937. doi:10.1111/brv.12426.

762 Sankey DWE, Storms RF, Musters RJ, Russell TW, Hemelrijk CK, Portugal SJ. 2021. Absence
763 of “selfish herd” dynamics in bird flocks under threat. *Curr Biol.* 31(14):3192-3198.e7.
764 doi:10.1016/j.cub.2021.05.009. <https://doi.org/10.1016/j.cub.2021.05.009>.

765 Samia DS, Møller AP, Blumstein DT, Stankowich T, Cooper Jr, WE. 2015. Sex differences in
766 lizard escape decisions vary with latitude, but not sexual dimorphism. *Proc Roy Soc B: Biol*
767 *Sci.* 282(1805): 20150050.

768 Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients.
769 *Methods Ecol Evol.* 1:103–113. doi:10.1111/j.2041-210x.2010.00012.x.

770 Schmidt AE, Ballard G, Lescroël A, Dugger KM, Jongsomjit D, Elrod ML, Ainley DG. 2021.
771 The influence of subcolony-scale nesting habitat on the reproductive success of Adélie penguins.
772 *Sci Rep.* 11:1–15. doi:10.1038/s41598-021-94861-7. [https://doi.org/10.1038/s41598-021-94861-](https://doi.org/10.1038/s41598-021-94861-7)
773 7.

774 Schmitt MH, Stears K, Wilmers CC, Shrader AM. 2014. Determining the relative importance of
775 dilution and detection for zebra foraging in mixed-species herds. *Anim Behav.* 96:151–158.
776 doi:10.1016/j.anbehav.2014.08.012. <http://dx.doi.org/10.1016/j.anbehav.2014.08.012>.

777 Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk
778 assessment. *Proc R Soc B Biol Sci.* 272:2627–2634. doi:10.1098/rspb.2005.3251.

779 Stier A, Viblanc VA, Massemin-Challet S, Handrich Y, Zahn S, Rojas ER, Saraux C, Le Vaillant
780 M, Prud'homme O, Grosbellet E, et al. 2014. Starting with a handicap: phenotypic differences
781 between early- and late-born king penguin chicks and their survival correlates. *Funct Ecol.*
782 28:601–611. doi:10.1111/1365-2435.12204.

783 Stonehouse B. 1960. The king penguin *Aptenodytes patagonica* of South Georgia. Falklands
784 Islands Dependencies Survey. Scientific Reports No. 23.

785 Taraborelli P. 2008. Vigilance and foraging behaviour in a social desert rodent, *Microcavia*
786 *australis* (rodentia caviidae). *Ethol Ecol Evol.* 20:245–256.
787 doi:10.1080/08927014.2008.9522524.

788 Tätte K, Ibáñez-Álamo JD, Markó G, Mänd R, Møller AP. 2019. Antipredator function of
789 vigilance re-examined: vigilant birds delay escape. *Anim Behav.* 156:97–110.
790 doi:10.1016/j.anbehav.2019.08.010.

791 Treves A. 2000. Theory and method in studies of vigilance and aggregation. *Anim Behav.*
792 60:711–722. doi:10.1006/anbe.2000.1528.

793 Uchida K, Suzuki KK, Shimamoto T, Yanagawa H, Koizumi I. 2019. Decreased vigilance or
794 habituation to humans? Mechanisms on increased boldness in urban animals. *Behav Ecol.*
795 30(6):1583–1590. doi:10.1093/beheco/arz117.

796 Viblanc VA. 2011. Coping with energy limitation, social constraints and stress in a colonial
797 breeder, the king penguin (*Aptenodytes patagonicus*). PhD Thesis. University of Strasbourg.

798 Viblanc VA, Gineste B, Stier A, Robin J.P., Groscolas, R. 2014a. Stress hormones in relation to
799 breeding status and territory location in colonial king penguin: a role for social density?
800 *Oecologia.* 175:763–772. doi:10.1007/s00442-014-2942-6.

801 Viblanc VA, Saraux C, Malosse N, Groscolas R. 2014b. Energetic adjustments in freely
802 breeding-fasting king penguins: does colony density matter? *Funct Ecol.* 28:621–631.
803 doi:10.1111/1365-2435.12212.

804 Viblanc VA, Smith AD, Gineste B, Groscolas R. 2012. Coping with continuous human
805 disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC*
806 *Ecol.* 12(10):1–11. doi:10.1186/1472-6785-12-10.

807 Viblanc VA, Smith AD, Gineste B, Kauffmann M, Groscolas R. 2015. Modulation of heart rate
808 response to acute stressors throughout the breeding season in the king penguin *Aptenodytes*
809 *patagonicus*. *J Exp Biol.* 218:1686–1692. doi:10.1242/jeb.112003.

810 Viera VM, Viblanc VA, Filippi-Codaccioni O, Côté SD, Groscolas R. 2011. Active territory
811 defence at a low energy cost in a colonial seabird. *Anim Behav.* 82:69–76.
812 doi:10.1016/j.anbehav.2011.04.001. <http://dx.doi.org/10.1016/j.anbehav.2011.04.001>.

813 Viscido S V., Miller M, Wethey DS. 2001. The response of a selfish herd to an attack from
814 outside the group perimeter. *J Theor Biol.* 208(3):315–328. doi:10.1006/jtbi.2000.2221.

815 Viscido S V., Wethey DS. 2002. Quantitative analysis of fiddler crab flock movement: evidence
816 for “selfish herd” behaviour. *Anim Behav.* 63(4):735–741. doi:10.1006/anbe.2001.1935.

817 Webster MM, Rutz C. 2020. How STRANGE are your study animals? *Nature.* 582:337–340.

818 Weimerskirch H, Stahl JC, Jouventin P. 1992. The breeding biology and population dynamics of
819 King Penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis (Lond 1859).* 134:107–117.
820 doi:10.1111/j.1474-919X.1992.tb08387.x.

821 Wiklund CG, Andersson M. 1994. Natural selection of colony size in a passerine bird. *J Anim*
822 *Ecol.* 63:765–774. doi:10.2307/5254.

823 Williams GC. 1966. Natural selection, the costs of reproduction, and a refinement of Lack’s
824 principle. *Am Nat.* 100(916):687–690.

825 Ydenberg RC, Dill LM. 1986. The economics of fleeing from predators. *Adv Study Behav.*
826 16:229–249. doi:10.1016/S0065-3454(08)60192-8.

827 Yee J, Lee J, Desowitz A, Blumstein DT. 2013. The costs of conspecifics: are social distractions
828 or environmental distractions more salient? *Ethology.* 119:480–488. doi:10.1111/eth.12085.

829 Zoratto F, Santucci D, Alleva E. 2009. Theories commonly adopted to explain the antipredatory
830 benefits of the group life: The case of starling (*Sturnus vulgaris*). *Rend Lincei.* 20:163–176.
831 doi:10.1007/s12210-009-0042-z.

832 Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common
833 statistical problems. *Methods Ecol Evol.* 1:3–14. doi:10.1111/j.2041-210x.2009.00001.x.

834 **FIGURE CAPTIONS**

835 **Figure 1. The linear relationship of colony density and relative local neighbour density in**
836 **incubating king penguins (*Aptenodytes patagonicus*).** Significant differences are distinguished
837 using the letters a, b, c, d. Dots represent the relative local density values; the horizontal bar
838 represents the median, shading represents the interquartile range, and the vertical line represents
839 the 95% confidence interval.

840

841 **Figure 2. Variables affecting Alert Distance (AD) in incubating king penguins (*Aptenodytes***
842 ***patagonicus*).** A) Standardized linear mixed model estimates (z-scores) and 95% confidence
843 intervals for the effects of the number of aggressions with conspecifics, relative local neighbour
844 density, colony density (low, medium, high, and maximal), and the interaction between relative
845 local neighbour density and colony density (n = 194 observations).

846

847 **Figure 3. The significant effect of the interaction between relative local neighbour density**
848 **(number of birds/m²) and colony density (low, medium, high, and max) on Alert Distance**
849 **(AD) is depicted in incubating king penguins (*Aptenodytes patagonicus*).** Dots represent the
850 raw AD values (n = 194 observations); shading represents the 95% confidence interval predicted
851 from the model while holding other variables in the model constant.

852

853 **Figure 4. Variables affected the probability of initiating flight in incubating king penguins**
854 **(*Aptenodytes patagonicus*).** A) A generalized linear mixed model depicting the decision to flee

855 (binomial; 0 = no flight initiated, 1 = flight initiated). Odds ratios and 95% confidence intervals
856 for the number of aggressions with conspecifics during the approach, relative local neighbour
857 density, and colony density (low, medium, high, and maximum) (n = 193 observations). B) The
858 significant predicted effect between the probability to initiate flight (binomial; 0 = no flight
859 initiated, 1 = flight initiated), and the number of aggressions during the approach against
860 neighbouring individuals by the focal individual. Shading represents the 95% confidence interval
861 predicted from the model while holding other variables in the model constant.

862

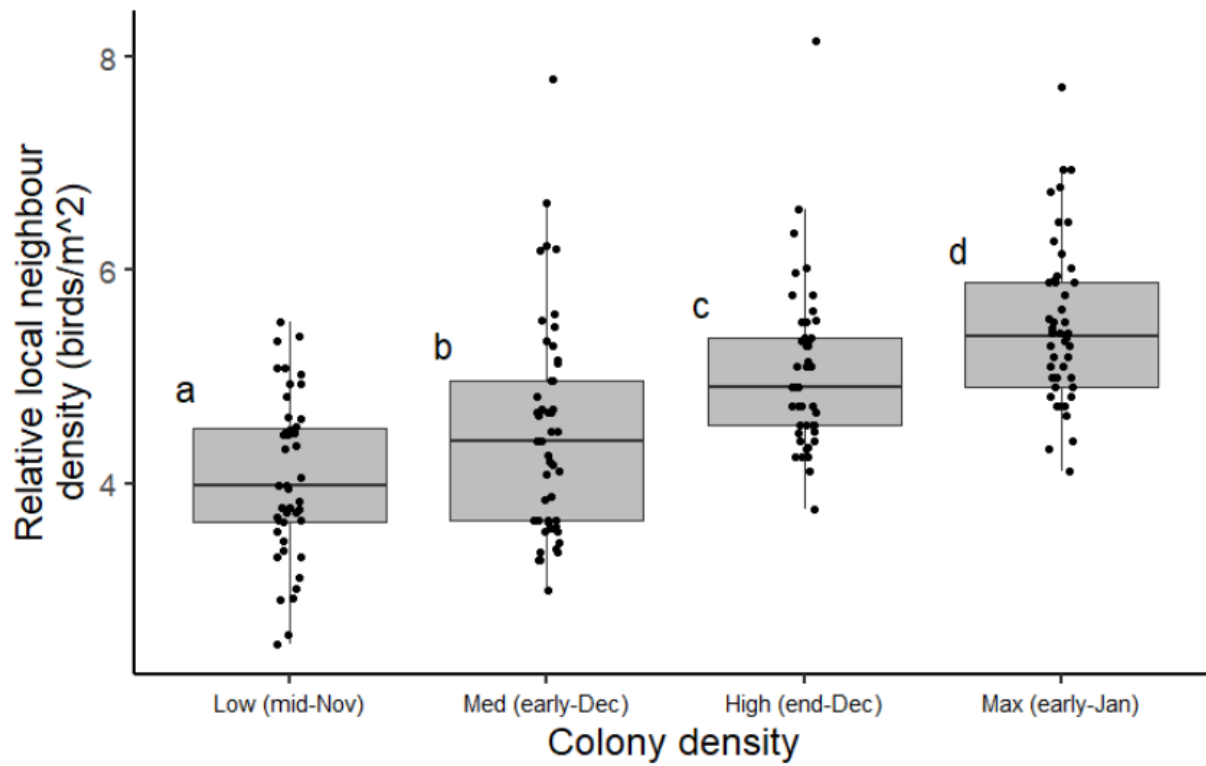
863 **Figure 5. Variables affecting Flight Initiation Distance (FID) in incubating king penguins**
864 **(*Aptenodytes patagonicus*).** A) Standardized linear mixed model estimates (z-scores) and 95%
865 confidence intervals for the effects of the number of aggressions against conspecifics, relative
866 local neighbour density, and colony density (low, medium, high, and maximum) (n = 93
867 observations). B) The significant predicted effect of approach speed on log FID is depicted. Dots
868 represent log FID values; shading represents the 95% confidence interval predicted from the
869 model while holding other variables in the model constant.

870

871

	Hypothesis	Predictions	References
1	Many eyes hypothesis	Alert distance should occur earlier in larger or denser groupings, as more vigilant individuals are present to raise an alarm	Pulliam 1973; Lima and Dill 1990; Lima 1995
2	Dilution hypothesis	Flight initiation distance should be delayed at high social density, as individual predation risk is reduced	Pulliam 1973; Alexander 1974; Ydenberg and Dill 1986; Lima and Dill 1990
3	Selfish herd hypothesis	Alert and flight initiation distances should be higher when individuals are in the periphery of a group, as predation risk is higher than in the center	Hamilton 1971
4	Distracted prey hypothesis	Alert and/or flight initiation distances should be delayed in denser groups, as increased stimuli (e.g. noise) may hijack finite attention resources and hinder predator detection. The distracted prey hypothesis was originally proposed for distractions of anthropogenic origin, but can be extended to any kind of distraction.	Chan et al. 2010; Petrelli et al. 2017

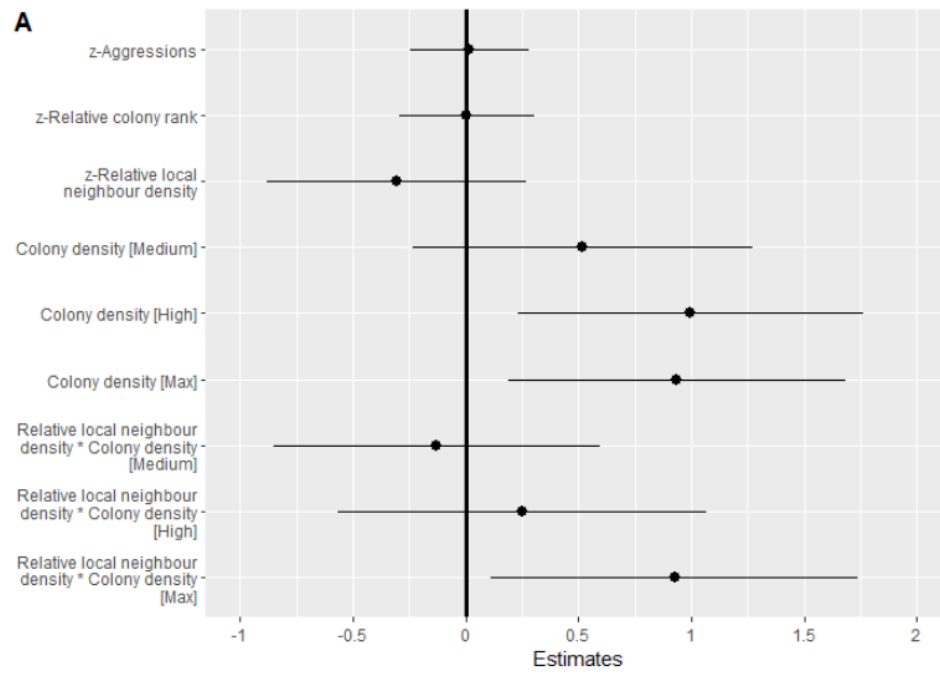
875 **Table 1.** Description of the four main hypotheses proposed to explain the effects of group size,
876 social density and social interactions on antipredator behavior measured by alert and flight
877 initiation distances. Note that these hypotheses are not mutually-exclusive.



879

880 Fig 1.

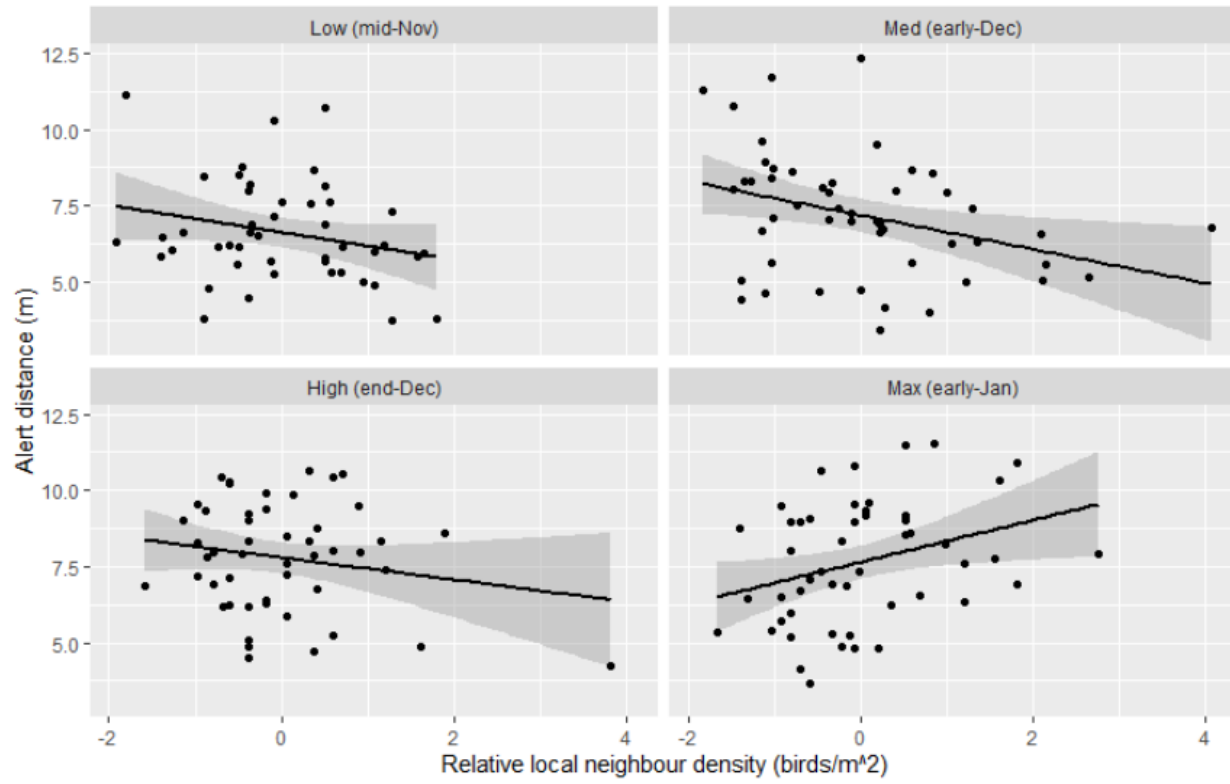
881



882

883 **Fig 2.**

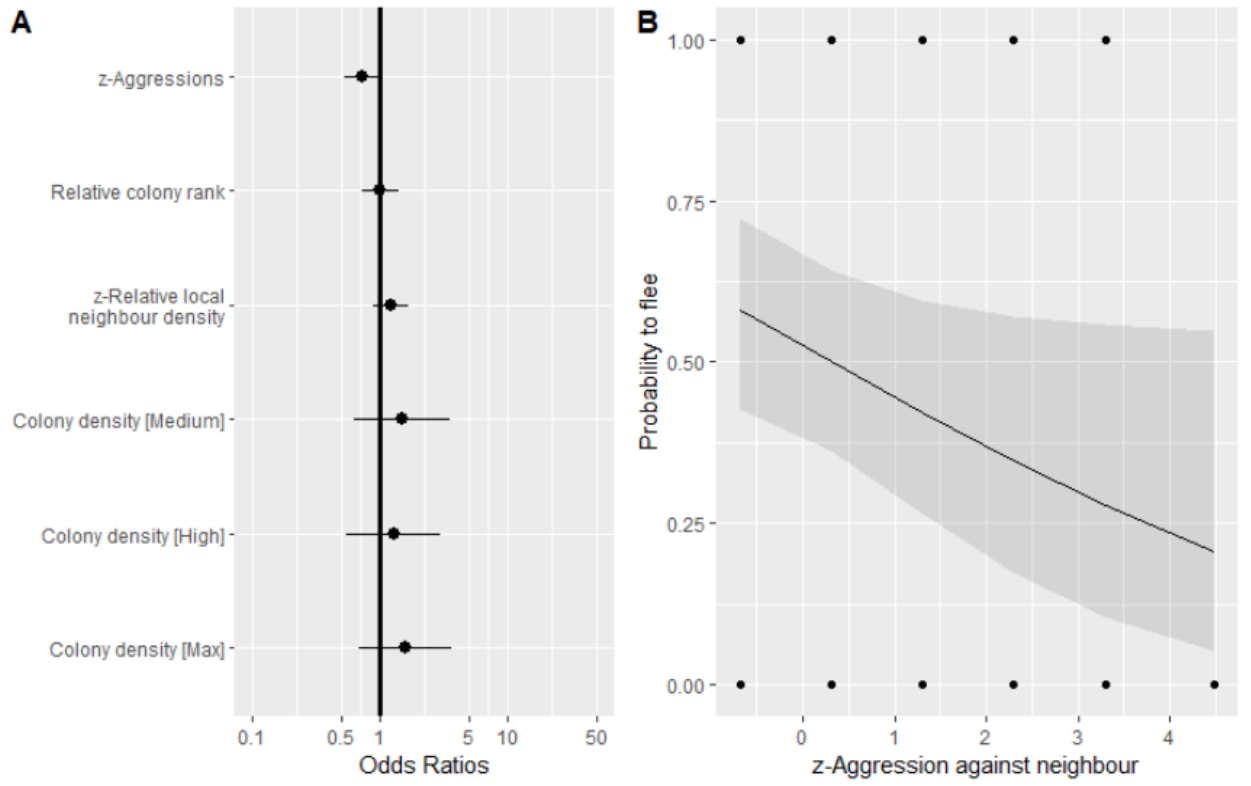
884



885

886 **Fig 3.**

887

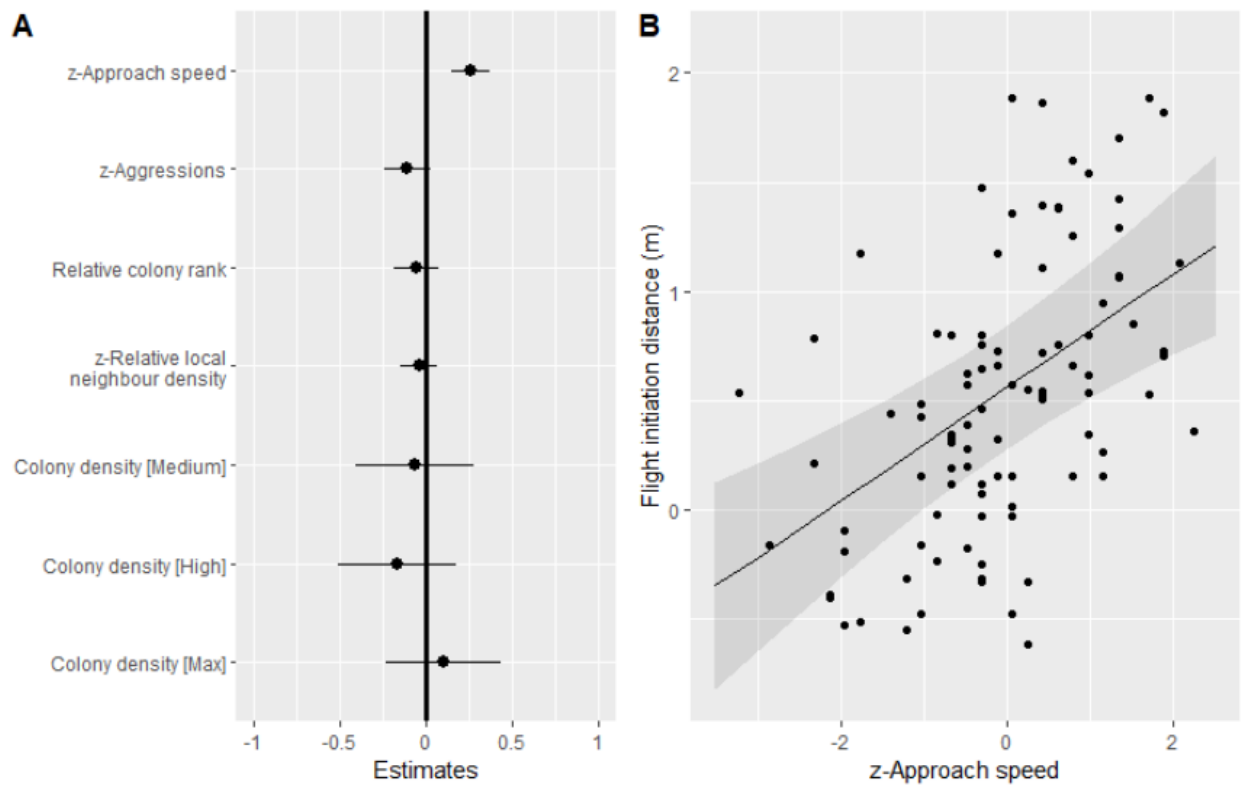


888

889 **Fig 4.**

890

891



892

893 **Fig 5.**

894