1 A matter of life and death – Hunting tactics of Southern

2 elephant seals *(Mirounga leonina)* and anti-predatory

3 behaviours of their prey

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10 **Running page head**

11 Elephant seals hunting tactics

12 Abstract

13 For air-breathing marine predators that must save energy during dives, the ability to

14 adopt hunting tactics that minimise the risk of triggering an escape reaction from the

15 prey is crucial for an efficient foraging. Female Southern elephant seals *(Mirounga*

16 *leonina,* SES hereafter) forage on small mesopelagic prey that they must hunt almost

17 continuously to meet their high-energy requirements. Here we aimed at understanding

18 how these large time-limited deep-divers can efficiently exploit their small sized prey.

19 To do so, we used data recorded by a new biologger, the sonar tag, deployed on SES

20 during their post-breeding foraging trips. This tag combines an active acoustic sensor

21 with ultra-high-resolution movement and bioluminescence sensors, offering a unique

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22   opportunity to simultaneously describe SES' hunting tactics to capture their prey and

23   defence mechanisms employed by prey. We analysed more than 5,800 prey capture

24   events in nine SES and show that they adopt a "stalking" hunting behaviour allowing

25   them to get as close as possible to their prey before attacking. The ability of SES to

26   adopt stealth approach tactics, minimising the risk of initiating a flight reaction from

27   their prey, might be a key factor in the success of this far-ranging generalist predator.

28   **Keywords**

31   1. INTRODUCTION

32   Predator-prey interactions play a key role in ecosystem structure and functioning.

33   While predators shape prey population dynamics (i.e., survival, growth, behaviour,

34   etc.), prey availability and accessibility regulate predator populations (Estes & Duggins

35   1995, Frederiksen et al. 2006, Letnic et al. 2012). Fine-scale interactions between

36   predators and their prey, i.e., how predators find, select, and capture their prey, and

37   alternatively how prey detect predators, and react to imminent predation, are key

38   factors in determining both predators' hunting efficiency and prey survival (Cooper Jr

39   1997, McHenry et al. 2009, Stewart et al. 2013). On one hand, to avoid capture, prey

40   can flee, fight back or stay still depending on hunting tactics of their predators, distance

41   from their predators, and accessibility to a shelter (Broom & Ruxton 2005, Eilam 2005).

42   On the other hand, predators must adopt hunting tactics that increases their chances

43   of successful capture while avoiding excessive energy expenditure. This is particularly

44   true for air-breathing marine predators, which are limited by oxygen availability and

45   must regularly return to the surface to breathe (Thompson 1993). For these predators,

46 active chase must be avoided in order to preserve oxygen reserves and increase time

47 spent diving and searching for prey. Therefore, the ability of air-breathing predators to

48 adopt hunting tactics that limit the risk of triggering an escape reaction from the prey is

49 crucial for an efficient foraging.

50 Studying fine-scale predator-prey interactions in the marine environment is particularly

51 challenging. Development of animal-borne biologging technologies advanced the

52 study of deep-diving animal foraging behaviour. GPS sensors for example can help

53 identifying the foraging areas of marine animals (e.g. (Hindell et al. 1991, Sommerfeld

54 et al. 2015, Reisinger et al. 2018)), whereas high-resolution head-mounted

55 accelerometers allow the detection of foraging events by measuring rapid head

56 movements potentially associated with prey capture attempts (Suzuki et al. 2009,

57 Viviant et al. 2010, Guinet et al. 2014, Ydesen et al. 2014). Accelerometers also record

58 the movements and postures of animals, providing a fine-scale description of their

59 hunting behaviour (e.g. (Johnson et al. 2008, Shepard et al. 2008, Jouma'a et al. 2016,

60 2017, Le Bras et al. 2016, 2017). Diet analyses (i.e. stomach contents, scat analyses,

61 stable isotopes analyses, genetic markers) provide an overview of prey consumed

62 during foraging trips (e.g. (Cherel et al. 2008, Jeanniard-du-Dot et al. 2017)) but fine-

63 scale information on prey size and behaviour is still challenging to obtain. Recently

64 developed miniature video cameras have provided the first direct information on prey

65 and predator-prey interactions (Adachi et al. (2021), Naito et al. (2013), Yoshino et al.

66 (2020) on Northern elephant seals *(Mirounga angustirostris)*, Bowen et al. (2002) on

67 harbour seals *(Phoca vitulina)*, Kernaléguen et al. (2016) on Australian fur seals

68 *(Arctocephalus pusillus doriferus)*, Davis et al. (1999) on Weddell seals *(Leptonychotes*

69 *weddellii)*).

70 Miniature cameras deployed on Northern elephant seals provided unique and novel

71 information on prey targeted by female elephant seals (Naito et al. 2013, Yoshino et

72 al. 2020, Adachi et al. 2021). As suggested by isotopic analyses (Cherel et al. 2008),

73 video footages confirmed that females mainly target myctophid species, and to a lesser

74 extent mesopelagic squids. Small size of prey relative to the large size of females

75 implies that they must feed continuously to meet their high-energy requirements. This

76 raises the question of how these large time-limited deep-divers can efficiently exploit

77 these small prey. Cameras require a light-source to illuminate dark waters where

78 elephant seals roam, which could potentially alter both predator and prey behaviour.

79 Moreover, high power consumption means these devices can only record selectively,

80 for relatively short periods, during multi-month foraging trips. Therefore, extensive

81 deployments are lacking and the way elephant seals can efficiently exploit their tiny

82 prey is still poorly known. In order to have a more complete and detailed picture on

83 predator-prey interactions in deep-diving predators such as elephant seals, we used a

84 miniature sonar tag, combining active acoustic signals with high-resolution movement

85 sensors. This tag uses a high-click rate narrow, forward directed beam that can insonify

86 prey at a distance up to 6 m in front of the animal. Even if data recorded by the tag do

87 not allow for the identification of the species of prey targeted by seals, it provides

88 information on their acoustic size – a proxy for actual size – gregarious and escape

89 behaviours (Goulet et al. 2019). Including high-resolution movement sensors, the tag

90 offer the opportunity to study the hunting tactics of seals and more generally fine-scale

91 predator-prey interactions. A more recent version of the sonar tag also include a high-

92 resolution bioluminescence sensor to study bioluminescent behaviour of prey,

93 especially how they might emit light flashes to defend themselves against predators

94 (Goulet et al. 2020) by temporarily dazzling predators and using the opportunity to

95   escape. Therefore, data recorded by this tag will enable the investigation of questions

96   raised by the results obtained with the camera deployments.

97   Previous sonar tag deployments on Southern elephant seals demonstrated that seals

98   have surprisingly a strong sensory advantage over their prey, allowing them to detect

99   prey several seconds before striking, well before they react (Chevallay et al. in

100   revision). As Northern elephant seals, they target small mesopelagic prey, which they

101   have to hunt continuously to meet their energy requirements. As they are constrained

102   to return to the surface to breathe, they must be efficient during their time-limited

103   hunting periods. Therefore, we hypothesised that the ability of Southern elephant seals

104   to detect their prey in a distance enabled them to adopt stealth approach tactics to

105   minimise the risk of initiating a flight reaction from their prey, therefore avoiding energy-

106   expensive chase. To test that hypothesis, we took advantage of data recorded by the

107   sonar tag to describe the hunting sequence of elephant seals and to describe the prey

108   defence mechanisms to see how it influences the seals' capture success.

109   2. MATERIALS AND METHODS

110   2.1.   Device deployments and data collection

111   Data were collected on 9 post-breeding female Southern elephant seals in October

112   2018 (n = 3), October 2019 (n = 3) and October 2020 (n = 3), in Kerguelen Islands

113   (49°20'S – 70°26'E). Females were captured with a canvas head-bag, anaesthetized

114   with a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100 – 0.7 to 0.8 ml/100

115   kg) either injected intravenously (McMahon et al. 2000) or using a deported

116   intramuscular injection system. Females were measured to the nearest centimetre and

117   weighted to the nearest kilogram. They were equipped with a neck-mounted Argos tag

118   (SPOT-293 Wildlife Computers, 72x54x24 mm, 119 g in air), a back-mounted CTD tag

119   (SMRU-SRDL, 115x100x40 mm, 680 g in air) and either a head-mounted DTAG-4

120   sonar tag (n = 7, 95x55x37 mm, 200 g in air, see Goulet et al. (2019) for further details

121   on the device) or a DTAG-4 sonar-light tag (n = 2, 92x69x37 mm, 250 g in air). Tags

122   were glued to the fur using quick-setting epoxy glue (Araldite AW 2101, Ciba). CTD

123   tags recorded conductivity, temperature and depth at 0.5 Hz. Sonar and sonar-light

124   tags were programmed to sample GPS position (up to every minute), tri-axial

125   acceleration (200 Hz), tri-axial magnetometer (50 Hz) and pressure (50 Hz). Sonar-

126   light tags also integrated a light sensor specifically designed to sample

127   bioluminescence events with a sampling frequency of 50 Hz (Goulet et al. 2020). The

128   active sonar within the tags recorded acoustic backscatter returning from 10 µs pings

129   with a centre frequency of 1.5 MHz, at a 25 Hz ping rate for 2018 and 2019

130   deployments and 12.5 Hz for 2020 deployments. The active sonar operated with a 3.4°

131   aperture beam width and a 6 m range (Goulet et al. 2019). Tags were recovered in late

132   December to January when females returned to shore to moult using the same capture

133   and sedation methods. All experiments were conducted under the ethical regulation

134   approval of the French Ethical Committee for Animal Experimentations

135   (2019070612143224 (#21375)) and the Committee for Polar Environment.

136   2.2.   Data analyses

137   Data recovered from tags were analysed using custom-written codes and functions

138   from www.animaltags.org in MATLAB version 2022b (The MathWorks 2022).

139   Statistical analyses were conducted in R software version 3.5.1 (R Core Team 2018).

140   *Prey capture attempts identification*

141   Prey capture attempts (PrCAs hereafter) were detected from the 200 Hz tri-axial

142   acceleration data recorded by the sonar tags, by computing the norm of the differential

143   of the tri-axial acceleration (norm-jerk hereafter), as described in Goulet et al.

144   (submitted). Spikes in the norm-jerk higher than 400 m.s^{-2} were classified as PrCAs.

145   As prey may be encountered in patches or may elude capture, leading to a bout

146   structure in prey strikes, strikes occurring less than 15 s from the previous strike were

147   grouped in the same bout as described by Goulet et al. (submitted).

148   *Sonar data analysis*

149   Sonar data recorded during bouts were displayed as echograms, showing the time on

150   the horizontal axis and the distance from the sonar tag on the vertical axis, extending

151   from 10 s before the bout start time to 2 s after the bout end. Because of the large

152   number of bouts detected (ranging from 4595 to 12039 per animal), only a random

153   subsample of 5 to 10% of bouts performed during acoustic data recordings were

154   analysed. Different variables describing predator-prey interactions were extracted

155   manually from echograms following the method described by Goulet et al. (submitted):

156   (1) number of prey, (2) prey evasive behaviour, (3) prey acoustic size, (4) capture

157   success. (1) The number of prey was defined as the maximum number of independent

158   echo traces within a same ping (Jones et al. 2008). It was scored as one, two or more

159   than two, i.e. a school of prey. (2) Prey evasive behaviour was identified from the

160   closing speed between predator and prey, which will vary in case of prey reaction,

161   resulting in a change in the slope of the prey echo trace (Goulet et al. 2019, Vance et

162   al. 2021). If a prey reaction was observed during the bout, prey was considered as

163   evasive. (3) Prey acoustic size was estimated from the -20 dB echo pulse width

164   measured on the widest part of the prey trace on evasive prey only (Burwen et al.

165   2003). Finally, (4) when prey trace was seen within 50 cm of the sonar transducer

166   within the last second of the bout, capture was considered successful. If prey trace

167   was seen further than 1 m away from the sonar transducer during the last second of

168   the bout or was evident after the bout ended, bout was classified as unsuccessful. All

169   other cases were classified as "unknown" (Goulet et al. submitted).

170   *Bioluminescence data analysis*

171   Bioluminescent flashes were detected as spikes in the 50 Hz light data recorded by

172   the sonar-light tags decimated at a 5 Hz sampling rate. Spikes in the data higher than

173   0.07 (arbitrary unit) were classified as flashes (Goulet et al. 2020). Events detected

174   within less than 5 s of each other were considered coming from the same

175   bioluminescence event (Goulet et al. 2020). If a bioluminescence event started

176   between 5 s before and 5 s after the bout, it was considered associated with the bout.

177   Flash events may consist of a series of short flashes, so the 5 Hz data may not have

178   sufficient resolution to accurately describe them. Therefore, we used 50 Hz light data

179   recorded during flash events to calculate the number of peaks in the light signal as well

180   as the intensity and duration of each peak.

181   *Predator approach behaviour*

182   Metrics describing seals' fine-scale behaviour during the approach and capture phase

183   (i.e. between the 10 s preceding each first strike of a bout (Chevallay et al. in revision)

184   and the last strike of the bout) were extracted from the 200 Hz tri-axial accelerometer

185   data decimated at 5 Hz. Posture of seals was inferred from Euler angles (i.e. pitch

186   angle (rotation around left-right axis), roll angle (rotation around longitudinal axis) and

187   heading angle (rotation around dorso-ventral axis)) (see Johnson and Tyack (2003) for

188   details of the formulas). Bouts were characterised in term of duration (time elapsed

189   during the first and last head strike of the bout) and intensity, defined as the RMS of

190   the norm-jerk signal during the bout. To know whether seals actively swam or passively

191   glided when hunting, we determined the number of flipper strokes between the 10 s

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192 preceding each bout and the last strike of the bout. Flipper strokes were detected from

193 dynamic acceleration of the lateral axis (Sato et al. 2007) by applying a high-pass filter

194 with a cut-off frequency of 0.6 Hz, i.e. 70% of the dominant stroke frequency, on the

195 lateral acceleration (Chevallay et al. in revision). Finally, the swimming effort, a proxy

196 of energy expenditure during swimming, was defined as the summed absolute values

197 of the filtered lateral acceleration (Maresh et al. 2004, Aoki et al. 2012). Seals are

198 usually negatively buoyant in the first week of the post-breeding foraging trips (Biuw et

199 al. 2003) and therefore in the period sampled by the sonar tags. Seals are thus

200 expected to glide when descending and swim actively when ascending. To avoid

201 conflating these two distinct movement styles when analysing hunting tactics, bouts

202 were grouped according to the vertical movement prior to each bout. Bouts with an

203 initial depth-rate higher than 0.25 m/s and lower than -0.25 m/s were grouped as,

204 respectively, descending and ascending bouts (Chevallay et al. in revision).

205 An exploratory analysis of seals' hunting tactics was first conducted on a sub-sample

206 of bouts by making a 3D animation of seals' behaviour during the approach phase.

207 This exploratory analysis identified three main approach modes, which differed in bout

208 duration, swimming effort, roll and heading ranges. Therefore, a K-means algorithm

209 with 3 clusters was applied on these behavioural metrics for ascending and descending

210 bouts separately. Each resulting cluster was described in terms of bout duration, bout

211 intensity, swimming behaviour and posture.

212 ## 2.3.   Statistical analyses

213 Approach behaviour between prey types were compared using generalized linear

214 mixed models (GLMM hereafter, R package 'MASS', (Ripley et al. 2013)) with gamma

215 distribution, with bout duration (s), bout intensity (m.s^{-2}), number of flipper strokes,

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216 swimming effort (m.s^{-2}), pitch, roll or heading angle extent (°) as response variables,

217 and prey type (schooling vs. single prey; single evasive prey vs. single non-evasive

218 prey) as fixed effect. Individual seal identities were used as random effects.

219 Influence of prey evasive behaviour on the likelihood of adopting an approach mode

220 was tested using mixed effects logistic regression, with approach mode (either high or

221 low-energy approach) as a binary response variable, flight initiation distance (m) as

222 fixed effect, and individual identities as random effects.

223 The impact of prey reaction on seals' capture success was modelled using mixed-

224 effect logistic regression models with capture success as a binary response variable

225 (scored as 1 or 0), reaction type (flash or escape attempt) or timing of reaction as fixed

226 effects and individual identities as random effects.

227 Finally, the effect of prey characteristics on capture difficulty was tested using GLMM

228 with gamma distribution with the bout duration, the number of head strokes and

229 swimming effort (proxies of prey capture difficulty, (Goulet 2020)) as response

230 variables, and acoustic size or flight initiation distance as fixed effects. Individual seal

231 identities were used as random effects.

232 For all models, assumptions were checked and any deviation from them were

233 corrected.

3. RESULTS

235 Tags recorded data during 29-79 days. Over that period, seals performed 69 ± 7 dives

236 per day (mean ± sd, min 57 dives per day, max 79 dives per day), and 510 ± 53 bouts

237 per day (range 443-610 bouts per day). Seals performed dives at 413 ± 89 m depth

238 (mean ± sd) for 19 ± 3 min, and spent 10 ± 2 min at the bottom of the dive. A diel diving

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239   pattern was observed for almost all individuals, with deeper and longer dives during

240   the day (449 ± 187 m, 21 ± 4 min) than at night (329 ± 70 m, 16 ± 1 min, LMM, P <

241   0.001).

3.1. Prey characteristics

243   Prey characteristics were inferred from sonar data during 5778 bouts for the nine

244   females equipped with sonar tags between 2018 and 2020. Single prey represented

245   99.2 ± 0.4% of prey targeted by our studied seals. Among single prey, 81.4 ± 8.1%

246   tried to escape (Table 1). For the two females equipped with sonar-light tags, flashing

247   prey represented 24.3 and 29.5% of their targeted prey. Acoustic size of prey ranged

248   from 5.0 to 9.0 cm (1st and 3rd quantiles, Q1-Q3 hereafter) (min 1.6 cm, max 32.8 cm,

249   Figure 1). We applied a mixture model to the distribution of prey acoustic sizes (R

250   package mixtools (Benaglia et al. 2010)), and identified three size groups (Figure 1):

251   small prey measuring 3 to 6 cm (4.3 ± 1.0 cm), medium-sized prey measuring 6 to 11

252   cm (7.6 ± 2.0 cm), and large prey measuring more than 11 cm and up to 35 cm (11.8

253   ± 4.1 cm).

3.2. Predator hunting behaviour

255   Gliding behaviour preceded 91% and 60% of descending and ascending bouts, with a

256   stop of active stroking 6.7 ± 1.4 s and 5.5 ± 1.6 s before the first strike of the bout

257   (Figure 2). Then, depending on prey behaviour, seals displayed three hunting modes:

258   low-energy mode, associated to non-evasive prey, high-energy mode, associated to

259   evasive prey, and sinuous mode, associated to schooling prey. Low-energy mode was

260   the most frequent in both descents (62% of bouts) and ascents (67% of bouts). Sinuous

261   mode was observed for 27% and 21% of descending and ascending bouts, and high-

262 energy mode was the least frequent mode, observed for only 11% and 12% of

263 descending and ascending bouts.

264 Low-energy modes were characterised by short bouts of 1 to 3 (Q1-Q3) intense head

265 strikes (406.5 ± 246.5 m.s^{-2}, Figure 3) lasting 0.3 to 3.7 s (Q1-Q3), and low swimming

266 efforts (37.2 ± 30.2 m.s^{-2}, Figure 3). High-energy modes were characterised by long

267 bouts of 4 to 12 (Q1-Q3) low intensity head strikes (287.7 ± 107.8 m.s^{-2}) usually lasting

268 5.0 to 20.2 s (Q1-Q3) and up to 36.6 s (90th percentile, Figure 2). This mode is

269 associated with the highest values of swimming effort (99.5 ± 83.7 m.s^{-2}), especially

270 during ascents (Figure 2). The probability of adopting low or high-energy hunting mode

271 depended on prey evasive behaviour: the greater the flight initiation distance (FID

272 hereafter), the greater the probability of adopting a high-energy hunting mode (mixed-

273 effects logistic regression, $P < 0.001$, Figure 2). Prey that reacted sooner were

274 associated with longer bouts (LMM, $P < 0.001$): bout duration (s) = (9.8 ± 2.0) + ($8.9 \pm$

275 0.7) * FID (m)) with a higher number of head strikes (LMM, $P < 0.001$, number of head

276 strikes = (6.4 ± 1.0) + (4.8 ± 0.3) * FID (m)) and a higher swimming effort (LMM, $P <$

277 0.001, swimming effort (m.s^{-2}) = (64.9 ± 10.2) + (41.5 ± 4.1) * FID (m)). Finally,

278 schooling prey were associated with sinuous approaches, characterised by the highest

279 values of roll and heading extent, short bouts of 1 to 3 intense head strikes ($435.3 \pm$

280 288.4 m.s^{-2}) lasting 0.3 to 10.0 s (Q1-Q3), and low swimming efforts (55.2 ± 73.9 m.s^{-}

281 ^{2}, Figures 2 and 3).

282 3.3. Prey anti-predatory behaviours

283 Anti-predatory behaviours of elephant seals' prey were studied on 1047 bouts for which

284 data on both evasive and flashing behaviours were available. Escape attempt was the

285 most frequent defence mechanism, detected in 59% of prey, while 19% of prey did not

286   show any reaction, 17% of prey flashed and tried to escape, and 5% only flashed. Prey

287   initiated flight reaction 2.4 ± 2.4 s (Q1-Q3: 3.5 – 0.4 s) before the first strike of the bout,

288   at 0.7 ± 0.4 m (Q1-Q3: 0.5 – 0.9 m) from seals. Prey flashed 1.9 ± 1.5 s (Q1-Q3: 3.3 –

289   0.5 s) before the first strike of the bout. Flash events usually lasted 1.7 ± 3.0 s (Q1-Q3:

290   0.2-1.6 s), as a series of 2 ± 2 flashes (Q1-Q3: 1-3 flashes) of 0.17 ± 0.24 s each (Q1-

291   Q3: 0.04-0.19 s) and of 0.18 ± 0.15 intensity (Q1-Q3: 0.10-0.18).

292   3.4.   Impact of prey behaviour on seals' capture success

293   We estimated prey capture success at 99% when prey did not react to the seals'

294   approach. Capture success was not significantly different between prey that tried to

295   escape and flashed (95%) and prey that only tried to escape (92%) (mixed-effect

296   logistic regression, P = 0.9999). On the opposite, when prey tried to escape, probability

297   of successful capture was 7% lower than when prey did not react (capture success =

298   92%, mixed-effects logistic regression, P < 0.001). The greater the flight initiation

299   distance, the lower the probability of seals successfully capturing the prey (mixed-

300   effects logistic regression, P < 0.001, Figure 4).

4. DISCUSSION

302   We used high-resolution bioluminescence and movement sensors combined with

303   active acoustics to study the functional relationships between Southern elephant seals

304   and their prey. Sonar tag recordings provided novel information on characteristics

305   (acoustic size) and fine-scale behaviour of prey targeted by seals. Tagged Southern

306   elephant seal females from Kerguelen Islands mostly targeted small, isolated prey,

307   while schools were almost never encountered. Prey acoustic size ranged between 4

308   and 10 cm, which is consistent with sizes of the main Southern elephant seals prey

309   species (Cherel et al. 2008, Guinet et al. 2014), i.e. *Electrona antarctica* 3-10 cm, *E.*

310   *carlsbergi* 4-10 cm and *Krefftichthys anderssoni* 1-8 cm (Collins et al. 2008), although

311   it is important to remember that acoustic and physical sizes are not necessarily similar.

312   Indeed, prey orientation has a strong influence on the measures of acoustic size

313   (Burwen et al. 2003): if a prey is oriented perpendicular to the beam, its acoustic size

314   reflects its width, while if it is oriented parallel to the beam, its acoustic size reflects its

315   length. When prey tries to escape, it will at some point likely be oriented along the

316   beam axis, so measuring the maximum length of given prey trace provides a strong

317   indication of the true prey size. A small but meaningful proportion of prey were 10 to

318   20 cm (up to 35 cm) in acoustic size. these prey sizes could correspond to other

319   abundant myctophid species in Kerguelen waters, such as *Gymnoscopelus braueri* or

320   *G. nicholsi*, up to 13 and 19 cm in length respectively. Finally, targets larger than 20

321   cm could be consistent with squids, species occasionally found in elephant seals' diet

322   (i.e. *Martialia hyadesi* and *Todarodes filippovae* that measure up to 40 and 55 cm

323   respectively (Cherel et al. 2008)). Further studies are needed to understand horizontal

324   and vertical distributions of these different-sized prey in relation to environmental

325   conditions.

326   High-resolution movement sensors integrated in the sonar tags also allowed us to

327   describe the hunting sequence of free-ranging Southern elephant seals. Seals

328   consistently started their approach by gliding towards their prey about 6 s before the

329   capture. This is consistent with results from Chevallay et al. (in revision) that showed

330   that elephant seals usually detect their prey between 6 and 10 s before the strike. Prey

331   usually reacted one to two seconds before the seals' capture, by trying to escape or

332   by emitting a bioluminescent flash. If prey did not respond, they were captured in a few

333   short head strikes. Larger prey likely need longer handling times and thus longer head

334   movements (Bowen et al. 2002, Hocking et al. 2016), as already observed by Goulet

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335   et al. (submitted) in Southern elephant seals, but also in Australian fur seals

336   *(Arctocephalus pusillus doriferus*, (Hocking et al. 2016)), sub-Antarctic fur seals

337   (*Arctocephalus tropicalis*, (Hocking et al. 2016)) and Northern elephant seals

338   (*Mirounga angustirostris,* (Adachi et al. 2019)) where the number of acceleration peaks

339   correlated with prey size. If prey tried to escape, seals responded by pursuing them for

340   several seconds, performing series of low intensity head movements before managing

341   to capture their prey in more than 90% of the cases. Therefore, our results show that

342   prey behaviour influences the predator's hunting tactics. These approach phases

343   characterised by bursts of acceleration to capture mobile prey and deceleration to

344   capture inactive prey were also observed in other aquatic top predators such as Adelie

345   penguins (*Pygoscelis adeliae*, (Wilson et al. 2002)) or Baikal seals (*Pusa sibirica*,

346   (Watanabe et al. 2004)). We observed these hunting modes similarly in descents and

347   ascents, which confirms prey-dependant behaviours in seals, rather than a

348   consequence of the prevailing movement direction.

349   *Predator approach tactics: how to stay stealthy?*

350   Seals usually stopped swimming several seconds before striking, as described by

351   Chevallay et al. (in revision). This type of approach resembles stalking observed in

352   terrestrial carnivorous species such as lions *(Panthera leo)*, pumas *(Puma concolor)*,

353   or tigers *(Panthera tigris)* (Elliott et al. 1977, Sunquist 1981, Van Orsdol 1984). Stalking

354   is defined as a slow approach without noisy body movements, allowing the predator to

355   get very close to their prey without alerting it (Curio 2012). This kind of approach is

356   usually observed in predators for which the costs of prey pursuit are high, as in sperm

357   whales for example that are known to stop swimming before initiating a pursuit (Aoki

358   et al. 2012). Elephant seals are hypometabolic predators performing long and deep

359   dives to feed. Consequently, active hunting with long prey pursuit could result in shorter

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360   dives, as dive duration at a given depth decreases with increasing swimming effort

361   (Génin et al. 2015). It may thus be advantageous to adopt a discreet approach that

362   limits the risks of triggering prey escape.

363   Fish can detect bow waves produced by an approaching predator through their lateral

364   lines (Blaxter & Fuiman 1990, McHenry et al. 2009, Stewart et al. 2013), a series of

365   small mechanoreceptors located under their skins. Therefore, by adopting a slow

366   approach, the mechanical disturbance generated by the forward movements of seals

367   may be considerably reduced, lowering the risk of being detected by prey. Gliding

368   before the strike was consistently observed during descending bouts. As seals are

369   usually negatively buoyant through most, if not all the duration of their post-breeding

370   foraging trip, they are likely to glide on descents, so they may take advantage of their

371   inertia to approach their prey discreetly. However, gliding was also observed for 60%

372   of strikes in ascending bouts, where seals usually swim actively. This suggests that

373   gliding is a deliberate manoeuvre adopted by seals and not only dictated by gravity

374   forces. The importance of slow approach to delay prey detection was highlighted in

375   many terrestrial and aquatic species (e.g. in desert iguanas *(Dipsosaurus dorsalis)*

376   (Cooper Jr 2003), in skinks *(Eumeces laticeps)* (Cooper Jr 1997), in Atlantic cods

377   *(Gadus morhua)* (Meager et al. 2006), and teleost fish (Webb 1984)).

378   A meaningful proportion of prey (26%) showed no evidence of reaction to the seals'

379   approach. While the proportion of non-evasive prey may be overestimated due to the

380   narrowness of the sonar beam (i.e. prey may have reacted outside the beam), the

381   systematic late prey reaction supports the hypothesis that gliding behaviour may be

382   used by seals to delay prey reaction, which may explain their very high capture

383   success. The ontogeny of how seals acquire this specific stalking tactic is unknown.

384   Stalking likely requires a high level of body movement control, and thus experience.

16

385 Learning and experience play a key role in the ability of predators to efficiently capture

386 their prey (Edwards & Jackson 1994, Guinet & Bouvier 1995, Morse 2000). However,

387 unlike other carnivorous species such as felids or killer whales whose young learn by

388 mimicking their mother or their conspecifics (e.g., (Guinet & Bouvier 1995, Elbroch et

389 al. 2013)), elephant seals forage individually from their first day at sea. They

390 consequently must develop their hunting tactics on their own. Equipping younger

391 individuals with sonar and movement tags from their first year at sea could provide a

392 better understanding of how seals develop their hunting tactics and how their hunting

393 efficiency increases with their experience.

394 *Prey defence mechanisms: how not to get captured?*

395 This study identified flash emission and escape attempt as the two types of prey

396 reaction to predators, which could be displayed simultaneously. Escape attempt was

397 the most frequent defence mechanism adopted by prey. Escape reaction was

398 associated with a reduction in seals' capture success, even though it remained high

399 (90% of the cases). Manoeuvrability being inversely proportional to body size

400 (Domenici 2001), small prey benefit from a greater manoeuvrability than their much

401 larger predator. However, their swimming speed is also much lower than that of

402 elephant seals (i.e. 0.1-0.3 m/s for myctophids (Ignatyev 1996) vs. 1-2 m/s for elephant

403 seals (Gallon et al. 2013)). Therefore, prey must react far enough from the seals to

404 take advantage of their higher manoeuvrability and escape capture. Indeed, we found

405 that the greater the prey flight initiation distance, the lower the seal capture success

406 rate.

407 On the opposite, flash did not seem to be an efficient defence mechanism as prey

408 capture success was the highest for flashing prey. Flash emission is a common

17

409 defence mechanism observed in marine organisms, used to temporarily dazzle

410 predators (Barnes & Case 1974). However, myctophid flashes might be too weak to

411 dazzle large elephant seals. Predation pressure from seal is likely lower than that from

412 other fish and squids, for which dazzling might significantly reduce predation risk. This

413 could explain why this flashing behaviour has been retained in fish populations even if

414 it fails to decrease capture success. A recent study showed that elephant seals may

415 trigger flash emission of their prey by performing a small head movement prior to

416 capture (Goulet et al. 2020). Several studies have found that predators may benefit

417 from flashes from their prey, e.g. Pacific angel sharks (*Squatina californica,* (Fouts &

418 Nelson 1999)), blue sharks *(Prionace glauca,* (Tricas 1979)) and dogfish *Galeus*

419 *melastomus* (Bozzanao et al. 2001)) that use bioluminescence cues to locate and

420 capture their prey in dark areas.

421 This study suggests that prey characteristics and behaviours play an important role in

422 seals' energy expenditure and foraging efficiency. Larger prey were captured with

423 higher swimming efforts and longer handling times, as observed in harbour seals

424 *(Phoca vitulina*, (Bowen et al. 2002)). Similarly, approaches towards evasive prey were

425 characterised by high swimming efforts thus likely higher energy expenditure, even if

426 prey capture success of escaping prey remained high. In a study aiming at assessing

427 the relationship between prey type and net energy accumulation, Goulet et al.

428 (submitted) showed that seals foraging on evasive prey displayed a slower

429 improvement of body condition than seals foraging on less evasive prey. Similar results

430 were observed in double-crested cormorants *(Phalacrocorax auritus)* that have

431 increased oxygen consumption when foraging on mobile prey compared to sedentary

432 ones (Halsey et al. 2007).

18

5. CONCLUSION

This study offers new insight into fine-scale predator-prey interactions in Southern elephant seals. Sonar tag recordings allow for the description of the fine-scale foraging behaviour of seals and provide key information on the characteristics and behaviour of their prey. Seals' hunting behaviour appeared to be shaped by characteristics and behaviour of their prey. Capture success was high, however, evasive prey were associated with an active pursuit that can result in significant energy costs. As prey behaviour is likely influenced by environmental conditions such as temperature or light level, elephant seals may favour foraging activity in environment where prey are less likely to react. To test this hypothesis, further studies should assess the impact of environmental conditions on prey behaviour.

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658   RR, Naito Y (2020) Acceleration-triggered animal-borne videos show a dominance of
659   fish in the diet of female northern elephant seals. Journal of Experimental Biology
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661

662 # Tables

663 Table 1: proportion of single prey, schooling prey, evasive prey and flashing prey and
664 prey acoustic size targeted by nine female Southern elephant seals equipped with
665 high-resolution movement and sonar tags in Kerguelen Islands between 2018 and
666 2020. Seal ID comprises the two first letters of the Latin species binomial followed by
667 the year and Julian day of attachment, and a letter denoting the sequential animal of
668 day.

Seal ID	Number of analysed echograms (+% of the total)	Proportion of individual prey (%)	Proportion of schooling prey (%)	Proportion of single evasive prey (%)	Proportion of single flashing prey (%)	Prey acoustic size (cm)
ml18_292a	831 (9%)	98.4	1.6	85.3	NA	7.4 ± 2.9

ml18_293a	300 (7%)	99.0	1.0	93.7	NA	8.0 ± 3.6
ml18_294a	414 (7%)	99.2	0.8	71.8	NA	7.6 ± 3.5
ml19_295a	856 (10%)	99.5	0.5	88.5	NA	7.8 ± 3.0
ml19_295c	887 (8%)	99.2	0.8	79.7	NA	7.3 ± 3.0
ml19_296a	540 (10%)	99.1	0.9	88.0	NA	8.6 ± 3.7
ml20_295a	551 (4%)	99.5	0.5	80.5	24.3	6.1 ± 3.1
ml20_296a	496 (4%)	99.0	1.0	71.0	29.5	4.9 ± 2.3
ml20_296c	903 (7%)	99.7	0.3	73.9	NA	7.3 ± 2.9

669

Figures
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671
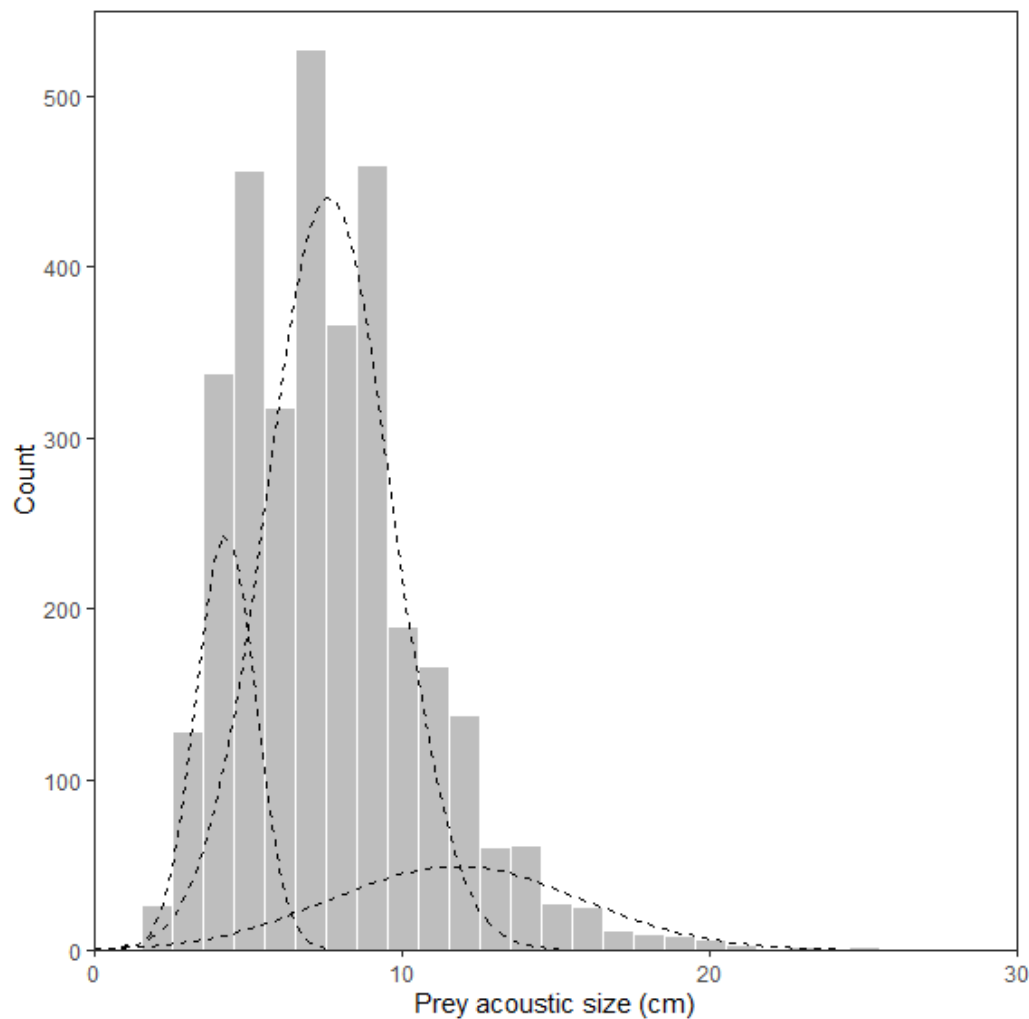
672 Figure 1: Acoustic size distribution of prey targeted by nine female Southern elephant

673 seals equipped with high-resolution movement and sonar tags in Kerguelen Islands

674 between 2018 and 2020. Prey acoustic sizes were estimated from the -20 dB echo

675 pulse width measured on the widest part of the prey echo trace. A mixture model was

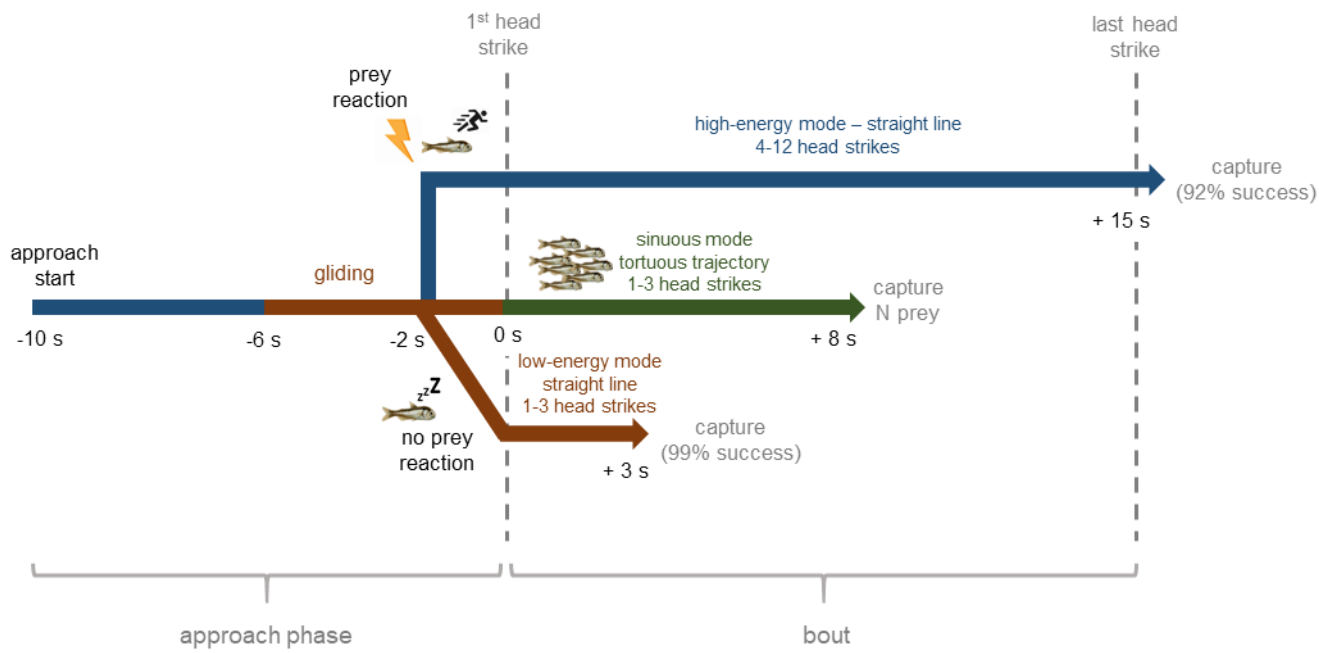676 applied which identified three normal distributions in the acoustic size data.

677

Figure 2: Summary of the hunting sequence of Southern elephant seals. Predator-prey interactions were described on nine females equipped with high-resolution movement and sonar tags in Kerguelen Islands between 2018 and 2020. The hunting sequence was described as the sequence of events from the beginning of the approach phase (i.e. 10 seconds preceding each bout) to the final head strike of the bout. Seal hunting behaviour was derived from accelerometer and magnetometer data, and prey behaviour was inferred from sonar data. Capture success was inferred from sonar data for individual prey only, as we were not able to determine the number of prey ingested in a school.
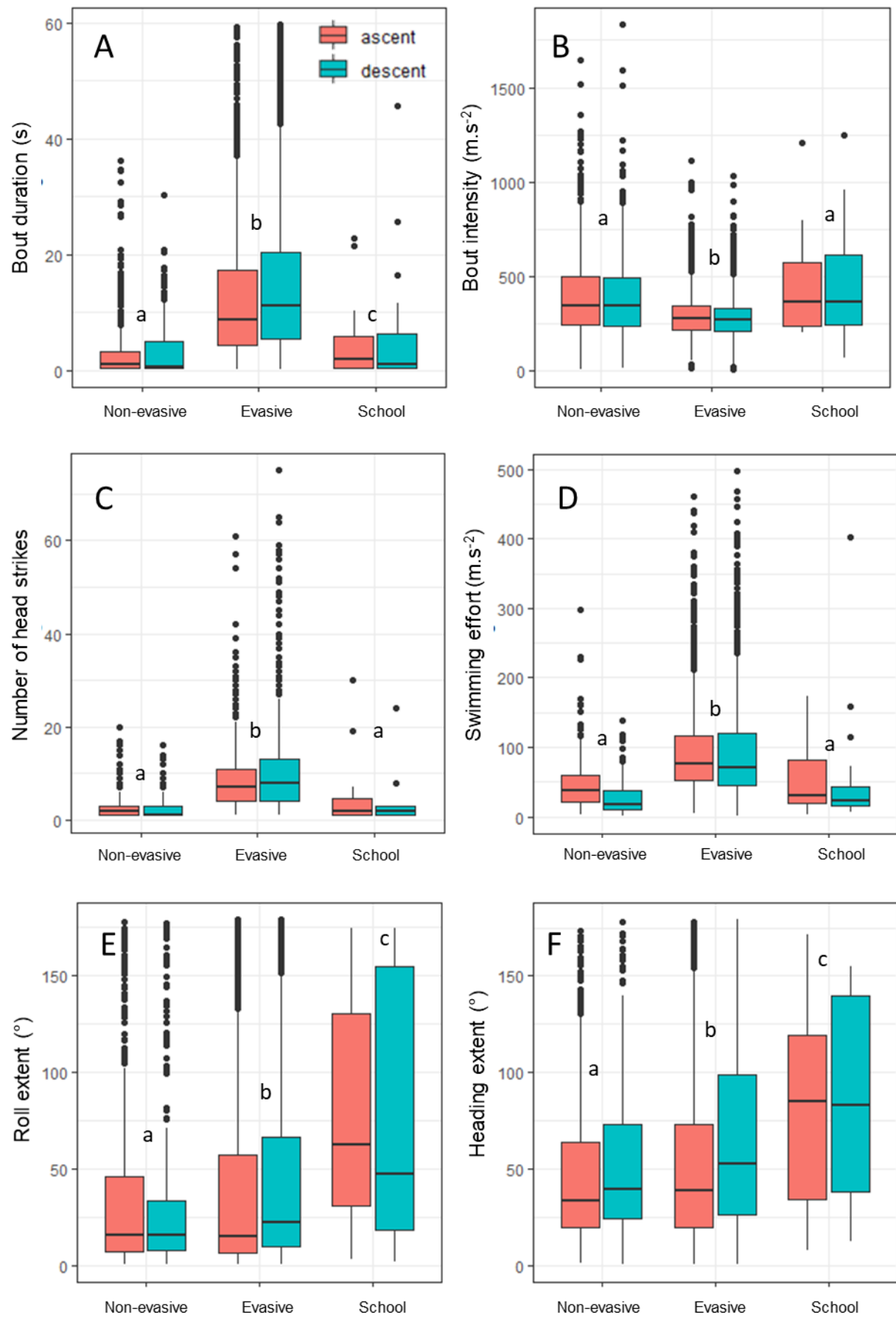
687

688   Figure 3: Characteristics of prey-dependant hunting behaviour of nine female Southern

689   elephant seals equipped with high-resolution movement and sonar tags in Kerguelen

690   Islands between 2018 and 2020. Behavioural metrics were derived from accelerometer

691   and magnetometer data recorded between the 10 seconds preceding each bout and

692   the last strike of the bout: ((A) bout duration (s), (B) bout intensity (m.s^{-2}), (C) number

693   of head strikes, (D) swimming effort (m.s^{-2}), (E) roll extent (°) and (F) heading extent

694   (°)). Letters in superscript indicate significant differences in behavioural parameters

695   between prey types (GLMM, P < 0.05).
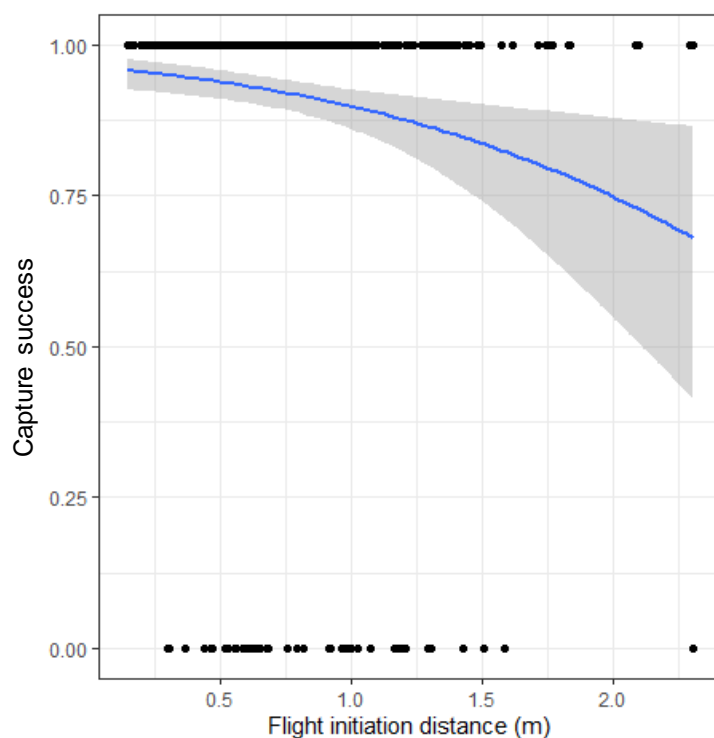

696

697   Figure 4: Effect of prey flight initiation distance (m) on prey capture success (%),

698   modelled using a mixed-effects logistic regression (P < 0.001). Prey capture success

699   was estimated from sonar recordings on 490 bouts for which prey reaction timing was

700   inferred, for nine female Southern elephant seals equipped with high-resolution

701   movement and sonar tags in Kerguelen Islands between 2018 and 2020.