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1 Hunting tactics of Southern elephant seals (*Mirounga*  
2 *leonina*) and anti-predatory behaviours of their prey

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9 **Running page head**

10 Elephant seals hunting tactics

11 **Abstract**

12 For air-breathing marine predators that must save energy during dives, the ability to  
13 adopt hunting tactics that minimise the risk of triggering an escape reaction from the  
14 prey is crucial for efficient foraging. Female Southern elephant seals (*Mirounga*  
15 *leonina*, SES hereafter) forage on small mesopelagic prey that they must hunt almost  
16 continuously to meet their high-energy requirements. Here we aimed at understanding  
17 how these large time-limited deep-divers can efficiently exploit their small sized prey.  
18 To do so, we used data recorded by a new bilogger, the sonar tag, deployed on SES  
19 during their post-breeding foraging trips. This tag combines an active acoustic sensor  
20 with ultra-high-resolution movement and bioluminescence sensors. This combination  
21 of sensors offers a unique opportunity to simultaneously describe SES' hunting tactics

22 and their prey's defence mechanisms. We analysed more than 5,800 prey capture  
23 events in nine SES and show that they adopt a "stalking" hunting behaviour allowing  
24 them to get as close as possible to their prey before attacking. The ability of SES to  
25 adopt stealth approach tactics, minimising the risk of initiating a flight reaction from  
26 their prey, might be a key factor in the success of this far-ranging generalist predator.

## 27 **Keywords**

28 Predator-prey interactions; hunting tactics; anti-predatory behaviours; Southern  
29 elephant seals; *Mirounga leonina*; biologging.

## 30 **1. INTRODUCTION**

31 Predator-prey interactions play a key role in ecosystem structure and functioning.  
32 While predators shape prey population dynamics (i.e., survival, growth, behaviour,  
33 etc.), prey availability and accessibility regulate predator populations (Estes & Duggins  
34 1995, Frederiksen et al. 2006, Letnic et al. 2012). Fine-scale interactions between  
35 predators and their prey, i.e., how predators find, select, and capture their prey, and  
36 alternatively how prey detect predators, and react to imminent predation, are key  
37 factors in determining both predators' hunting efficiency and prey survival (Cooper Jr  
38 1997, McHenry et al. 2009, Stewart et al. 2013). On one hand, to avoid capture, prey  
39 can flee, fight back or stay still depending on hunting tactics of their predators, distance  
40 from their predators, and accessibility to a shelter (Broom & Ruxton 2005, Eilam 2005).  
41 On the other hand, predators must adopt hunting tactics that increase their chances of  
42 successful capture while avoiding excessive energy expenditure. This is particularly  
43 true for air-breathing marine predators, which are limited by oxygen availability and  
44 must regularly return to the surface to breathe (Thompson 1993). In most cases,  
45 avoiding active chase helps preserving oxygen reserves and increasing time diving

46 and searching for prey. Therefore, the ability of air-breathing predators to adopt hunting  
47 tactics that limit the risk of triggering an escape reaction from the prey is crucial for an  
48 efficient foraging.

49 Studying fine-scale predator-prey interactions in the marine environment is particularly  
50 challenging. Development of animal-borne biologging technologies advanced the  
51 study of deep-diving animal foraging behaviour. GPS sensors for example can help  
52 identifying the foraging areas of marine animals (e.g., Hindell et al. 1991, Sommerfeld  
53 et al. 2015, Reisinger et al. 2018), whereas high-resolution head-mounted  
54 accelerometers allow the detection of foraging events by measuring rapid head  
55 movements potentially associated with prey capture attempts (Suzuki et al. 2009,  
56 Viviant et al. 2010, Guinet et al. 2014, Ydesen et al. 2014). Accelerometers also record  
57 the movements and postures of animals, providing a fine-scale description of their  
58 hunting behaviour (e.g., Johnson et al. 2008, Shepard et al. 2008, Jouma'a et al. 2016,  
59 Le Bras et al. 2017). Diet analyses (i.e., stomach contents, scat analyses, stable  
60 isotopes analyses, genetic markers) provide an overview of prey consumed during  
61 foraging trips (e.g., Cherel et al. 2008, Jeanniard-du-Dot et al. 2017) but fine-scale  
62 information on prey size and behaviour is still challenging to obtain. Recently-  
63 developed miniature video cameras have provided the first direct information on prey  
64 and predator-prey interactions (Adachi et al. 2021, Naito et al. 2013, Yoshino et al.  
65 2020 on Northern elephant seals (*Mirounga angustirostris*), Bowen et al. 2002 on  
66 harbour seals (*Phoca vitulina*), Kernaléguen et al. 2016 on Australian fur seals  
67 (*Arctocephalus pusillus doriferus*), Davis et al. 1999 on Weddell seals (*Leptonychotes*  
68 *weddellii*)).

69 Miniature cameras deployed on Northern elephant seals provided unique and novel  
70 information on prey targeted by female elephant seals (Naito et al. 2013, Yoshino et

71 al. 2020, Adachi et al. 2021). As suggested by isotopic analyses (Cherel et al. 2008),  
72 video footages confirmed that females mainly target myctophid species, and to a lesser  
73 extent mesopelagic squids. Small size of prey relative to the large size of females  
74 implies that they must feed continuously to meet their high-energy requirements. This  
75 raises the question of how these large time-limited deep-divers can efficiently exploit  
76 these small prey. Cameras require a light-source to illuminate dark waters where  
77 elephant seals forage, which could potentially alter both predator and prey behaviour.  
78 Moreover, high power consumption means these devices can only record selectively,  
79 for relatively short periods, during multi-month foraging trips. Therefore, extensive  
80 deployments are lacking and the way elephant seals can efficiently exploit their tiny  
81 prey is still poorly known. In order to have a more complete and detailed picture on  
82 predator-prey interactions in deep-diving predators such as elephant seals, we used a  
83 miniature sonar tag, combining active acoustic signals with high-resolution movement  
84 sensors. This tag uses a high-click rate narrow, forward directed beam that can insonify  
85 prey at a distance up to 6 m in front of the animal. Even if data recorded by the tag do  
86 not allow for the identification of the species of prey targeted by seals, it provides  
87 information on their acoustic size – a proxy for actual size – gregarious and escape  
88 behaviours (Goulet et al. 2019). Including high-resolution movement sensors, the tag  
89 offers the opportunity to study the hunting tactics of seals and more generally fine-  
90 scale predator-prey interactions. A more recent version of the sonar tag also includes  
91 a high-resolution bioluminescence sensor to study bioluminescent behaviour of prey,  
92 especially how they might emit light flashes to defend themselves against predators  
93 (Goulet et al. 2020) by temporarily dazzling predators and using the opportunity to  
94 escape. Therefore, data recorded by this tag will enable the investigation of questions  
95 raised by the results obtained with the camera deployments.

96 Previous sonar tag deployments on SES demonstrated that SES have surprisingly  
97 strong sensory advantage over their prey, allowing them to detect prey several  
98 seconds before striking, well before they react (Chevallay et al. 2023). As Northern  
99 elephant seals, they target small mesopelagic prey, which they have to hunt  
100 continuously to meet their energy requirements. As they are constrained to return to  
101 the surface to breathe, they must be efficient during their time-limited hunting periods.  
102 Therefore, we hypothesised that the ability of SES to detect their prey in a distance  
103 enabled them to adopt stealth approach tactics to minimise the risk of initiating a flight  
104 reaction from their prey, therefore avoiding energy-expensive chase. To test that  
105 hypothesis, we took advantage of data recorded by the sonar tag to describe the  
106 hunting sequence of SES and to describe the prey defence mechanisms to see how it  
107 influences the SES capture success.

## 108 2. MATERIALS AND METHODS

### 109 2.1. Device deployments and data collection

110 Data were collected on 9 post-breeding female SES in October 2018 (n = 3), October  
111 2019 (n = 3) and October 2020 (n = 3), in Kerguelen Islands (49°20'S – 70°26'E).  
112 Females were captured with a canvas head-bag, anaesthetized with a 1:1 combination  
113 of Tiletamine and Zolazepam (Zoletil 100 – 0.7 to 0.8 ml/100 kg) either injected  
114 intravenously (McMahon et al. 2000) or using a deported intramuscular injection  
115 system without restraint. Females were measured to the nearest centimetre and  
116 weighted to the nearest kilogram. They were equipped with a neck-mounted Argos tag  
117 (SPOT-293 Wildlife Computers, 72x54x24 mm, 119 g in air), a back-mounted CTD tag  
118 (SMRU-SRDL, 115x100x40 mm, 680 g in air) and either a head-mounted DTAG-4  
119 sonar tag (n = 7, 95x55x37 mm, 200 g in air, see Goulet et al. (2019) for further details

120 on the device) or a DTAG-4 sonar-light tag (n = 2, 92x69x37 mm, 250 g in air). Tags  
121 were glued to the fur using quick-setting epoxy glue (Araldite AW 2101, Ciba). CTD  
122 tags recorded conductivity, temperature and depth at 0.5 Hz. Sonar and sonar-light  
123 tags were programmed to sample GPS position (up to every minute), tri-axial  
124 acceleration (200 Hz), tri-axial magnetometer (50 Hz) and pressure (50 Hz). Sonar-  
125 light tags also integrated a light sensor specifically designed to sample  
126 bioluminescence events with a sampling frequency of 50 Hz (Goulet et al. 2020). The  
127 active sonar within the tags recorded acoustic backscatter returning from 10  $\mu$ s pings  
128 with a centre frequency of 1.5 MHz, at a 25 Hz ping rate for 2018 and 2019  
129 deployments and 12.5 Hz for 2020 deployments. The active sonar operated with a 3.4°  
130 aperture beam width and a 6 m range (Goulet et al. 2019). Tags were recovered in late  
131 December to January when females returned to shore to moult using the same capture  
132 and sedation methods. All experiments were conducted under the ethical regulation  
133 approval of the French Ethical Committee for Animal Experimentations  
134 (2019070612143224 (#21375)) and the Committee for Polar Environment.

## 135 2.2. Data analyses

136 Data recovered from tags were analysed using custom-written codes and functions  
137 from [www.animaltags.org](http://www.animaltags.org) in MATLAB version 2022b (The MathWorks 2022).  
138 Statistical analyses were conducted in R software version 3.5.1 (R Core Team 2018).

### 139 2.2.1. Prey capture attempts identification

140 Prey capture attempts (PrCAs hereafter) were detected from the 200 Hz tri-axial  
141 acceleration data recorded by the sonar tags, by computing the norm of the differential  
142 of the tri-axial acceleration (norm-jerk hereafter) (Chevallay et al. 2023). Histograms of  
143 the norm-jerk showed a clear bimodal distribution for all SES. High jerk modes

144 associated with prey strikes were separated from the lower modes using a threshold  
145 at 400 m.s<sup>-2</sup>. Therefore, spikes in the norm-jerk higher than 400 m.s<sup>-2</sup> were classified  
146 as PrCAs (Chevallay et al. 2023). As prey may be encountered in patches or may elude  
147 capture, leading to a bout structure in prey strikes, strikes occurring less than 15 s from  
148 the previous strike were grouped in the same PrCA bout (bout hereafter) according to  
149 the distribution of the inter-strike interval (Chevallay et al. 2024). Our estimations of the  
150 number of PrCAs using the norm-jerk are consistent with the ones obtained with  
151 mandible accelerometers (Naito et al. 2013, Adachi et al. 2021).

### 152 2.2.2. *Sonar data analysis*

153 Sonar data recorded during bouts were displayed as echograms, showing the time on  
154 the horizontal axis and the distance from the sonar tag on the vertical axis, extending  
155 from 10 s before the bout start time to 2 s after the bout end. Because of the large  
156 number of bouts detected (ranging from 4595 to 12039 per animal), only a random  
157 subsample of 5 to 10% of bouts performed during acoustic data recordings were  
158 analysed. They were selected by randomly selecting bouts from a global (all animals  
159 dataset (all animals together). Different variables describing predator-prey interactions  
160 were extracted manually from echograms: (1) number of prey, (2) prey evasive  
161 behaviour, (3) prey acoustic size, (4) capture success. (1) The number of prey was  
162 defined as the maximum number of independent echo traces within a same ping  
163 (Jones et al. 2008). It was scored as one, two or more than two, i.e., a school of prey.  
164 (2) Prey evasive behaviour was identified from the closing speed between predator  
165 and prey, which will vary in case of prey reaction, resulting in a change in the slope of  
166 the prey echo trace (Goulet et al. 2019, Vance et al. 2021). If a prey reaction was  
167 observed during the bout, prey was considered as evasive. Prey flight initiation  
168 distance was defined as the distance between the tag and the prey when prey first



169 showed an escape reaction (Vance et al. 2021, Chevallay et al. 2023). (3) Prey  
170 acoustic size was estimated from the -20 dB echo pulse width measured on the widest  
171 part of the prey trace on evasive prey only (Burwen et al. 2003). The measurement  
172 was done ping by ping and we used the maximum of all measurements for the final  
173 size estimate. Echo duration was only measured on evasive prey on the assumption  
174 that escaping prey will typically be oriented parallel with the predator providing a  
175 relatively consistent orientation for which to estimate size. Finally, (4) when prey trace  
176 was seen within 50 cm of the sonar transducer within the last second of the bout,  
177 capture was considered successful. If prey trace was seen further than 1 m away from  
178 the sonar transducer during the last second of the bout or was evident after the bout  
179 ended, bout was classified as unsuccessful. All other cases were classified as  
180 “unknown”.

### 181 2.2.3. *Bioluminescence data analysis*

182 Bioluminescent flashes were detected as spikes in the 50 Hz light data recorded by  
183 the sonar-light tags decimated at a 5 Hz sampling rate, as this resolution is sufficient  
184 to detect flashes. Spikes in the data higher than 0.07 (arbitrary unit) were classified as  
185 flashes (Goulet et al. 2020). Events detected within less than 5 s of each other were  
186 considered coming from the same bioluminescence event (Goulet et al. 2020). If a  
187 bioluminescence event started between 5 s before and 5 s after the bout, it was  
188 considered associated with the bout. Flash events may consist of a series of short  
189 flashes, so the 5 Hz data may not have sufficient resolution to accurately describe  
190 them. Therefore, we used 50 Hz light data recorded during flash events to calculate  
191 the number of peaks in the light signal as well as the intensity and duration of each  
192 peak.

193        *2.2.4. Predator approach behaviour*

194 Metrics describing SES fine-scale behaviour during the approach and capture phase,  
195 i.e., between the 10 s preceding each first strike of a bout (Chevallay et al. 2023) and  
196 the last strike of the bout, were extracted from the 200 Hz tri-axial accelerometer data  
197 decimated at 5 Hz. Posture of SES was inferred from Euler angles, i.e., pitch angle  
198 (rotation around left-right axis), roll angle (rotation around longitudinal axis) and  
199 heading angle (rotation around dorso-ventral axis), (see Johnson and Tyack 2003 for  
200 details of the formulas). Bouts were characterised in term of duration (time elapsed  
201 during the first and last head strike of the bout) and intensity, defined as the root-mean  
202 square of the norm-jerk signal during the bout. To know whether SES actively swam  
203 or passively glided when hunting, we determined the number of flipper strokes between  
204 the 10 s preceding each bout and the last strike of the bout. Flipper strokes were  
205 detected from dynamic acceleration of the lateral axis (Sato et al. 2007) by applying a  
206 high-pass filter with a cut-off frequency of 0.6 Hz, i.e., 70% of the dominant stroke  
207 frequency, on the lateral acceleration (Chevallay et al. 2023). Finally, the swimming  
208 effort, a proxy of energy expenditure during swimming, was defined as the summed  
209 absolute values of the filtered lateral acceleration (Maresh et al. 2004, Aoki et al. 2012).  
210 SES are usually negatively buoyant in the first weeks of the post-breeding foraging  
211 trips (Biuw et al. 2003) and therefore in the period sampled by the sonar tags. SES are  
212 thus expected to glide when descending and swim actively when ascending. To avoid  
213 conflating these two distinct movement styles when analysing hunting tactics, bouts  
214 were grouped according to the vertical movement prior to each bout. Bouts with an  
215 initial depth-rate higher than 0.25 m/s and lower than -0.25 m/s were grouped as,  
216 respectively, descending and ascending bouts (Chevallay et al. 2023).

217 An exploratory analysis of SES hunting tactics was first conducted on a sub-sample of  
218 bouts by making a 3D animation of SES behaviour during the approach phase. This  
219 exploratory analysis identified three main approach modes, which differed in bout  
220 duration, swimming effort, roll and heading ranges. Therefore, a K-means algorithm  
221 with 3 clusters was applied on these behavioural metrics for ascending and descending  
222 bouts separately. Each resulting cluster was described in terms of bout duration, bout  
223 intensity, swimming behaviour and posture.

### 224 2.3. Statistical analyses

225 Approach behaviour between prey types were compared using generalized linear  
226 mixed models (GLMM hereafter, R package 'MASS', Ripley et al. 2013) with gamma  
227 distribution, with bout duration (s), bout intensity ( $\text{m}\cdot\text{s}^{-2}$ ), number of head strikes,  
228 swimming effort ( $\text{m}\cdot\text{s}^{-2}$ ), roll or heading angle extent ( $^{\circ}$ ) as response variables, and prey  
229 type (schooling vs. single prey; single evasive prey vs. single non-evasive prey) as  
230 fixed effect. Individual SES identities were used as random effects.

231 Influence of prey evasive behaviour on the likelihood of adopting an approach mode  
232 was tested using mixed effects logistic regression, with approach mode (either high or  
233 low-energy approach) as a binary response variable, flight initiation distance (m) as  
234 fixed effect, and individual identities as random effects.

235 The impact of prey reaction on SES capture success was modelled using mixed-effect  
236 logistic regression models with capture success as a binary response variable (scored  
237 as 1 or 0), reaction type (flash or escape attempt) or timing of reaction as fixed effects  
238 and individual identities as random effects.

239 Finally, the effect of prey evasive behaviour on capture difficulty was tested using  
240 GLMM with gamma distribution with the bout duration, the number of head strikes and

241 swimming effort (proxies of prey capture difficulty, Goulet 2020) as response variables,  
242 and flight initiation distance as fixed effect. Individual SES identities were used as  
243 random effects.

244 For all models, assumptions were checked (i.e. autocorrelation, heteroscedasticity)  
245 and any deviation from them were corrected. Particularly, as data represent a time  
246 series, an autocorrelation structure of order 1 was added to the models. Details on the  
247 models are presented in Table A1 in the Appendix.

## 248 3. RESULTS

249 Tags recorded data during 29-79 days. Over that period, SES performed  $69 \pm 7$  dives  
250 per day (mean  $\pm$  sd, min 57 dives per day, max 79 dives per day), and  $510 \pm 53$  bouts  
251 per day (range 443-610 bouts per day). SES performed dives at  $413 \pm 89$  m depth  
252 (mean  $\pm$  sd) for  $19 \pm 3$  min, and spent  $10 \pm 2$  min at the bottom of the dive. A diel diving  
253 pattern was observed for almost all individuals, with deeper and longer dives during  
254 the day ( $449 \pm 187$  m,  $21 \pm 4$  min) than at night ( $329 \pm 70$  m,  $16 \pm 1$  min, GLMM,  $P <$   
255  $0.001$ ).

### 256 3.1. Prey characteristics

257 Prey characteristics were inferred from sonar data during 5778 bouts for the nine  
258 females equipped with sonar tags between 2018 and 2020. Single prey represented  
259  $99.2 \pm 0.4\%$  of prey targeted by our studied SES. Among single prey,  $81.4 \pm 8.1\%$  tried  
260 to escape (Table 1). For the two females equipped with sonar-light tags,  
261 bioluminescence flash occurred in 24.3 and 29.5% of their targeted prey. Acoustic size  
262 of prey ranged from 5.0 to 9.0 cm (1<sup>st</sup> and 3<sup>rd</sup> quantiles, Q1-Q3 hereafter) (min 1.6 cm,  
263 max 32.8 cm, Figure 1). A mixture model applied to the distribution of prey acoustic

264 sizes (R package mixtools, Benaglia et al. (2010)) identified three size groups (Figure  
265 1): small prey measuring 3 to 6 cm ( $4.3 \pm 1.0$  cm, 33% of prey), medium-sized prey  
266 measuring 6 to 11 cm ( $7.6 \pm 2.0$  cm, 55% of prey), and large prey measuring more  
267 than 11 cm and up to 35 cm ( $11.8 \pm 4.1$  cm, 12% of prey).

### 268 3.2. Predator hunting behaviour

269 Gliding behaviour preceded 91% and 60% of descending and ascending bouts, with a  
270 stop of active stroking  $6.7 \pm 1.4$  s and  $5.5 \pm 1.6$  s before the first strike of the bout  
271 (Figure 2). Then, depending on prey behaviour, SES displayed three hunting modes:  
272 i) low-energy mode, observed for 79% of non-evasive prey, ii) high-energy mode,  
273 observed for 61% of evasive prey, and iii) sinuous mode, observed for 63% of  
274 schooling prey and 24% of evasive prey. Low-energy mode was the most frequent in  
275 both descents (62% of bouts) and ascents (67% of bouts). Sinuous mode was  
276 observed for 27% and 21% of descending and ascending bouts, and high-energy  
277 mode was the least frequent mode, observed for only 11% and 12% of descending  
278 and ascending bouts. Low-energy modes were characterised by short bouts of 1 to 3  
279 (Q1-Q3) intense head strikes (Figure 3) lasting 0.3 to 3.7 s (Q1-Q3), and low swimming  
280 efforts (Figure 3). High-energy modes were characterised by long bouts of 4 to 12 (Q1-  
281 Q3) low intensity head strikes (Figure 3) usually lasting 5.0 to 20.2 s (Q1-Q3) and up  
282 to 36.6 s (90<sup>th</sup> percentile, Figure 2). This mode is associated with the highest values of  
283 swimming effort (Figure 3), especially during ascents. The probability of adopting low  
284 or high-energy hunting mode depended on prey evasive behaviour: the greater the  
285 flight initiation distance (FID hereafter), the greater the probability of adopting a high-  
286 energy hunting mode (mixed-effects logistic regression,  $P < 0.001$ , Figure 2). Prey that  
287 reacted sooner were associated with longer bouts (GLMM,  $P < 0.001$ ): bout duration  
288 (s) =  $(10.2 \pm 1.7) + (7.8 \pm 0.7) * \text{FID (m)}$ ) with a higher number of head strikes (GLMM,

289  $P < 0.001$ , number of head strikes =  $(6.1 \pm 0.9) + (5.1 \pm 0.3) * \text{FID (m)}$ ) and a higher  
290 swimming effort (GLMM,  $P < 0.001$ , swimming effort ( $\text{m}\cdot\text{s}^{-2}$ ) =  $(65.9 \pm 8.9) + (39.0 \pm$   
291  $4.0) * \text{FID (m)}$ ). Finally, sinuous approaches were characterised by the highest values  
292 of roll and heading extent, short bouts of 1 to 3 intense head strikes (Figure 3) lasting  
293 0.3 to 10.0 s (Q1-Q3), and low swimming efforts (Figure 3) and were consistently  
294 observed for schooling prey, but also for single evasive prey.

### 295 3.3. Prey anti-predatory behaviours

296 Anti-predatory behaviours of SES prey were studied on 1047 bouts for which data on  
297 both evasive and flashing behaviours were available. For these bouts, escape attempt  
298 without bioluminescence flash was the most frequent defence mechanism, detected in  
299 59% of prey, while 19% of prey did not show any reaction, 17% of prey flashed and  
300 tried to escape, and 5% only flashed. Prey initiated flight reaction  $2.4 \pm 2.4$  s (Q1-Q3:  
301  $3.5 - 0.4$  s) before the first strike of the bout, at  $0.7 \pm 0.4$  m (Q1-Q3:  $0.5 - 0.9$  m) from  
302 SES. Prey flashed  $1.9 \pm 1.5$  s (Q1-Q3:  $3.3 - 0.5$  s) before the first strike of the bout.  
303 Flash events usually lasted  $1.7 \pm 3.0$  s (Q1-Q3:  $0.2-1.6$  s), as a series of  $2 \pm 2$  flashes  
304 (Q1-Q3: 1-3 flashes) of  $0.17 \pm 0.24$  s each (Q1-Q3:  $0.04-0.19$  s) and of  $0.18 \pm 0.15$   
305 intensity (Q1-Q3:  $0.10-0.18$ ).

### 306 3.4. Impact of prey behaviour on SES capture success

307 We estimated prey capture success at 99% when prey did not react to the SES  
308 approach. Capture success was not significantly different between prey that tried to  
309 escape and flashed (95%) and prey that only tried to escape (92%) (mixed-effect  
310 logistic regression,  $P = 0.9999$ ). On the opposite, when prey tried to escape, probability  
311 of successful capture was 7% lower than when prey did not react (capture success =  
312 92%, mixed-effects logistic regression,  $P < 0.001$ ). The greater the flight initiation

313 distance, the lower the probability of SES successfully capturing the prey (mixed-  
314 effects logistic regression,  $P = 0.0026$ , Figure 4).

## 315 4. DISCUSSION

316 We used high-resolution bioluminescence and movement sensors combined with  
317 active acoustics to study the functional relationships between SES and their prey.  
318 Sonar tag recordings provided novel information on characteristics (acoustic size) and  
319 fine-scale behaviour of prey targeted by SES. Tagged SES females from Kerguelen  
320 Islands mostly targeted small, isolated prey, while schools were almost never  
321 encountered. Prey acoustic size ranged between 4 and 10 cm, which is consistent with  
322 sizes of the main SES prey species (Cherel et al. 2008, Guinet et al. 2014), i.e.,  
323 *Electrona antarctica* 3-10 cm, *E. carlsbergi* 4-10 cm and *Krefflichthys anderssoni* 1-8  
324 cm (Collins et al. 2008), although it is important to remember that acoustic and physical  
325 sizes are not necessarily similar. Indeed, prey orientation has a strong influence on the  
326 measures of acoustic size (Burwen et al. 2003): if a prey is oriented perpendicular to  
327 the beam, its acoustic size reflects its width, while if it is oriented parallel to the beam,  
328 its acoustic size reflects its length. When prey tries to escape, it will at some point likely  
329 be oriented along the beam axis, so measuring the maximum length of given prey trace  
330 provides a strong indication of the true prey size. A small but meaningful proportion of  
331 prey were 10 to 20 cm (up to 35 cm) in acoustic size. These prey sizes could  
332 correspond to other abundant myctophid species in Kerguelen waters, such as  
333 *Gymnoscopelus braueri* or *G. nicholsi*, up to 13 and 19 cm in length respectively.  
334 Finally, targets larger than 20 cm could be consistent with squids, species occasionally  
335 found in SES diet (i.e., *Martialia hyadesi* and *Todarodes filippovae* that measure up to  
336 40 and 55 cm respectively, Cherel et al. 2008). Further studies are needed to

337 understand horizontal and vertical distributions of these different-sized prey in relation  
338 to environmental conditions.

339 High-resolution movement sensors integrated in the sonar tags also allowed us to  
340 describe the hunting sequence of free-ranging SES. SES consistently started their  
341 approach by gliding towards their prey about 6 s before the capture. This is consistent  
342 with results from Chevallay et al. (2023) that showed that SES usually detect their prey  
343 between 6 and 10 s before the strike, i.e. between 7-17 m considering an average  
344 swimming speed of 1.3 to 1.7 m/s (Chevallay et al. 2023). Prey usually reacted one to  
345 two seconds before the SES capture, by trying to escape or by emitting a  
346 bioluminescent flash. If prey did not respond, they were captured in a few short head  
347 strikes. Larger prey likely need longer handling times and thus longer head movements  
348 (Bowen et al. 2002, Hocking et al. 2016), as already observed by Goulet et al.  
349 (unpublished data) in SES, but also in Australian fur seals (*Arctocephalus pusillus*  
350 *doriferus*, Hocking et al. 2016), sub-Antarctic fur seals (*Arctocephalus tropicalis*,  
351 Hocking et al. 2016) and Northern elephant seals (*Mirounga angustirostris*, Adachi et  
352 al. 2019) where the number of acceleration peaks correlated with prey size. If prey tried  
353 to escape, SES responded by pursuing them for several seconds, performing series of  
354 low intensity head movements before managing to capture their prey in more than 90%  
355 of the cases. These approach phases characterised by bursts of acceleration to  
356 capture mobile prey and deceleration to capture inactive prey were also observed in  
357 other aquatic top predators such as Adélie penguins (*Pygoscelis adeliae*, Wilson et al.  
358 2002) or Baikal seals (*Pusa sibirica*, Watanabe et al. 2004). We observed these  
359 hunting modes similarly in descents and ascents, which confirms prey-dependant  
360 behaviours in SES, rather than a consequence of the prevailing movement direction.  
361 Classifying SES approach behaviours into categories of hunting modes can shadow



362 the actual complexity of predator-prey interactions. It is likely that SES display a more  
363 various set of approach tactics depending on other characteristics of their prey than  
364 we were able to identify with sonar data. However, this classification still allowed to  
365 identify patterns in the SES approach behaviours and to explore how SES tailor their  
366 approach tactics according to the different behaviours of their prey.

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

368 SES usually stopped swimming several seconds before striking, as described by  
369 Chevally et al. (2023). This type of approach resembles stalking observed in terrestrial  
370 carnivorous species such as lions (*Panthera leo*, Elliott et al. 1977, Van Orsdol 1984),  
371 or tigers (*Panthera tigris*, Sunquist 1981). Stalking is defined as a slow approach  
372 without noisy body movements, allowing the predator to get very close to their prey  
373 without alerting it (Curio 2012). This kind of approach is usually observed in predators  
374 for which the costs of prey pursuit are high, as in sperm whales for example that are  
375 known to stop swimming before initiating a pursuit (Aoki et al. 2012). SES are  
376 hypometabolic predators performing long and deep dives to feed. Consequently, active  
377 hunting with long prey pursuit could result in shorter dives, as dive duration at a given  
378 depth decreases with increasing swimming effort (Génin et al. 2015). It may thus be  
379 advantageous to adopt a discreet approach that limits the risks of triggering prey  
380 escape.

381 Fish can detect bow waves produced by an approaching predator through their lateral  
382 lines (Blaxter & Fuiman 1990, McHenry et al. 2009, Stewart et al. 2013), a series of  
383 small mechanoreceptors located under their skins. Therefore, by adopting a slow  
384 approach, the mechanical disturbances generated by the forward movements of SES  
385 may be considerably reduced, lowering the risk of being detected by prey. Gliding

386 before the strike was consistently observed during descending bouts. As SES are  
387 usually negatively buoyant through most, if not all the duration of their post-breeding  
388 foraging trips, they are likely to glide on descents, so they may take advantage of their  
389 inertia to approach their prey discreetly. However, gliding was also observed for 60%  
390 of strikes in ascending bouts, where SES usually swim actively. This suggests that  
391 gliding is a deliberate manoeuvre adopted by SES and not only dictated by gravity  
392 forces. The importance of slow approach to delay prey detection was highlighted in  
393 many terrestrial and aquatic species (e.g., in desert iguanas (*Dipsosaurus dorsalis*),  
394 Cooper Jr. 2003, in skinks (*Eumeces laticeps*), Cooper Jr. 1997, in Atlantic cods  
395 (*Gadus morhua*), Meager et al. 2006, and teleost fish, Webb 1984).

396 A meaningful proportion of prey (26%) showed no evidence of reaction to the SES  
397 approach. While the proportion of non-evasive prey may be overestimated due to the  
398 narrowness of the sonar beam (i.e., prey may have reacted outside the beam), the  
399 systematic late prey reaction supports the hypothesis that gliding behaviour may be  
400 used by SES to delay prey reaction, which may explain their very high capture success.  
401 The ontogeny of how SES acquire this specific stalking tactic is unknown. Stalking  
402 likely requires a high level of body movement control, and thus experience. Learning  
403 and experience play a key role in the ability of predators to efficiently capture their prey  
404 (Edwards & Jackson 1994, Guinet & Bouvier 1995, Morse 2000). However, unlike other  
405 carnivorous species such as felids or killer whales whose young learn by mimicking  
406 their mother or their conspecifics (e.g., Guinet & Bouvier 1995, Elbroch et al. 2013),  
407 SES forage individually from their first day at sea. They consequently must develop  
408 their hunting tactics on their own. Equipping younger individuals with sonar and  
409 movement tags from their first year at sea could provide a better understanding of how  
410 SES develop their hunting tactics and how their hunting efficiency increases with their

411 experience. The SES stealth approach tactics might explain their very high capture  
412 success. Moreover, SES are known to use suction feeding to capture their prey (Kienle  
413 & Berta 2016), and this might also help them to achieve such a high success rate.  
414 Indeed, combining an undetected close range approach with suction of a relatively  
415 large volume of water, SES are likely limiting the possibility for prey to escape.

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

417 This study identified flash emission and escape attempt as the two types of prey  
418 reaction to predators, which could be displayed simultaneously. Escape attempt was  
419 the most frequent defence mechanism adopted by prey. It was associated with a  
420 reduction in SES capture success, even though it remained high (90% of the cases).  
421 Manoeuvrability being inversely proportional to body size (Domenici 2001), small prey  
422 benefit from a greater manoeuvrability than their much larger predator. However, their  
423 swimming speed is also much lower than that of SES, i.e., 0.1-0.3 m/s for myctophids  
424 (Ignatyev 1996) vs. 1-2 m/s for SES (Gallon et al. 2013). Therefore, prey must react  
425 far enough from the SES to take advantage of their higher manoeuvrability and escape  
426 capture. Indeed, we found that the greater the prey flight initiation distance, the lower  
427 the SES capture success rate.

428 On the opposite, flash did not seem to be an efficient defence mechanism as prey  
429 capture success was the highest for flashing prey. Flash emission is a common  
430 defence mechanism observed in marine organisms, used to temporarily dazzle  
431 predators (Barnes & Case 1974). However, myctophid flashes might be too weak to  
432 dazzle large SES. Predation pressure from SES is likely lower than that from other fish  
433 and squids, for which dazzling might significantly reduce predation risk. This could  
434 explain why this flashing behaviour has been retained in fish populations even if it fails

435 to decrease capture success. A recent study showed that SES may trigger flash  
436 emission of their prey by performing a small head movement prior to capture (Goulet  
437 et al. 2020). Several studies have found that predators may benefit from flashes from  
438 their prey, e.g., Pacific angel sharks (*Squatina californica*, Fouts & Nelson 1999), blue  
439 sharks (*Prionace glauca*, Tricas 1979) and dogfish *Galeus melastomus* Bozzanao et  
440 al. 2001) that use bioluminescence cues to locate and capture their prey in dark areas.

441 This study suggests that prey characteristics and behaviours play an important role in  
442 SES energy expenditure and foraging efficiency. Larger prey were captured with higher  
443 swimming efforts and longer handling times, as observed in harbour seals (*Phoca  
444 vitulina*, Bowen et al. 2002). Similarly, approaches towards evasive prey were  
445 characterised by high swimming efforts thus likely higher energy expenditure, even if  
446 prey capture success of escaping prey remained high. In a study aiming at assessing  
447 the relationship between prey type and net energy accumulation, Goulet et al.  
448 (unpublished data) showed that SES foraging on evasive prey displayed a slower  
449 improvement of body condition than SES foraging on non evasive prey. Similar results  
450 were observed in double-crested cormorants (*Phalacrocorax auritus*) that have  
451 increased oxygen consumption when foraging on mobile prey compared to sedentary  
452 ones (Halsey et al. 2007).

## 453 5. CONCLUSION

454 This study offers new insights into fine-scale predator-prey interactions in SES. Sonar  
455 tag recordings allow for the description of the fine-scale foraging behaviour of SES and  
456 provide key information on the characteristics and behaviour of their prey. We show  
457 that SES target different types of prey with specific behaviours, and that they display  
458 three hunting modes that they tailor to the different behaviours of these prey types.

459 Capture success was high, however, evasive prey were associated with an active  
460 pursuit that can result in significant energy costs. Further investigation using  
461 bioenergetics modelling could be done to study the trade-off between effort expended  
462 and the potential energetic advantages of pursuing larger and more responsive prey.  
463 As prey behaviour is likely influenced by environmental conditions such as temperature  
464 or light level (Chevallay et al. 2024), SES may favour foraging activity in environment  
465 where prey are less likely to react. To test this hypothesis, further studies should  
466 assess the impact of environmental conditions on prey behaviour.

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 699

## 700 Tables

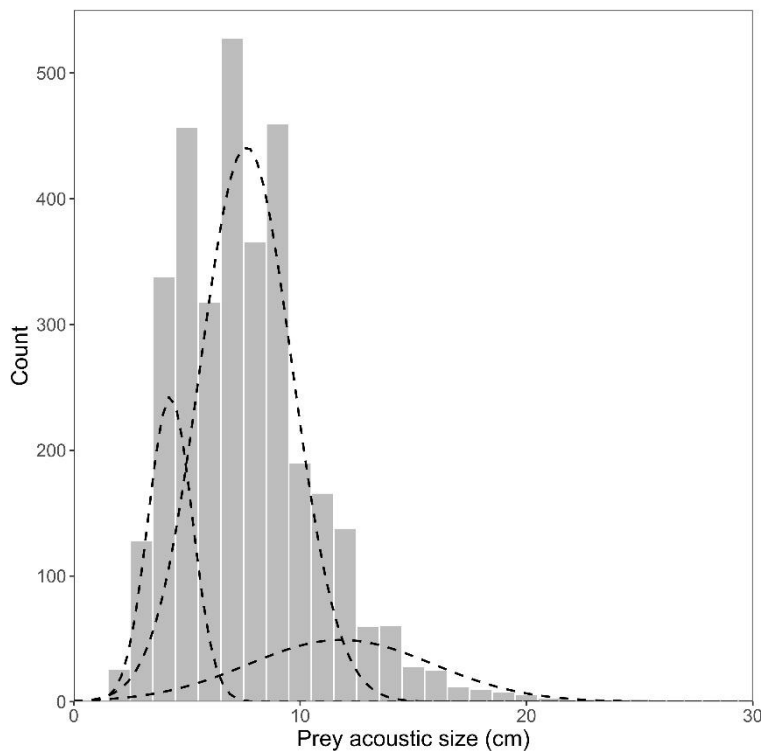
701 Table 1: proportion of single prey, schooling prey, evasive prey and flashing prey and  
 702 prey acoustic size targeted by nine female SES equipped with high-resolution  
 703 movement and sonar tags in Kerguelen Islands between 2018 and 2020. SES ID  
 704 comprises the two first letters of the Latin species binomial followed by the year and  
 705 Julian day of attachment, and a letter denoting the sequential animal of day.

SES 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

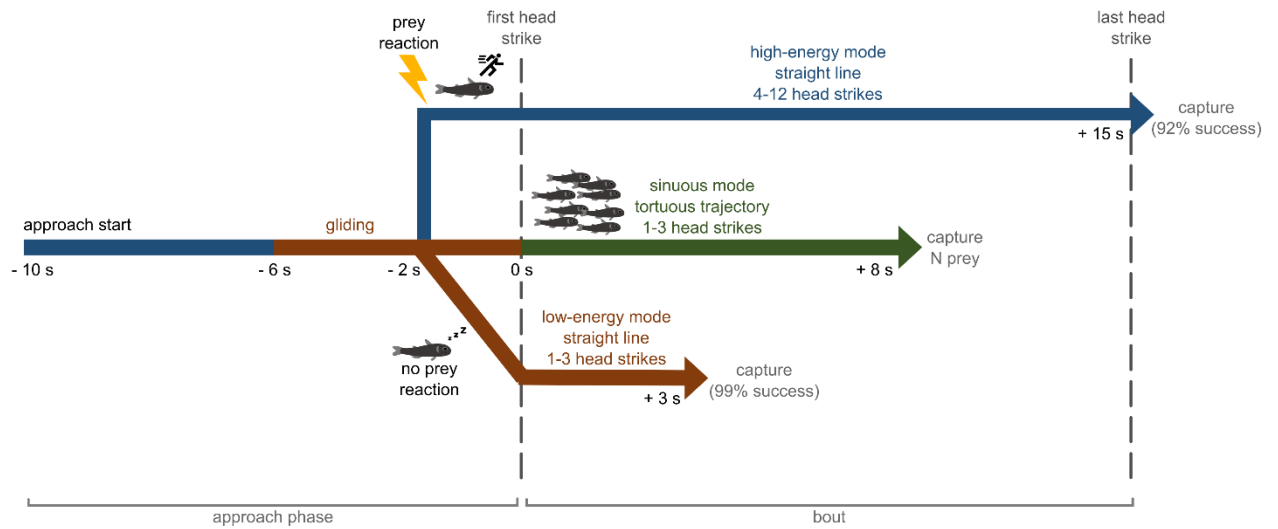
706

## 707 Figures



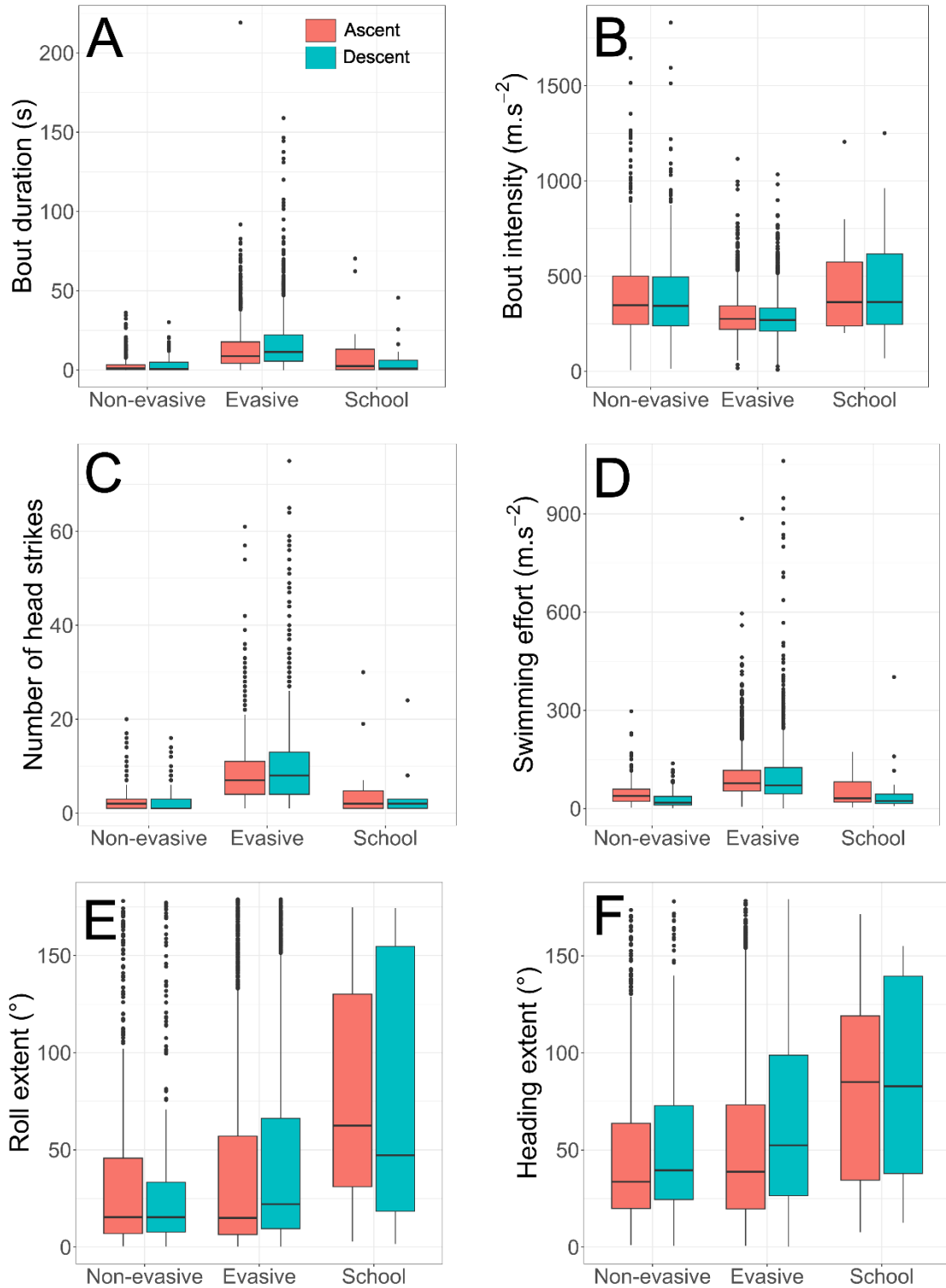
708

709 Figure 1: Acoustic size distribution of prey targeted by nine female SES equipped with  
710 high-resolution movement and sonar tags in Kerguelen Islands between 2018 and  
711 2020. Prey acoustic sizes were estimated from the -20 dB echo pulse width measured  
712 on the widest part of the prey echo trace. A mixture model was applied which identified  
713 three normal distributions in the acoustic size data. The number of components of the  
714 mixture model was chosen *a priori* after visualising the prey acoustic size distribution.



715

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

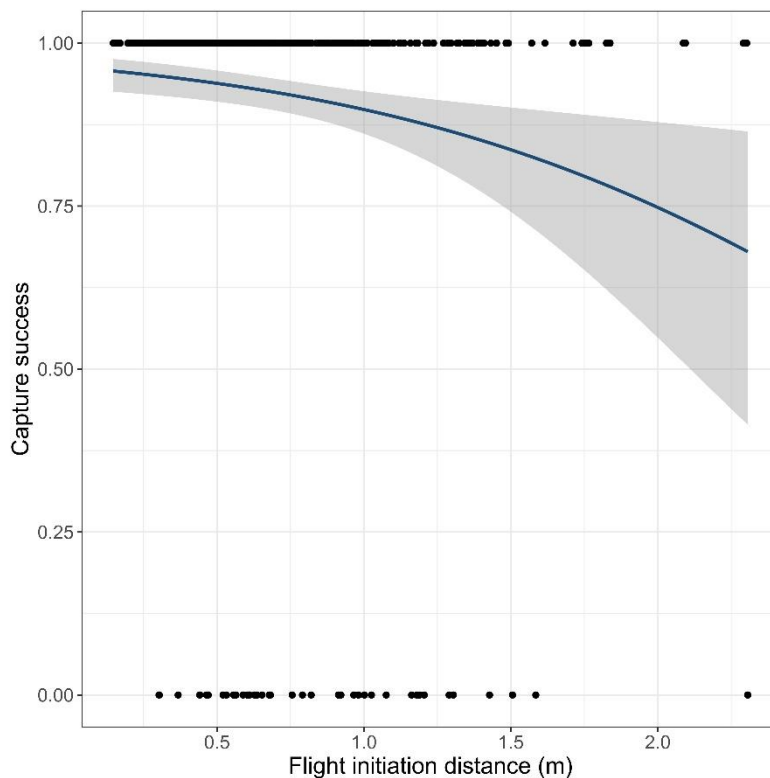


724

725 Figure 3: Characteristics of prey-dependant hunting behaviour of nine female SES

726 equipped with high-resolution movement and sonar tags in Kerguelen Islands between

727 2018 and 2020. Behavioural metrics were derived from accelerometer and  
728 magnetometer data recorded between the 10 seconds preceding each bout and the  
729 last strike of the bout: ((A) bout duration (s), (B) bout intensity ( $m.s^{-2}$ ), (C) number of  
730 head strikes, (D) swimming effort ( $m.s^{-2}$ ), (E) roll extent ( $^{\circ}$ ) and (F) heading extent ( $^{\circ}$ )).  
731 Letters in superscript indicate significant differences in behavioural parameters  
732 between prey types (GLMM,  $P < 0.05$ ). The box's bottom side represents the first  
733 quartile of the data, the line in the middle of the box represents the median of the data  
734 and the box's upper side represents the third quartile of the data. The bottom whisker  
735 shows the minimum data value and the upper whisker shows the maximum data value.  
736 Dots represent outlier values.



737  
738 Figure 4: Effect of prey flight initiation distance (m) on prey capture success, modelled  
739 using a mixed-effects logistic regression ( $P = 0.0026$ ). Prey capture success was  
740 estimated from sonar recordings on 490 bouts for which prey reaction timing was

741 inferred, for nine female SES equipped with high-resolution movement and sonar tags  
 742 in Kerguelen Islands between 2018 and 2020.

## 743 Appendix

744 Table A1. Definitions, parameters and p-values of models presented in the main text.  
 745 We build multiple models because parameters on prey type (schooling vs. single prey,  
 746 prey evasive behaviour, flight initiation distance) were strongly interrelated.

<b>Response variable</b>	<b>Fixed effect (the base category is italicized)</b>	<b>Random effect</b>	<b>Intercept</b>	<b>Coefficient</b>	<b>P-value</b>
Bout duration (s)	Prey type (schooling vs. <i>single prey</i> )	SES identities	4.0 ± 0.6	5.3 ± 1.7	< 0.001
	Prey type (single evasive prey vs. <i>single non-evasive prey</i> )	SES identities	4.0 ± 0.6	11.3 ± 0.4	< 0.001
	Flight initiation distance (m)	SES identities	10.2 ± 1.7	7.8 ± 0.7	< 0.001
Bout intensity (m.s <sup>-2</sup> )	Prey type (schooling vs. <i>single prey</i> )	SES identities	390.7 ± 15.2	54.1 ± 28.6	0.0588
	Prey type (single evasive prey vs. <i>single non-evasive prey</i> )	SES identities	390.7 ± 15.2	-107.7 ± 5.7	< 0.001

Number of head strikes	Prey type (schooling vs. <i>single</i> prey)	SES identities	3.2 ± 0.4	1.9 ± 0.6	0.0019
	Prey type (single evasive prey vs. <i>single non-evasive</i> prey)	SES identities	3.2 ± 0.4	6.2 ± 0.2	< 0.001
	Flight initiation distance (m)	SES identities	6.1 ± 0.9	5.1 ± 0.3	< 0.001
Swimming effort (m.s <sup>-2</sup> )	Prey type (schooling vs. <i>single</i> prey)	SES identities	39.9 ± 4.1	9.3 ± 7.6	0.2218
	Prey type (single evasive prey vs. <i>single non-evasive</i> prey)	SES identities	39.9 ± 4.1	55.4 ± 2.2	0.001
	Flight initiation distance (m)	SES identities	65.9 ± 8.9	39.0 ± 4.0	< 0.001
Roll extent (°)	Prey type (schooling vs. <i>single</i> prey)	SES identities	39.5 ± 3.7	43.1 ± 15.2	0.0045
	Prey type (single evasive prey vs. <i>single non-evasive</i> prey)	SES identities	39.5 ± 3.7	3.8 ± 1.6	0.0213



Heading extent (°)	Prey type (schooling vs. <i>single</i> prey)	SES identities	51.6 ± 2.9	34.9 ± 10.5	< 0.001
	Prey type (single evasive prey vs. <i>single non-evasive</i> prey)	SES identities	51.6 ± 2.9	6.9 ± 1.4	< 0.001
Approach mode (high vs. low energy mode)	Flight initiation distance (m)	SES identities	0.05 ± 0.4	0.85 ± 0.19	< 0.001
Capture success (binary)	Flight initiation distance (m)	SES identities	0.96 ± 0.34	-0.26 ± 0.36	0.0026

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