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Inter-site variability in the Cape fur seal's behavioural response to boat noise exposure

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Abstract

The impact of man-made noise on wildlife is recognised as a major global concern affecting many taxa in both terrestrial and aquatic ecosystems, with the degree of impact varying among individuals or species. Understanding the factors inducing intra-species differences in response to noise is essential for the development of adapted and effective mitigation measures. This study compares the behavioural response of Cape fur seals to boat noise exposures at two study sites showing differences in their level of exposure to anthropogenic activities, and individual composition. Increased vigilance was found for Lambert’s Bay seals exposed to high noise level (70-80 dB) compared to those tested at Cape Town harbour. Comparisons with a similar study performed in Namibia were made. Intrinsic factors such as individuals’ age-class, sex or arousal state as well as extrinsic factors such as the ambient noise and the nature/extent of human-seal interactions were suggested to induce such variation.

Keywords

Noise pollution - Cape fur seal - Playback experiment - Intra-species variation - Animal Behaviour

Highlights

- Cape fur seals’ reaction to boat noise exposure was compared across study sites
- Multiple intrinsic and extrinsic factors could drive their behavioural response
- Individuals’ age, sex and arousal state may induce behavioural inter-site variation
- Ambient noise and human-seal interactions are suggested to be influential factors

1. Introduction

25 Due to the continuous expansion of human activities on earth, anthropogenic noise exposure is
26 a widespread phenomenon, involving both terrestrial and aquatic ecosystems (Buxton et al.,
27 2017; Shannon et al., 2015). It is therefore an issue that has received great attention in the last
28 decade. (Duarte et al., 2021; Shannon et al., 2015). Based on an extensive body of research
29 applying both experimental and observational approaches, it is now well documented that
30 anthropogenic noise exposure may have various negative impacts on animals ranging from
31 behavioural modifications (e.g. alteration of anti-predator, foraging or communication-related
32 behaviours), physical or physiological impacts (e.g. hearing ability, body condition, stress level,
33 physical trauma), to reproductive or developmental issues (e.g. fecundity changes, egg/larval
34 development), and even death (for reviews see Barber et al., 2010; Duarte et al., 2021; Erbe et
35 al., 2016; Shannon et al., 2015). The effects of these impacts, alone or in combination, have
36 critical consequences for the survival and reproduction of individuals, jeopardising the
37 sustainability of populations and species (Barber et al., 2010).

38 Many factors are known to cause intra-species variations in animals' response to
39 anthropogenic disturbance (Harding et al., 2019; Radford et al., 2015), making the
40 interpretation of studies (and their direct application within conservation strategies) subject to
41 limitations. First, variation in behavioural responses can be caused by extrinsic factors such as
42 the time of day (Neo et al., 2018) or the characteristics of the habitat, i.e. urban vs. rural (Davies
43 et al., 2017; Gentry et al., 2017) or protected vs. unprotected (Mensinger et al., 2018). Secondly,
44 intrinsic factors such as anatomical or physiological characteristics can have a significant effect
45 on how noise exposure impacts individuals themselves. Such variations can be the result of
46 differences in sex (Bruitjes and Radford, 2013; Mancera et al., 2017), age-class (Casper et al.,
47 2013; Houser et al., 2013; McClure et al., 2017), body condition (Potvin and MacDougall-
48 Shackleton, 2015; Purser et al., 2016), hearing abilities (Radford et al., 2015) or personality
49 (Naguib et al., 2013). As many of these intrinsic and extrinsic factors are dynamic over time,
50 the responses of specific individuals to the same noise disturbance may also change over time:
51 individuals may become sensitised or habituated to these stimuli (Bejder et al., 2009). When
52 under repeated exposure, the basal or naïve response level of an individual may be progressively
53 lowered, leading to greater tolerance of the disturbance, a process defined as 'habituation'
54 (Bejder et al., 2009; Harding et al., 2019). On the contrary, a repeated exposure can also lead
55 to an increase in the individual's responsiveness over time; this is defined as 'sensitisation'

56 (Bejder et al., 2009). For these reasons, extrapolating results obtained on a limited size group
57 or cohort of animals could therefore lead to under- or over-estimating the effect of man-made
58 noise exposure (or even in a broader sense, to an anthropogenic disturbance) on a particular
59 species (Bejder et al., 2009). Despite a large number of studies assessing the impact of noise on
60 a given species, inter-individual variation to noise impact is an aspect that is often overlooked
61 (Harding et al., 2019). Yet, understanding how biological or environmental drivers can play a
62 role in animals' response to anthropogenic noise should be considered in the development of
63 mitigation strategies. This may allow policies to be adapted to populations with different life
64 histories and living in different conditions.

65 Pinnipeds (seals, fur seals, sea lions and walruses) are semi-aquatic marine mammals
66 exposed to anthropogenic noise both under water and on land due to their amphibious lifestyle.
67 For colonial breeding pinniped species such as fur seals, the existence of different cohorts of
68 animals (breeding animals in colony vs non-breeding animals in haul-out sites) is likely to result
69 in different noise exposure conditions and responses between groups. In addition, as the
70 geographical range of these species is generally wide, colonies and haul-out sites are established
71 in very different environments with varying natural characteristics and for which the proximity
72 and the level of exposure to human activities may differ as well. For fur seals, the time spent
73 onshore during the breeding season is challenging as all behaviours related to reproduction and
74 young rearing are energetically demanding. Anthropogenic disturbance during this time will
75 therefore likely impact their fitness and breeding success.

76 Little is known about the effect of anthropogenic airborne noise on the behaviour and/or
77 physiology of colonial pinnipeds on land. A few studies have assessed the effect of extreme
78 events (such as missile or rocket launches and military explosions, Demarchi et al., 2012; Holst
79 et al., 2011, 2005; Stewart, 1993, 1981), but to date, only two studies have investigated the
80 effect of chronic noise exposure on land-based pinnipeds: car and/or boat motor noise on
81 Australian (*Arctocephalus pusillus doriferus*) and Cape fur seals (*Arctocephalus pusillus*
82 *pusillus*) (Martin et al., 2022; Tripovich et al., 2012). Both studies were conducted at a single
83 study site, limiting the potential for generalisation across the species range. Further
84 investigations are thus needed to better understand whether intra specific differences in
85 response (e.g., noise avoidance, increase of vigilance or aggressive behaviour, decrease of
86 resting, stress) to noise exposure exists and whether such differences relate to intrinsic or
87 extrinsic factors (environment, prior exposure, physiological/behavioural contexts).

88 The Cape fur seal is distributed along the southwest and south coasts of Southern Africa,
89 from Southern Angola to Algoa Bay in South Africa. Across this large distribution range, Cape
90 fur seal populations are exposed to different types and levels of anthropogenic activities. This
91 species is therefore a good model to investigate intra-species variation in responses to human-
92 made noise exposure. In a recent study, Martin *and colleagues* (2022) have evaluated the
93 behavioural response of Cape fur seals to short-term boat motor noise exposure at Pelican Point
94 breeding colony in Namibia. The number of seals in the focal groups was reported to decrease
95 during the noise exposure (Martin et al., 2022). Energetically costly behaviours such as the time
96 individuals spend awake, vigilant or in locomotion were increased to the detriment of vital
97 activities like resting and nursing (Martin et al., 2022). The present study aimed to use the same
98 experimental approach (playback experiments with broadcast of in-air boat motor noise) at two
99 other sites located in South Africa: Lamberts Bay (LB, a breeding colony adjacent to a small
100 harbour, low ambient noise) and Cape Town Harbour (CT, a haul-out site within the limits of
101 a major commercial harbour, high ambient noise). The sites have different levels of exposure
102 to anthropogenic activities, as well as different individual compositions (mother-pup pairs for
103 LB vs mostly juveniles and subadult males for CT), enabling comparisons of factors that might
104 contribute to intra-species variation in the behavioural response of Cape fur seals to boat motor
105 noise. We expect that animals from CT already exposed to anthropogenic activities will be less
106 impacted by our noise exposure experiments than those from LB less habituated to high level
107 of human activities.

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2. Materials and methods

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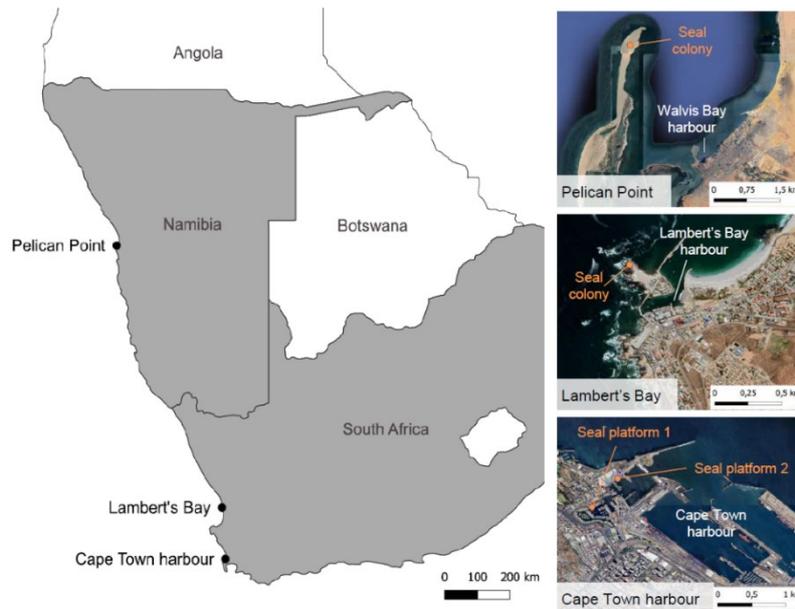
2.1 Study sites

111 Playback experiments were conducted outside the breeding season, at two sites in South Africa:
112 Lambert's Bay and Cape Town Harbour (Figure 1). At Lambert's Bay, data were collected on
113 six days, between the 26th of April and the 1st of May 2021. Experiments at Cape Town harbour
114 were conducted on nine days, between the 2nd and the 20th of April 2021.

115 The Lambert's Bay Cape fur seal breeding colony is located on Bird Island (South
116 Africa, 32°05'18"S 18°18'03"E), a protected nature reserve about 360 meters adjacent to the
117 small coastal town of Lambert's Bay and its associated harbour (between the two nearest
118 points). The island has been joined to the mainland by a causeway which forms the harbour

119 wall. Seals are gathered in the western part of the island (ocean side), in a small area which is
120 approximately 100 meters wide and 60 meters long, although the number of seals using the
121 island has not been formally quantified. The eastern side of the island hosts a Cape Gannet
122 (*Morus capensis*) colony which is the main public viewing attraction on the island and the only
123 place the general public can access. Cape fur seals thus have very low exposure to humans on
124 the island, there are no vehicles on the island and they only experience occasional visits from
125 the reserve rangers on foot. The rangers gently keep the seals away from the gannets when the
126 seals spread out too much or when there is a risk of agonistic interactions with the birds. The
127 area is rocky and depending on the weather conditions, highly exposed to wind and swell, with
128 waves breaking on the rocks of the island. As the colony is located in close proximity to the
129 harbour, seals resting on land are exposed to daily passage of vessels (mostly small to medium-
130 sized fishing vessels powered by either outboard motors or inboard diesel engines). During the
131 time of our study, the colony was composed of mother-pup pairs (4 to 6-month old pups), as
132 well as juveniles and subadult individuals.

133 At the Cape Town harbour, seals rest on two floating platforms in the Victoria Basin.
134 The first is a wooden platform (33°54'29"S 18°25'05"E) measuring about 10 by 10 meters and
135 that has been installed right next to the Two Oceans Aquarium for public observation of these
136 wild Cape fur seals. The second (33°54'13" 18°25'19"E) is about 600 meters further on and is
137 a permanent floating pontoon for boat access on which seals haul out. Around these harbour
138 haul-out sites, seals are exposed on a daily (even hourly) basis to passing vessels ranging from
139 small outboard powered tour ferries and launches to yachts and larger fishing vessels as well as
140 commercial shipping in the outer reaches of the harbour. They are additionally exposed
141 to human activities and noises from the land side including tourists and loud noises from the
142 shipyards. Seals hauling-out at the harbour were only males, ranging from juvenile to full adult
143 individuals while we carried out our study, but females can be also seen at this site.



144 **Figure1:** Map of Southern Africa with locations of Lambert's Bay breeding colony and Cape
 145 Town harbour (left, Pelican Point breeding colony in which a similar study was conducted
 146 recently (Martin et al., 2022) is indicated as well). Satellite view of the three study sites (right).
 147

148 2.2 Boat noise playback procedure

149 Since the aim of this study was to replicate an experimental study conducted on Cape fur seals
 150 in Namibia at different locations in South Africa, we used the exact same protocol as the one
 151 described by Martin *and colleagues* (2022).

152 Focal groups were defined as clusters of a minimum of 4 individuals positioned in close
 153 proximity to each other, within a 3 to 4 m diameter. The behaviour of all individuals had to be
 154 visible from the observer's location during the experiment. We minimised the risk of testing
 155 the same individual several times by carrying out the experiments over several days and/or at
 156 several locations (different places in the colony for Lambert's Bay and by testing the two
 157 platforms of Cape Town harbour once a day only).

158 The boat motor noise playback experiments were performed with the same stimulus
 159 broadcasted in Martin *and colleagues'* study (2022) in order to mimic the presence of a boat.
 160 In the present study, we used a waterproof and wireless high-powered loudspeaker (JLB Xtreme
 161 3, 2 x 25W, frequency response: 53.5-20,000 Hz) connected to a Bluetooth sound player
 162 (Roland – R-07 RD). Received levels were as followed: 60.9–64.4 dB re 20 μ Pa RMS SPL for
 163 low, 64.4–70.5 dB re 20 μ Pa RMS SPL for medium and 70.5–80 dB re 20 μ Pa RMS SPL for

164 high exposure, and were verified with a ‘Testo 815’ sound level meter (‘A’ weighting, fast
165 response). The loudspeaker was positioned at 10 meters from the focal group and the broadcast
166 amplitude was pre-calibrated to match the above received levels in the focal group (the range
167 of RLs corresponds to the level received at the front and at the back of the focal group). Each
168 focal group was exposed to only one of the three noise levels and the broadcast level was chosen
169 randomly. We conducted a 10-min habituation period after placing the speaker at 10 m from
170 the focal group, and each test session was composed of the same three phases: a pre-playback
171 phase of 10 min of observation (from t_0 to t_{10}), a 2-min boat motor noise exposure (from t_{10} to
172 t_{12}) and a post-playback phase lasting 10 min (from t_{12} to t_{22}) (Martin et al., 2022). At Lambert’s
173 Bay, experiments were carried out whenever possible during the day while at Cape Town
174 Harbour, we avoided the noisy time of day (due to intense boat traffic or works on boats) and
175 we conducted playback experiments early in the morning (between 6.30 am and 9 am) or late
176 afternoon (after 5 pm).

177 **2.3 Boat motor noise playback procedure and statistical analyses**

178 The videos of the Lambert’s Bay and Cape Town harbour sessions were analysed in the same
179 way as in Martin *and colleagues*’ study (2022) to investigate the same four aspects of the seal’s
180 behavioural response to the exposure of boat motor noise: avoidance of the noise source, overall
181 behavioural response to the playback, behavioural modification during noise exposure and
182 behavioural modification following noise exposure. Seals exposed to the boat motor noise were
183 divided into five age/sex categories: pups (< 1-year-old), juveniles (1- to 3-year old and not
184 sexually mature), subadult males (< 8-year-old), adult females and full adult males i.e. bulls.

185 *Avoidance of the noise source* – The number of individuals present in the focal group
186 was noted at the start and end of each of the three phases (t_0 , t_{10} , t_{12} and t_{22}). To test whether the
187 number of individuals varied significantly during experiments, we fitted a generalized linear
188 mixed-effects model (GLME) assuming a Poisson error structure (as the response variable is a
189 count). The number of individuals was set as a ‘response variable’ while the phase (t_0 , t_{10} , t_{12}
190 and t_{22}), the study site (Lambert’s Bay and Cape Town harbour) and the noise level (low,
191 medium or high) were set as ‘fixed effects’. In addition, playback experiment was defined as a
192 ‘random effect’ to account for the fact that data are not independent (each experiment consists
193 of monitoring one focal group over time). The model was run with the *lme4* R package (Bates
194 et al., 2015) and p-values were obtained using the *car* package (Fox and Weisberg, 2019). The

195 absence of over-dispersion in the model was verified using the *performance* package (Lüdecke
196 et al. 2021). A pairwise analysis of estimated marginal means was conducted to compare
197 significant fixed effects using the *emmeans* package in R (Lenth, 2021). It included a Šidák
198 correction for multiple comparisons.

199 *Behavioural response to noise exposure* – The overall response of each individual to the
200 2-minute boat motor noise exposure was rated on an ethological scale as follow: 0: no response,
201 1: eye-movement towards the noise source without change of posture, 2: prolonged look
202 towards the noise source, change of posture (e.g. lying down to sitting) and signs of alertness,
203 3: slight retreat from the noise source defined as a 1-3 m movement away from the source, 4:
204 significant retreat from the noise source defined as the individual leaves the focal group (i.e.,
205 on video, individual is out of view) (Martin et al., 2022). Individual responses were compared
206 among study sites and noise levels through a cumulative link mixed model (CLMM) using the
207 *ordinal* R package (Christensen, 2019). As above, the focal group was set as ‘random effect’.
208 A pairwise analysis of estimated marginal means was conducted to compare significant effects
209 using the *emmeans* package in R (Lenth, 2021).

210 *Behavioural modification during noise exposure* – The activity budget of individuals
211 was evaluated during the last 2 min of pre-playback and the 2 min of noise playback. The
212 activity of each individual was point sampled once every 10 s for each 2-min period and
213 described as: sleep, awake, vigilance, nursing, agonistic interaction, nuzzling, locomotion
214 (Table1). In the case of coexistence between two behaviours, we prioritized vital activities. For
215 instance, a female showing signs of vigilance while nursing her pup was assigned as nursing.
216 Observations were converted into percentage of time spent in each activity. A linear mixed-
217 effects model (LME) was performed with the phase, the study site and the noise level set as
218 ‘fixed effects’ and the individual defined as ‘random effect’ for each of the seven behavioural
219 variables reported (Martin et al., 2022). A pairwise analysis of estimated marginal means was
220 conducted to compare pre-playback and playback values for each site and each noise level.

221 To investigate possible differences in seals’ behavioural modification according to their
222 age/sex category (pup, juvenile, subadult male or adult female), additional LME models were
223 performed per study site with the phase, the noise level and the age/sex category set as ‘fixed
224 effects’ for each of the seven behavioural variables and the individual was defined as a ‘random
225 effect’. LME were performed using the *lme4* package in R (Bates et al., 2015).

226 **Table 1:** Description of the behavioural activities considered in the study (extracted from
 227 Martin et al., 2022).

Activity	Description
Sleep	A seal lying down with closed eyes
Awake	A seal sitting in a resting position and looking at its surroundings
Vigilance	An alert seal, sitting and looking attentively towards a conspecific or the noise source
Nursing	A suckling pup or a nursing female
Agonistic interaction	A seal threatening a conspecific e.g. production of growl(s) or bark(s), open-mouth displays, physical aggression (bites)
Nuzzling	A seal touching the muzzle or any other part of another seals body, using its muzzle
Locomotion	A seal walking or running

228

229 *Behavioural modification following noise exposure* – The activity budget of individuals
 230 was compared between the 10 min of pre-playback phase and the 10 min of post-playback phase
 231 (one observation every 30 s). We used the same method as the previous section: a LME with
 232 the three ‘fixed effects’ and the ‘random effect’ for each of the seven behavioural variables
 233 considered. Differences between age/sex categories were also investigated using the same
 234 method as the previous section.

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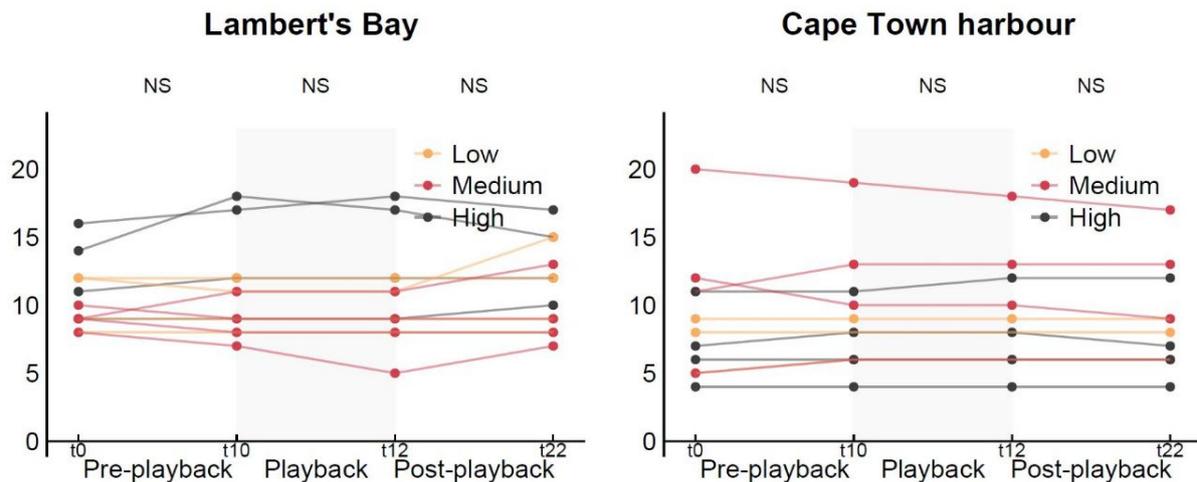
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3. Results

237 A total of 23 sessions were carried out: 12 at Lambert’s Bay and 11 at Cape Town harbour. In
 238 both study sites, four groups were exposed to a high level of noise and four to a medium level.
 239 For the low level, four experiments were performed at Lambert’s and three at Cape Town
 240 harbour. At Lambert’s Bay, the 12 experiments involved a total of 131 individuals present in
 241 focal groups at the time of the playback (focal group size ranged from 8 to 16 individuals).
 242 Focal groups consisted mostly of females (n=70), pups (n=30) and juveniles (n=23), with a
 243 small number of subadult males (n=8). At Cape Town harbour, a total of 99 individuals were
 244 tested during experiments and all were male. Here the focal groups, ranging in size from 4-20
 245 individuals, consisted of mostly subadults (n=73), with some juveniles (n=25) and one adult.

3.1 Avoidance of the noise source

247 Results reported no change in the number of seals in the focal group throughout each of
 248 the three playback phases (GLME; $p=0.989$) in both Lambert's Bay and Cape Town harbour,
 249 and for the three playback levels (GLME; no significant interactions between phase*study site,
 250 phase*noise level or phase*study site*noise level, $p > 0.05$ in all cases) (Figure 2). Therefore,
 251 we found no avoidance response to boat motor noise during our experiments in South Africa.



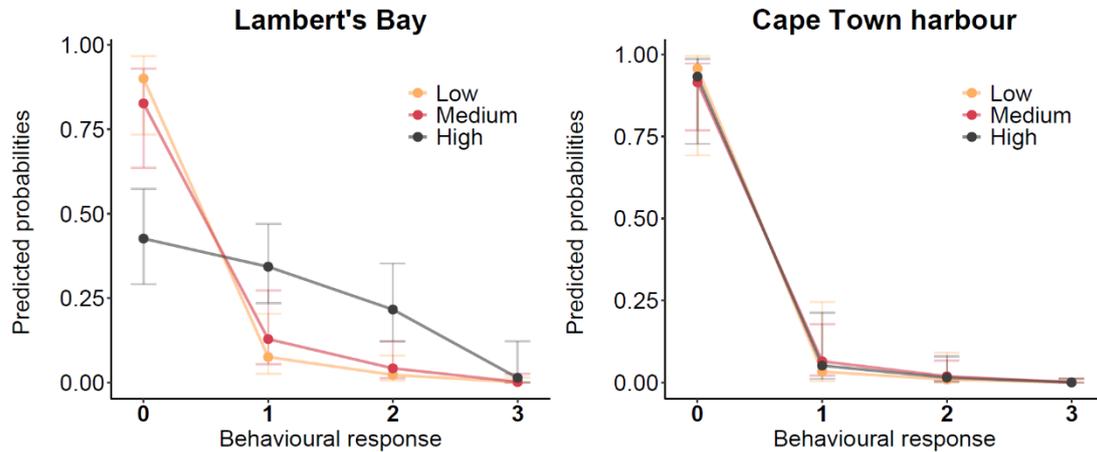
252 **Figure 2:** Number of individuals within the focal groups throughout each of the 3 playback
 253 phases for experiments conducted at Lambert's Bay and Cape Town harbour. *The significance*
 254 *of the results was tested using a pairwise analysis of estimated marginal means following a*
 255 *linear mixed effects model (NS: not significant).*

3.2 Behavioural response to noise exposure

257 Both the study site and the noise level had a significant effect on the behavioural
 258 response of seals (CLMM; $p = 0.0012$ for both) but no interaction between the two variables
 259 was found (CLMM; level*study site, $p = 0.1030$). At Lamberts Bay, seals' behaviour remained
 260 unchanged at low and medium playback levels i.e. no response, coded 0 on the ethological
 261 scale. Conversely, the high-level noise exposure elicited stronger behavioural responses: the
 262 proportion of responses 0, 1 and 2 is more similar between these 3 levels of the ethological
 263 scale, showing a net decrease in no responses (0) and an increase in the proportion of response
 264 1 and 2 compared to the low and medium playback levels. Almost half of the seals did not react
 265 and the other half increased vigilance during high noise level exposures (look towards the
 266 loudspeaker, change of posture, sign of alertness, Figure 3). For Cape Town harbour, the

267 behaviour of most seals remained unchanged across playback phases for all noise levels
268 (response 0).

269 **Figure 3:** Predicted probabilities and 95% confidence interval (from CLMM) of seals'
270 individual behavioural responses across the four levels of the ethological scale from 0 – no
271 response to 3 – strong responses, for experiments conducted at Lambert's Bay and Cape Town
272 harbour, South Africa.



273 3.3 Behavioural modification during noise exposure

274 The proportion of time spent by individuals in each behavioural activity was compared
275 between the last 2' of the pre-playback phase and the 2'-playback phase, for each level of noise
276 exposure (low, medium and high) at Lambert's Bay and Cape Town harbour (Supplementary
277 Fig. S1). Linear mixed-effects models revealed a significant variation in the time seals spent
278 sleeping and vigilant between the pre-playback and the playback phase, with an effect of both
279 the study site and the noise level (the interaction phase*study site*noise level had $p = 0.042$ for
280 the activity 'sleep' and $p = 0.001$ for 'vigilance'). Time spent sleeping decreased by 19.9% for
281 the high level of noise in Lambert's Bay and did not change for low and medium levels while
282 it did not change at all for the three levels in Cape Town harbour (Table 2). Similarly, time
283 spent vigilant increased only at Lambert's Bay during high-level exposures (+13.3%) while no
284 change was found for low and medium levels, or for any level played at Cape Town harbour
285 (Table 3). The five other behavioural variables ('awake', 'nursing', 'agonistic interactions',
286 'nuzzling' and 'locomotion') did not show any change between the two phases at both sites.

287 The behavioural response of individual seals during noise exposure was investigated
288 according to their age/sex category for each study site separately because the composition of
289 focal groups differed among sites (Table 3). Only age/sex categories with more than 10

290 individuals were included. For both Lambert’s Bay and Cape Town harbour experiments, no
 291 effect of the age/sex category of individuals on their behavioural response during noise
 292 exposure was found for any behavioural variable (p always > 0.05 for phase*noise
 293 level*age/sex category interaction and for phase*age/sex category interaction).

294 **Table 2:** Changes in seals’ activity budget between the pre-playback and the playback phases
 295 for experiments conducted at Lambert’s Bay and Cape Town harbour. *Stars results from*
 296 *pairwise analysis of estimated marginal means following a linear mixed effects model and*
 297 *indicate whether the activity budget is significantly different between the two phases*
 298 *(Significance code: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘NS’ 1). An increase of the activity during*
 299 *the noise playback (PRE < PB) is indicated in dark grey and a decrease (PRE > PB) in light*
 300 *grey. The intensity of the variation is expressed in percentage of time spent in this activity.*

301

		Sleep	Awake	Vigilance	Nursing	Agonistic interaction	Nuzzling	Locomotion
Lambert’s Bay	Low	NS	NS	NS	NS	NS	NS	NS
	Medium	NS	NS	NS	NS	NS	NS	NS
	High	*** - 19.9%	NS	*** + 13.2 %	NS	NS	NS	NS
Cape Town harbour	Low	NS	NS	NS	NA	NS	NS	NS
	Medium	NS	NS	NS	NA	NS	NS	NS
	High	NS	NS	NS	NA	NS	NS	NS

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303

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305

306 **Table 3:** Summary of the number of seals included in the analysis of parts 3.3 and 3.4 of the
 307 present study, for each age/sex category and per study site. *Categories with less than 10*
 308 *individuals were not included in the study of seals’ behavioural response per age/sex category*
 309 *and are indicated in grey in Table 2.*

310

		Pups	Juveniles	Subadult males	Adult females
3.3 Behavioural modification during noise exposure					
Lambert’s Bay		26	21	8	64
Cape Town harbour		0	24	72	0
3.4 Behavioural modification following noise exposure					
Lambert’s Bay		21	16	8	60
Cape Town harbour		0	22	69	0

341 With regard to the comparison between Lambert's Bay and Cape Town harbour, the first
342 analysis showed that both seals tested at LB and CT did not spatially avoid the disturbance zone
343 during noise exposure, regardless of the broadcast noise level. At these sites, boat noise was not
344 considered as a severe and immediate threat that would force individuals to urgently leave the
345 area. Although individuals from both sites reacted similarly in this aspect, differences in their
346 behavioural responses to the noise and in the modification of their activity budget were
347 observed both between sites and within focal groups. Seals at Cape Town harbour, displayed a
348 high threshold to noise disturbance, with no apparent behavioural changes to any received levels
349 of engine noise. The threshold of response differed at Lambert's Bay, with changes in behaviour
350 and activity budget indicated when the received level was considered high but not for medium
351 or low levels. Consequently, the Lambert's Bay seals were considered more sensitive to noise
352 disturbance compared to those in Cape Town Harbour.

353 The only significant difference in behavioural responses between the two study sites
354 was obtained for the high level of noise. While Cape Town harbour individuals did not show
355 any behavioural changes at this level, the Lambert's Bay seals showed greater behavioural
356 modifications. Indeed, while less than half of the animals did not respond at all, the other half
357 looked briefly or extensively at the noise source. Regarding their activity budget, we reported
358 a decrease of 19.9% in time they spent sleeping and a 13.2% increase in time spent vigilant.
359 Exposure to boat noise at high levels (70 to 80 dB re 20 μ Pa RMS SPL) appeared to be more
360 threatening to the animals of Lambert's Bay colony than to those hauling-out at Cape Town
361 harbour. Such inter-site variation may have multiple explanations as the two sites differ in many
362 ways: one is a breeding colony and the other is a haul-out site. First, the social groups differed
363 greatly in their composition between the two sites. At Lambert's Bay, tested animals were
364 mainly adult females, 4-6-month old pups and juveniles whereas focal groups of Cape Town
365 harbour were composed of only juveniles and subadult males. Age-class or sex of individuals
366 were reported to influence the individuals' behavioural reaction to anthropogenic noise in
367 several species such as birds (Injaian et al., 2018; McClure et al., 2017), pinnipeds (Houser et
368 al., 2013), fishes (Bruitjes & Radford, 2013) or rodents (Avaliani et al., 2018). A second
369 explanation would be the behavioural and/or arousal state of the tested animals, due in particular
370 to different social contexts between the two sites. Although it was out of the breeding season
371 (mating and pupping) and subadult males do not breed, subadult males stay in colonies and
372 exhibit similar behaviours to that of bulls holding harems. They compete for space and engage
373 in agonistic behaviours, with a relatively high state of arousal. This can thus impact the females'

374 behaviour as they are caught in these agonistic interactions and sometimes it leads to fights
375 between females trying to protect their pup or to keep their own space in the colony. In contrast,
376 the platforms in Cape Town port are resting places for males that come and go. Competition
377 for space is very limited and social interactions between males can be considered as practicing
378 breeding behaviour but without any strong aggressiveness. For instance, we have observed
379 juvenile males trying to mount older males. The latter were moving to escape but not biting the
380 young conspecifics. It is a behavioural response that would not happen during the breeding
381 season. These differences in individuals' behaviours and arousal states are likely to induce
382 differences in response to noise between sites. It can be hypothesized that because of the
383 instability of interactions on the colony at Lambert's Bay, seals would be more reactive and
384 alert to high-levels of disturbance. In two fish species, inter-individual variation in response to
385 boat-noise playback was related to reproductive context (presence or absence of eggs in the
386 nest, Bruintjes & Radford, 2013) or territorial status (resident vs intruder, Sebastianutto et al.,
387 2011). Another potential source of behavioural differences in the response to high levels of
388 noise is the density of seals at each site. On Cape Town seal platforms, a maximum of several
389 dozen individuals can be found together at a time while at Lambert's Bay the total population
390 represents several thousand individuals (Kemper et al., 2007). Group size is a factor whose
391 effect on the response to anthropogenic noise has been demonstrated before (Filiciotto et al.,
392 2014; Handegard et al., 2015). In fur seals, observations showed that the reaction of one or few
393 individuals can spread to many other individuals very rapidly through allelomimetic behaviours
394 (Martin et al., 2022). In large groups, a strong global reaction is thus expected compared to
395 small groups.

396 The consistency in methodology between this study and the previous one at Pelican
397 Point, Namibia (Martin et al., 2022) enables comparisons to be made between three very
398 different colonies. At Pelican Point, Cape fur seals' behavioural response to boat-noise
399 exposure were significantly stronger than in South Africa. At this site, no difference was
400 observed between the three noise levels. A significant part of the tested seals exposed to noise
401 levels ranging from 60.9 to 80 dB dB re 20 μ Pa RMS SPL left the exposure area during the
402 broadcast of noise. About half of them were reported to look at the noise source and for a long
403 duration during the 2-min playback phase. About 20% of them moved 1 to 3 meters away from
404 the source and the same proportion clearly left the focal group area. Finally, both females and
405 pups' activity budget (subadult males and juveniles were not considered in this analysis) were
406 significantly modified during the playback phase: activities such as sleeping or nursing

407 decreased from 15.4 to 45 % (nursing was unchanged for low noise level exposures) and the
408 time spent awake, vigilant or in locomotion increased from 2.1 to 31.2 % (Martin et al., 2022).

409 Pelican Point is a large breeding colony with a high abundance of individuals compared
410 to Lambert's Bay and the size of the groups hauling-out in Cape Town harbour. Again, recent
411 counts are lacking but the number of individuals is estimated to be around 90,000 during the
412 breeding season (N. Dreyer, 2023, personal communication). As mentioned above, differences
413 in animal density could be a possible explanation for such increased behavioural response there.
414 At Pelican Point, tested groups had a similar composition to Lambert's Bay: it was mostly
415 females with their 4-6-month old pup and few yearlings and subadult males (n=14 and 8
416 respectively). Intrinsic factors such as age, sex as well as reproductive context could therefore
417 contribute to the differences in response of individuals between Cape Town harbour and Pelican
418 Point, but are less likely to explain differences between Lambert's Bay and Pelican Point.

419 We suggest that additional extrinsic factors may drive intra-species differences in Cape
420 fur seals' behavioural response to boat-noise exposure. The first concerns the level of boat
421 motor noise – or more generally – low-frequency anthropogenic noise, to which the site is
422 exposed on a daily basis. At Cape Town harbour, the ambient noise generated by vessels in the
423 harbour (boat traffic and work at shipyards) is very high. Although not systematic, several
424 measurements of ambient noise levels performed in the middle of the day (next to the platforms
425 where the seals were tested) revealed an average level ranging from 67 to 80 dB re 20 μ Pa RMS
426 SPL (measured with a 'Testo 815' sound level meter). The noise levels that were broadcast
427 during our experiments correspond to lower or similar noise levels to which these animals are
428 exposed on a daily basis. At Lambert's Bay, seals experience the passage of small to medium-
429 sized fishing vessels at the edge of the colony. Exposure to boat noise is irregular as it depends
430 on the season and relatively limited to certain hours of the day (departure and return of boats).
431 In addition, Lambert's Bay seal colony is located on a rocky island and therefore highly exposed
432 to low frequency noise from swell and waves breaking against the rocks. Pelican Point is the
433 least noisy site. Although subject to daily seal-watching boat approaches, those activities occur
434 mostly in the morning. The eastern side of the colony (where playback experiments were
435 performed) is not exposed to breaking waves as it borders the shallow waters of the Walvis Bay
436 lagoon. Considering this, our results support a negative relationship between ambient noise
437 level and the intensity of seals' behavioural response to noise playback experiments. At Cape
438 Town harbour, habituation to the high and chronic noise exposure could explain why seals did

439 not show any behavioural response to boat motor noise playback. Seals at the other two sites
440 with less exposure to boat noise are probably more alert when exposed to these disturbances.
441 Such findings are consistent with other studies showing that animals from noisy areas have
442 lower levels of response when exposed to experimental noise playback compared to individuals
443 from quiet areas (Harding et al., 2018; Lazerte et al., 2016; Radford et al., 2016; Senzaki et al.,
444 2018).

445 A key point to discuss is that the absence of seals' behavioural reaction during noise
446 exposure at Cape Town harbour does not indicate an absence of physiological changes such as
447 hearing damage, elevated stress hormones levels, hypertension or immune system deficiencies
448 (Barber et al., 2010; Hammerschlag et al., 2022; Shannon et al., 2015). These impairments are
449 very likely to cause difficulties in undertaking vital activities such as feeding (foraging rate or
450 success) or defence against predators. It can also have negative consequences for social
451 interactions among individuals (e.g. attraction of a sexual partner, territorial behaviour or
452 parental care, Shannon et al., 2015) through impaired communication systems. Even in the
453 absence of an obvious behavioural response to noise exposure, the stress induced by chronic
454 exposure to anthropogenic noise and its consequences on individuals' fitness and survival
455 should not be underestimated.

456 A final factor that may drive intra-species variation in response to anthropogenic noise
457 in Cape fur seals is the extent and the nature of their interactions with humans. Among the three
458 study sites, the degree of human presence is highly variable. At Cape Town harbour, seals
459 hauling-out on platforms are constantly in close proximity to people. They are very habituated
460 to them. Based on their behaviour, it seems that the presence of humans is not considered as an
461 immediate threat to them, unless they get very close. Even close, seals often do not react to
462 humans, and each morning, they can be seen being gently moved when sleeping on the docks.
463 Conversely, seal-human interactions at Lambert's Bay are very rare. Since the access to the
464 colony is restricted, only a few rangers or people working under permit are allowed to
465 occasionally enter the seal colony. Regular passages of boats in the vicinity of the colony are
466 therefore not likely to be associated with the presence of humans or threats to the seals. This
467 would explain why their behaviour changes only for a high noise level of exposure, unusual for
468 them at this site. A third and intermediate situation occurs at Pelican Point, central Namibia. In
469 this breeding colony, the presence of humans occurs daily but at low levels as the peninsula is
470 only accessible by 4x4 vehicles or by boats. Tour boats from the ocean side and kayak tours

471 launching from the land side approach the same areas of the colony daily and typically result in
472 relatively low disturbance. While independent tourist vehicles are more haphazard but less well
473 behaved. In our experience of working in the area, tourist vehicles would typically result in
474 disruption of 2 or 3 groups per day with vehicles and people often getting too close and scaring
475 the seals, causing stampedes of dozens to hundreds of individuals into the water. A final
476 potential factor that may increase seals' alertness towards humans in central Namibia is the
477 annual Cape fur seal harvest (seals are rounded up on land killed for the manufacture of fur and
478 leather products as well as meat, oil and aphrodisiac applications using male seal genitalia,
479 Hofmeyr, 2017; Webber, 2014). Although it does not take place at Pelican Point colony but at
480 Cape Cross (about 150 km further north), movements of individuals between colonies are
481 known to occur in this area (Oosthuizen, 1991). Noise generated by motor vehicles could thus
482 be associated with the approach of humans and would be perceived as a potential threat. This
483 hypothesis is in line with previous studies reporting that the lack of fishing pressure in marine
484 protected area results in diminished behavioural responses to motorboat noise exposure for
485 several fish species (Mensing et al., 2018; Picciulin et al., 2010). As mentioned by Harding
486 and colleagues (2019), animal responses could depend upon the level of perceived threats rather
487 than on the level of noise. Similarly, harvest has been suggested to induce selective pressure
488 for shyer and more vigilant individuals (Leclerc et al., 2017), and such individual behavioural
489 traits are often heritable. It is thus possible that seals from Pelican Point even if they have not
490 experienced directly the harvest pressure, they are descendants of individuals who did.

491 The present findings reinforced the idea that different populations from the same animal
492 species may respond differently to anthropogenic disturbances depending on their life history
493 traits and experience (Harding et al., 2019). Multiple intrinsic (such as the age or sex of
494 individuals, their breeding status or the behavioural context) and extrinsic factors (such as the
495 ambient noise and the extent and nature of seal-human interactions at a specific site) were
496 suggested to play a role in the occurrence of intra-species variation in Cape fur seals'
497 behavioural reaction to boat-noise exposure. It would be interesting to carry out further
498 investigations at study sites that would allow better control of certain factors (such as the
499 composition of the groups tested and the behavioural context) in order to test precisely and
500 separately the effect of the intrinsic and extrinsic factors suggested in this study. Depending on
501 how they interact, such factors may have synergistic or cumulative effects (as well as agonistic
502 effects) (Harding et al., 2019).

503 In this study, it is suggested that some anthropogenic disturbances may modify the
504 tolerance threshold of a species to other perturbations and thus induce negative impacts on the
505 behaviour and physiology of individuals, affecting their long-term survival. These are important
506 aspects to consider when establishing mitigation measures for the impact of human activities
507 on wildlife. As far as possible, assessments of the potential effects of human activities should
508 be evaluated on a case-by-case basis to improve the effectiveness of particular measures.

Ethical Statement

This research has been conducted under the research permits reference 'Res2020-67' from the South African Department Environment, Forestry and Fisheries (DEFF) and CN 44-87-16854 from Western Cape Nature Conservation Board. It received approval from the Research Ethics Committee: Animal Care and Use of Stellenbosch University (Protocol number ACU-2021-15015).

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