



HAL
open science

Assessment of the impact of anthropogenic airborne noise on the behaviour of Cape fur seals during the breeding season in Namibia

Mathilde Martin, Tess Gridley, Simon Harvey Elwen, Isabelle Charrier

► To cite this version:

Mathilde Martin, Tess Gridley, Simon Harvey Elwen, Isabelle Charrier. Assessment of the impact of anthropogenic airborne noise on the behaviour of Cape fur seals during the breeding season in Namibia. *Journal of Experimental Marine Biology and Ecology*, 2022, 550, pp.151721. 10.1016/j.jembe.2022.151721 . hal-03823702

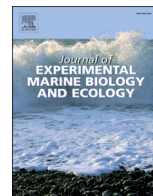
HAL Id: hal-03823702

<https://hal.science/hal-03823702>

Submitted on 21 Oct 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Assessment of the impact of anthropogenic airborne noise on the behaviour of Cape fur seals during the breeding season in Namibia

Mathilde Martin^{a,b,*}, Tess Gridley^{b,c}, Simon Harvey Elwen^{b,c}, Isabelle Charrier^a

^a Université Paris-Saclay, CNRS, Institut des Neurosciences Paris-Saclay, 151 rue de la Rotonde, 91400, Saclay, France

^b Sea Search Research and Conservation NPC, 4 Bath Road, Muizenberg, Cape Town, 7945, South Africa

^c Department of Botany and Zoology, Faculty of Science, Stellenbosch University, Stellenbosch 7605, South Africa

ARTICLE INFO

Keywords:

Noise pollution
Cape fur seal
Animal behaviour
Activity budget
Playback experiment
Pinnipeds

ABSTRACT

The increase of anthropogenic noise in the environment is a global phenomenon occurring in various types of habitats. Its impact on wildlife is therefore a growing research concern for many taxa. Due to their amphibious lifestyle, pinnipeds are exposed to anthropogenic noise in both aquatic and terrestrial environments. Using playback experiments, the present study assessed the impact of engine noise (car and boat) on the behaviour of Cape fur seals at the Pelican Point breeding colony, Namibia. Groups of individuals (35 groups, 369 individuals) were exposed either to low, medium or high amplitude levels of in-air noise, broadcast from the land or sea side. During the noise exposure, we found a significant increase in energetically costly behaviours: time spent awake, vigilance and locomotion for both females and pups. This was to the detriment of vital activities such as resting and nursing that decreased considerably (from 5.9 to 45% decrease) compared to the pre-playback phase without noise exposure. Animals' behavioural disturbance was limited to the 2-min period of noise exposure and we observed a rapid recovery when the noise ceased. We found stronger responses to boat motor noise broadcast from the sea side compared to car motor noise from land. Noise pollution from vehicles and boats in the vicinity of seal breeding colonies may threaten their health and the survival of their young by modifying their natural behaviour. It is therefore important to develop regulations for vehicles (speed, distance) in these areas with increasing tourist and recreational activities to limit disturbance.

1. Introduction

Human activities such as transport, construction, or exploration have developed considerably over the past decades and generate anthropogenic noise in many types of habitats (Shannon et al., 2015). Noise can be produced occasionally but also on a chronic basis and can reach levels exceeding natural ones (Buxton et al., 2017). Understanding the impact of anthropogenic noise on wildlife including marine wildlife is therefore a growing area of research (for a recent review see Duarte et al., 2021). Extensive studies have demonstrated that underwater anthropogenic noise can have a variety of detrimental effects (direct or indirect) on marine species ranging from behavioural modifications, acoustic disturbance (e.g. masking communication) to physiological impact (e.g. hearing damage, stress, physiological trauma) and even death (Erbe et al., 2018; Halliday et al., 2020; Southall et al., 2007).

Pinnipeds are semi-aquatic mammals that spend time both in water for foraging (and mating) and on land for mating and raising young (or

on ice depending on the species). Due to their amphibious lifestyle, pinnipeds are exposed to anthropogenic noise in both aquatic and terrestrial environments. Underwater anthropogenic noise (mainly frequencies below 10 kHz, Erbe et al., 2018) is known to have multiple potential negative impacts on pinnipeds: behavioural avoidance has been documented in wild seals exposed to ship noise (harbour seal *Phoca vitulina* and grey seal *Halichoerus grypus*, Mikkelsen et al., 2019), seismic survey airguns (ringed seal *Pusa hispida*, Kelly et al., 1986; ringed seal, bearded seals *Erignathus barbatus* and spotted seal *Phoca largha*, Harris et al., 2001), tidal turbine noise (harbour seal, Hastie et al., 2018), and pile driving (harbour seal, Russell et al., 2016). Vocal adjustment i.e. an increase in vocalisation amplitude in response to an elevation in the ambient noise level (Lombard effect) has been reported in bearded seals (Fournet et al., 2021). Finally, seals have been shown to experience temporary or permanent hearing threshold shifts in response to noise (harbour seal, Kastak et al., 2008; Kastelein et al., 2013; Reichmuth et al., 2019).

* Corresponding author at: Université Paris-Saclay, CNRS, Institut des Neurosciences Paris-Saclay, 151 rue de la Rotonde, 91400, Saclay, France.
E-mail address: mathilde.martin@universite-paris-saclay.fr (M. Martin).

The impact of in-air noise disturbance when pinnipeds are on land is not well understood (Tripovich et al., 2012) but may be detrimental to critical activities such as resting or nursing offspring. In highly polygynous land-breeding species such as sea lions and fur seals this breeding period is associated with a high energy expenditure for individuals of all ages (Champagne et al., 2012). Males fast throughout the breeding season while holding harems and displaying territorial behaviours whereas females give birth, nurse and provide maternal care to their young (Riedman, 1990). For newborn pups, the first months of life are often crucial for their survival because they exclusively rely on their mother for milk and protection (Campagna and Harcourt, 2021). The on-land breeding season is therefore a sensitive time and any disturbance that would affect their natural behaviour and/or physiological state could be detrimental for their reproduction and survival.

Previous studies of anthropogenic activities on pinnipeds haul-out sites have largely focused on the effect of human presence, often associated with tourism. Impacts of human exposure (e.g. approaching on foot, kayak or motorboat) include changes in the animals' state of alertness, physiological state (e.g. stress), modification of their natural activities (e.g. changes in their activity budget) and can even lead to stampedes (Andersen et al., 2012; Back et al., 2018; Barton et al., 1998; Boren et al., 2002; Engelhard et al., 2002; Kovacs and Innes, 1990; Pavez et al., 2015; Shaughnessy et al., 2008). As pinnipeds have sensory systems that are adapted to both aerial and aquatic environment, they use sight, sound and smell to perceive changes in their environment (Riedman, 1990). The behavioural responses reported in previous studies of human presence likely result from a multi-sensory process, without isolating the effect of noise alone on animal responses. When investigated explicitly, the impact of noise on seal behaviour on land has focused on localized geographic areas exposed to isolated extreme events such as missile or rocket launches and military explosions (Demarchi et al., 2012; Holst et al., 2011, 2005; Stewart, 1993, 1981; Stewart et al., 1994). Only one experimental study on the impact of a common anthropogenic noise (airborne motor boat noise) on Australian fur seals' *Arctocephalus pusillus pusillus* behaviour during the breeding season has been published (Tripovich et al., 2012). The seals tested showed variable responses depending on the noise levels they were exposed to, with stronger reactions and more energetically costly behaviours to louder noise levels (i.e. seals moved away, ceased vital activities such as nursing or resting), highlighting the impact of airborne noise on pinnipeds breeding colonies. As boat and land based marine wildlife tourism has increased markedly over the past decades (Birtles et al., 2001; Kirkwood et al., 2003), often focused on pinniped viewing and interaction at haul-out sites (Newsome and Rodger, 2008), additional knowledge of the impact of in-air noise pollution on seals is required.

The Cape fur seal *Arctocephalus pusillus pusillus* is an extremely colonial pinniped species with colonies up to hundreds of thousands of individuals (210,000 individuals at Cape Cross breeding colony, Namibia - Ministry of Environment and Tourism, 2021). Cape fur seal are highly polygynous, socially mature males (older than 10 years) hold harems composed of 10 to 30 females that they establish through aggressive behaviours and physical conflicts at the beginning of the breeding season (Rand, 1955). Territorial bulls fast during the entire breeding time while maintaining their territory boundaries and mating. Females give birth to a single pup each year which they exclusively nurse for an extended lactation period of 8 to 11 months (David and Rand, 1986; Rand, 1955). About 6 days after parturition, females depart to sea and then intersperse foraging trips with short periods ashore until weaning (Gentry and Kooyman, 2014). Because of this social organization and reproductive system, the breeding period of the Cape fur seal represents a period of high-energetic costs for all animals living in the colony, combined with low energy gain for males which effectively starve while defending their harem. Hence, human-induced disturbance during this time may have a critical impact on individual fitness. In addition, as colonies are extremely dense and seals are gregarious mammals, the behavioural response of seals to a local disruption (flee or

stampede for instance) could be propagated across a large group of animals (i.e. allelomimetic behaviour) and have a more generalized impact than just a local disturbance (Born et al., 2021). The Cape fur seal is therefore a good model to investigate the potential effect of anthropogenic noise on land.

Seal watching contributes significantly to the tourism economy in Namibia (USD\$2 million in 2008, Campbell et al., 2011). This activity has been experiencing a boom since the 1990s: in 2011, 30% of non-African visitors took part in seal watching tours, which at that time represented more than 100,000 people (Campbell et al., 2011). These estimates are likely to have continued to rise to the present day with the growth of tourism in Namibia. Over the past 15 years, the Pelican Point Cape fur seal colony has evolved from a haul-out site (Kirkman et al., 2007) to an established breeding colony with 12,000 pups estimated at the last aerial census in 2011 (Ministry of Fisheries and Marine Resources, unpubl. data). The increase in tourist activities around this breeding colony may be causing disturbance, due to the production of anthropogenic noise, and such increase can be seen on other breeding colonies in Namibia and South Africa. Assessing the consequences of human activities at seal breeding colonies is essential to reduce disruption and to reconcile economic activity with the protection of wildlife, especially when species experience rapid changes in their environment and have only a limited opportunity to adapt (Blickley and Patricelli, 2010).

The present study aims to empirically assess the impact of boat and car motor noise in-air on Cape fur seals at Pelican Point breeding colony, Namibia. Playback experiments were conducted using three controlled noise exposure levels. Seals' responses were evaluated from four different perspectives: assessing a potential avoidance phenomenon of the noise source, describing their behavioural response to noise exposure, quantifying behavioural modifications (in their activity-budget) during the noise exposure and finally, the behavioural modifications following noise exposure (i.e. recovery).

2. Materials and methods

2.1. Study site

The study took place at Pelican Point (Walvis Bay, Namibia, 25°52'S, 14°26'E) in February 2020 (Fig. 1). Cape fur seals occur all around the sandy peninsula and extend from the shoreline to 20 to 100 m inland, depending on the time of day and the movement of the tides. Experiments were performed on the east side of the peninsula, as this area is sheltered from ocean waves and exposed daily to both boat-based marine tourism (marine mammals watching boat tours) and land-based 4 × 4 all-terrain vehicles (for both recreational and tourism activities).

2.2. Stimuli

To test the impact of in air anthropogenic noise on Cape fur seals, boat and car motor noise were played back to different groups of seals. The stimuli were previously recorded in-air using a Sennheiser ME67 directional shotgun microphone (frequency range: 40–20,000 Hz +/- 2.5 dB) with a 44,100 Hz sampling rate and connected to a NAGRA LB digital audio recorder. Stimuli recordings were made by placing the microphone 50 cm from the switched-on engine (4 × 4 3.2 l Diesel Ford Ranger car or 25 hp Yamaha 2 stroke outboard boat motor) for 2 min, generating a representative sample of the motor noise (Fig. 2). We recorded the engines at 50 cm to get a loud and pristine recording (no wind, electrical noise or other additional background noise of the environment), and thus we were in the near-field of the engine.

2.3. Playback procedure

Each playback experiment consisted of testing a focal group of seals (Altmann, 1974). Focal groups were chosen for their accessibility in the

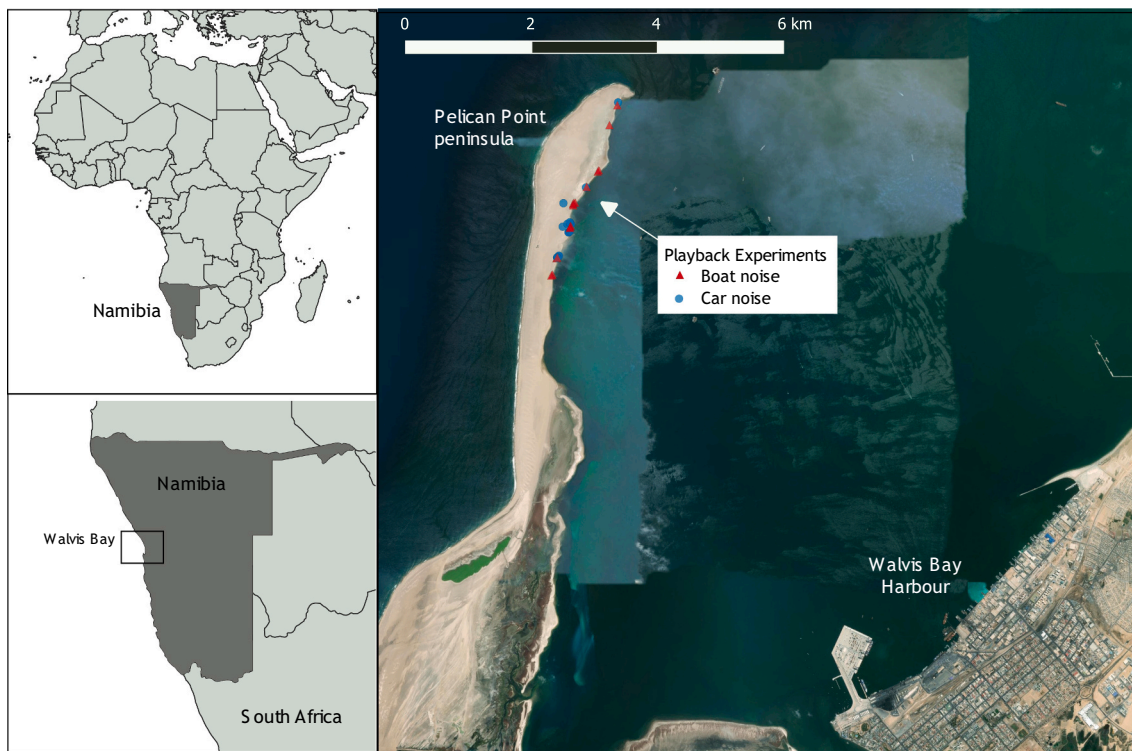


Fig. 1. Map of the study area and locations of playback experiments.

colony (on the colony edge, at the land side or on the sea side). Focal groups were defined as clusters (with a minimum of 6 individuals) positioned in close proximity to each other, within a 3 m diameter. The behaviour of all individuals had to be visible from the experimenter's location during the experiment. During playback experiments, we broadcast the noise stimulus from the direction the seals would normally experience it, i.e. car motor noise was broadcast from the land side to mimic the passage of a car and boat motor noise was broadcast from the sea side i.e. the beach, to mimic the presence of an outboard motor boat. Experiments had the same playback protocol and behavioural analysis method. All sessions were video-recorded by the experimenter using a Fujifilm FinePix XP90 camera for further analysis.

Playback experiments were conducted using a waterproof and wireless high-powered speaker (JBL Charge 3, 2×10 W, frequency response: 65–20,000 Hz) connected to a Bluetooth sound player (Sony NW-A35). Focal groups were approached slowly and carefully by crawling to avoid visual detection or disturbance, defined as increased vigilance, fleeing movements or stampedes. The experimenter stopped 6 m from the focal group. Received level of the playback noise was modified by the proximity of the loudspeaker to the focal group (6, 3 or 1 m), using a 5 m pole. Indeed, the maximum source level obtained with our loudspeaker was 80 dB re 20 μ Pa RMS SPL (sound pressure level) at 1 m and at 0° , so to get the different noise levels, we changed the distance between the speaker and the focal group. Based on the protocol described by Tripovich et al. (2012), focal groups were exposed either at a low, medium or high noise level. For both car and boat motor noise experiments, received levels of the playback stimulus were 60.9–64.4 dB re 20 μ Pa RMS SPL for low exposure (broadcast at 6 m), 64.4–70.5 dB re 20 μ Pa RMS SPL for medium (broadcast at 3 m) and 70.5–80 dB re 20 μ Pa RMS SPL (broadcast at 1 m). Ranges correspond to the level received by individuals at the forefront of the focal group (facing the speaker, so at 0°) compared to the back as focal groups were up to 3 m wide. The broadcast distance for each level was calibrated for each of the two stimuli by verifying the received levels with a 'Testo 815' sound level meter set as 'A' weighting at fast response.

Once in position, a 10-minute habituation period was provided to

ensure the seals returned to baseline conditions i.e. no experimenter-related vigilance behaviour. Following the habituation period, the experiment began and consisted of three phases (Fig. 3). The initial pre-playback phase (i.e. control phase) lasting 10 min of observation was immediately followed by a two-minute playback exposure phase where engine noise (car or boat) was broadcast. The observational post-playback phase (i.e., recovery phase) lasted 10 min (Fig. 3). To ensure independence, each group was randomly assigned a stimuli and intensity, and tested only once.

2.4. Behavioural responses and statistical analyses

Videos of the experiments were analysed in order to investigate four aspects of the seals' behavioural response to the playback (Fig. 3).

2.4.1. Avoidance of the noise source

Avoidance of the noise broadcast area was assessed through the seals movement. The number of individuals present in the focal group was noted at the start and end of each of the three phases (t_0 , t_{10} , t_{12} and t_{22} , Fig. 3). To test whether the number of individuals varied significantly during the experiment, we fitted a generalized linear mixed-effects model (GLME) assuming a Poisson error structure (as the response variable is a count). The number of individuals (variable 'Nind') was set as a 'response variable' while the phase (t_0 , t_{10} , t_{12} and t_{22}), the type of stimulus (car or boat motor noise) and the playback level (low, medium or high) were set as fixed effects. In addition, playback experiment was defined as a 'random effect' to account for the fact that data are non-independent (each experiment consists of monitoring one focal group over time). The model was run with the *lme4* R package (Bates et al., 2015) and *p*-values were obtained using the *car* package (Fox and Weisberg, 2019). A pairwise analysis of estimated marginal means was conducted to compare significant fixed effects using the *emmeans* package in R (Lenth, 2021). It included Šidák correction for multiple comparisons. Although the seals at Pelican Point experience car and boat passage every day these are concentrated within the morning hours, peaking at 10 am. To investigate whether the seals' reaction to

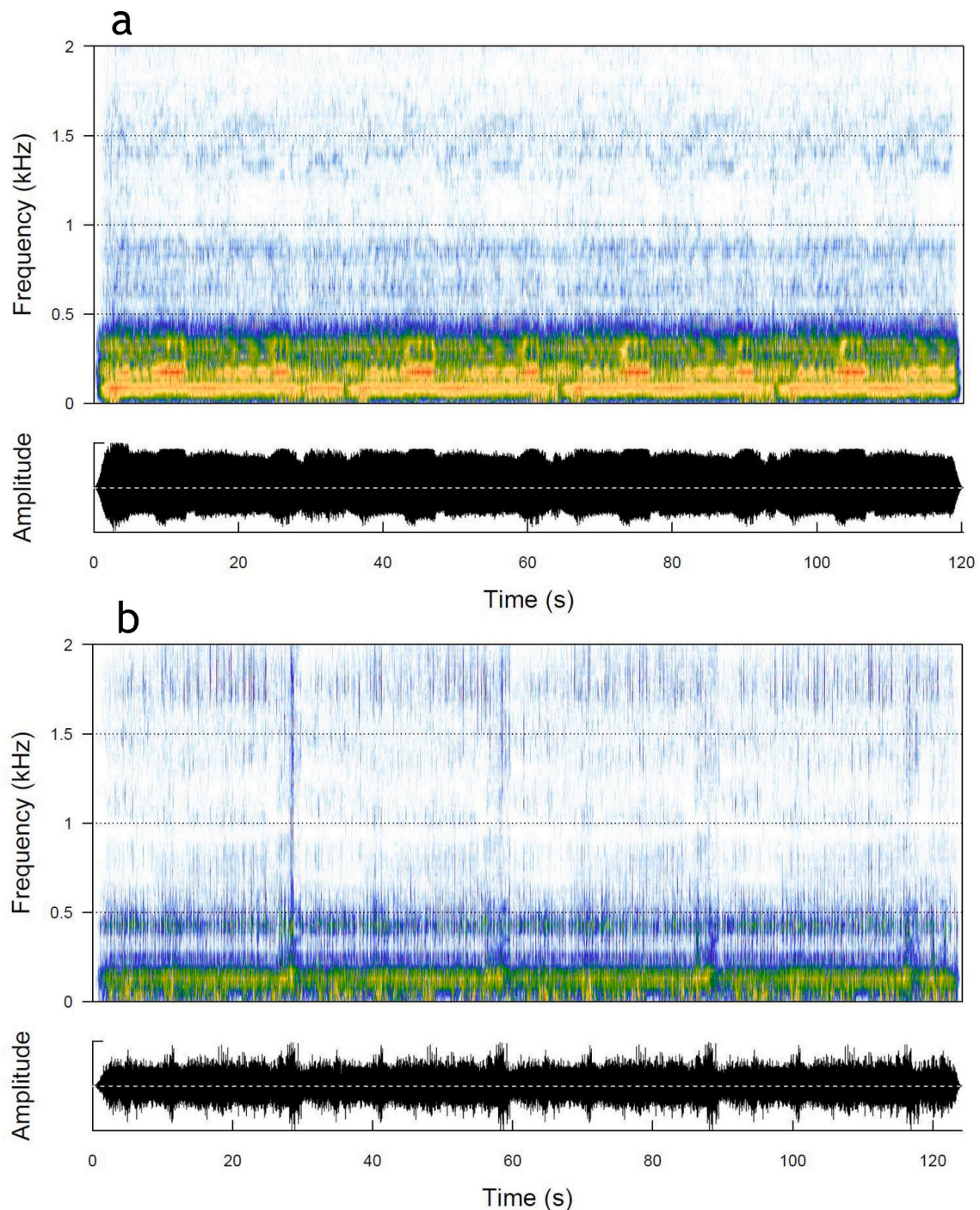


Fig. 2. Spectrograms and oscillograms of the two stimuli used for playback experiments: (a) car motor noise and (b) boat motor noise. Spectrograms (Hamming window size: 512 pts., 90% overlap) generated using Seewave (Sueur et al., 2008).

motor noise has a temporal component, we built another model including the timing of playback experiment as a ‘fixed effect’ in the model. This variable called ‘Hour’ had two levels: ‘early hours’ for trials started after 8 am and before 10 am and ‘late hours’ for trials started from 10 am to 12 pm.

2.4.2. Behavioural response to noise exposure

Behavioural reactions to the 2-minute noise exposures were assessed through detailed video analysis. For each individual (adult females, subadult males, yearlings and pups) present in the focal group at the start of the playback phase, reactions were assessed according to the

following ethological scale: 0: no response, 1: eye-movement towards the noise source without change of posture, 2: prolonged look towards the noise source, change of posture (e.g. lying down to sitting) and signs of alertness, 3: slight retreat from the noise source defined as a 1–3 m movement away from source, 4: significant retreat from the noise source defined as the individual leaves the focal group (i.e., on video, individual is out of view). The effect of the type of stimulus (i.e. car or boat motor noise) and the playback experiment level (i.e. low, medium, high) on seals’ behavioural response was assessed with a cumulative link mixed model (CLMM) using the *ordinal* R package (Christensen, 2019), performed with the playback experiment (i.e. the focal group) set as a

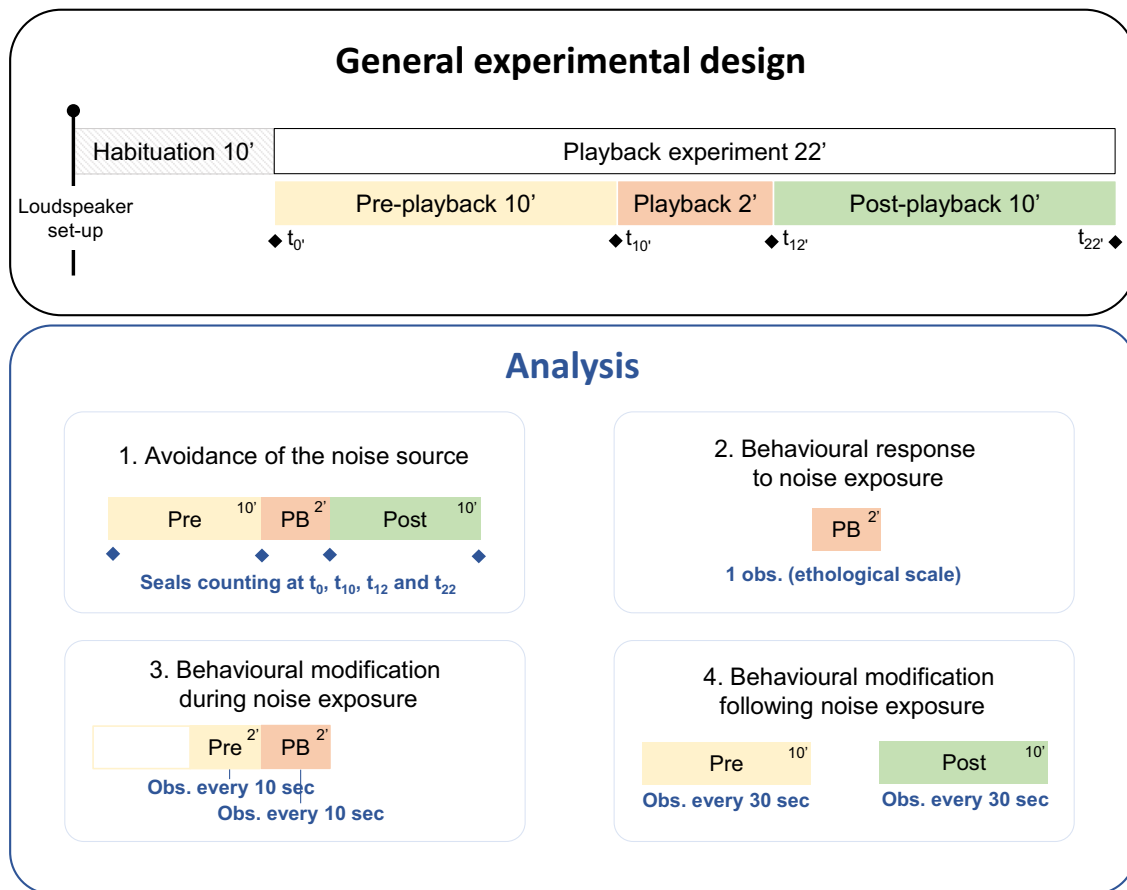


Fig. 3. Playback experiments general design and summary of the video-based analyses carried out.

‘random effect’. The effect of a variable was tested (and *p*-values were obtained) by performing an analysis of variance comparing a full model and a reduced model that did not include this variable.

2.4.3. 2.4.3 Behavioural modification during noise exposure

To investigate a potential behavioural modification during the noise exposure time, we assessed the behaviour of individuals during the last 2 min of the pre-playback phase and during the 2 min of playback. These observations were limited to individuals that were present in the focal group during this entire 4-minute period. The activities of each individual were point sampled once every 10 s and designated as: sleep, awake, vigilance, nursing, agonistic interaction, nuzzling, locomotion (Table 1). In cases where behaviours were not mutually exclusive, we assigned vital activities as the priority state. For example, a female showing signs of vigilance while nursing her pup was reported as nursing so that any changes in nursing activity could be accurately

Table 1

Description of the behavioural activities considered in the study.

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

captured. For each individual, the activity budget (percentage of time spent in each activity) was compared between the pre-playback and the playback phases, using a linear mixed-effects model (LME). The phase was set as a ‘fixed effect’ and the individual defined as a ‘random effect’. Behavioural changes were investigated by age/sex category (adult female, subadult male, yearling or pup) by investigating also the interaction between the two variables ‘Phase’ and ‘Age/sex category’ for each activity (except nursing). When an effect of the age/sex category was found (significant interaction Phase*Age/sex category), we evaluated the effect of the phase separately for each age/sex category. Since suckling is a shared behaviour for a female and her pup, the effect of age/sex category on the variation of this behaviour during the playback phase was not studied. This analysis was performed separately for the three levels of intensity (low, medium, high) and the two noise stimuli (car and boat). Linear mixed-effects model were performed using the *lme4* package in R (Bates et al., 2015).

2.4.4. Behavioural modification following noise exposure

The behaviour of individuals that were present in the focal group during the entire duration of the experiment (i.e. 22 min) was point sampled every 30 s during the pre-playback (10 min) and the post-playback (10 min) phase using the ethogram Table 1. As above, a LME model approach was used (*lme4* package in R, Bates et al., 2015) with the individual included as a ‘random effect’ for each activity and for each intensity level. Interaction between the two variables ‘phase’ and ‘age/sex category’ was also considered.

3. Results

In total, 35 playback experiments were performed over a 30-day

period (from the 30th of January to the 28th of February 2020), with experiments conducted on 19 of the days. A total of 18 experiments tested the impact of car motor noise played back from the land side (6 for each noise level) and 17 of motor boat noise played from the seaward side of the colony (6 for low and 6 medium level, 5 of high) (Fig. 1). In total, 369 individuals (190 car exposures and 179 boat) from 35 different groups were assessed. Groups mainly consisted of adult females ($n = 231$) and pups ($n = 113$), while subadult males ($n = 9$) and yearlings ($n = 16$) were relatively rare in our target groups.

3.1. Avoidance of the noise source

According to the generalized linear mixed-effects model performed to investigate the variation in the number of seals in a focal group during the 22-minute experiment, no significant interaction was found between the phase time (i.e. t_0 , t_{10} , t_{12} and t_{22}) and the type of stimulus (i.e. car or boat motor noise, $p = 0.876$). Similarly, no interaction was found between the phase time and the playback level (i.e. low, medium and high, $p = 0.719$). However, the phase of the experiment alone had a significant effect on the variation of the number of individuals in the focal group ($p = 2.787 \cdot 10^{-11}$). There was a significant reduction in the number of individuals during the noise exposure phase (i.e. playback phase, from t_{10} to t_{12}) for both car motor ($p = 0.018$) and boat motor noise ($p = 0.0005$) playbacks and regardless the noise level (Fig. 4). In contrast, no significant variation was observed during the pre- and post-playback phases (Fig. 4). Some groups showed a large number of individuals leaving the area during motor noise exposure, in particular for the three experiments conducted from the land side with a low sound level (Fig. 4). Lastly, there was no interaction between the phase time and the timing of the experiment (i.e. ‘early’ or ‘late’ experiment, $p = 0.401$).

3.2. Behavioural response to noise exposure

The response of 369 individuals was investigated and scored using an ethological scale ranging from 0 to 4. The responses of the seals to the playback experiments were diverse with a slight predominance of the second level of the ethological scale i.e. prolonged look towards the noise source, change of posture (e.g. lying down to sitting) and signs of alertness for both car and boat motor noise exposures (Fig. 5). The CLMM revealed significant differences in seals' response depending on the type of stimulus broadcast ($p = 0.037$). More vigilance reactions (responses 1 or 2) were reported in seals exposed to car noise while more individuals moved away from the noise source (responses 3 or 4) when exposed to boat motor noise (Fig. 5). No effect of noise level exposure on

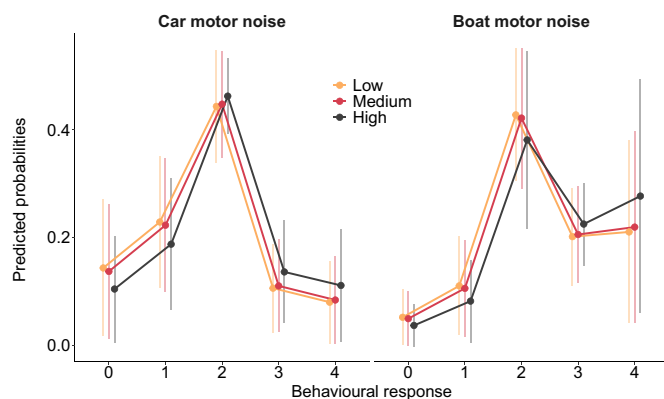


Fig. 5. Predicted probabilities and 95% confidence interval of seals' behavioural responses from CLMM for both car and boat motor noise playback experiments.

seals' behavioural response was reported ($p = 0.832$) (Fig. 5).

3.3. Behavioural modification during noise exposure

The activity budget of 187 adult females and 56 pups was compared between the two phases (last 2 min of pre-playback and the 2 min of noise playback). Although present, sub adult males and yearlings represented a very small part of our population sample (14 and 8 individuals respectively) and were therefore excluded from this analysis due to sample size restrictions.

In general, we found no significant interaction between the two variables ‘Phase’ and ‘Age/sex category’ (except for the for medium-level playback of boat noise - Table 2) meaning that mothers and pups responded similarly to the broadcasted noise. Response patterns were consistent between playbacks from sea side and from land side: we observed a significant reduction in time spent sleeping (in average 17% to 18% decrease for car motor noise exposures, 24.8% to 45% decrease for boat motor noise – all noise levels) and reductions in nursing time (5.9% to 19.8% decrease for car noise, 15.4% to 31.8% decrease for boat noise - all noise levels; Table 2). Conversely, females and pups spent more time awake (13.8 to 26.3% increase – all noise levels), vigilant (7.6 to 31.2% increase – all noise levels) or in locomotion (2.1 to 4.6% increase – all noise levels). There was no variation in ‘agonistic interaction’ and ‘nuzzling’ behaviour. We identified a more pronounced increase in vigilance by mothers to the medium-level playback of boat

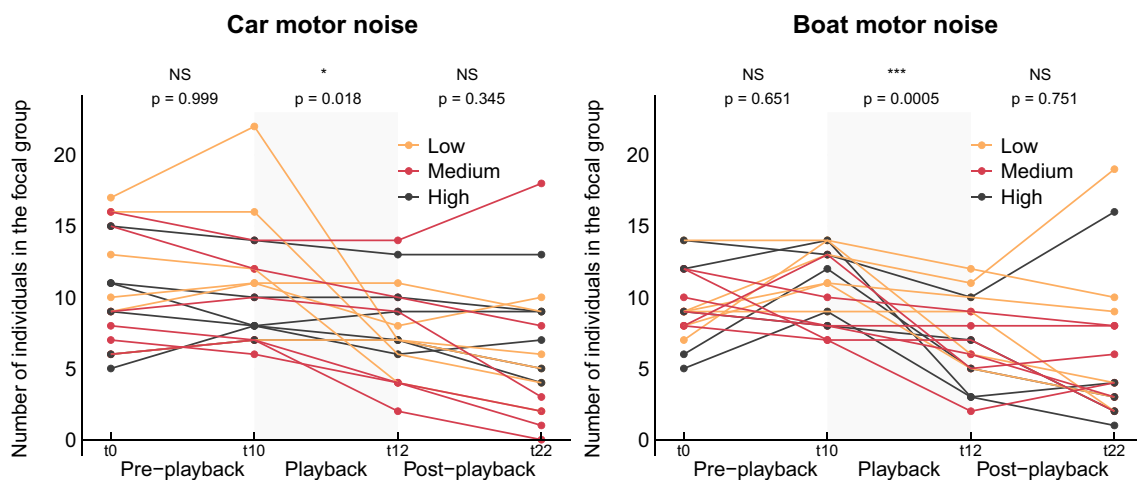


Fig. 4. Number of individuals within the focal groups throughout each of the 3 phases of the playback experiments, for car motor noise and boat motor noise exposures. Stars indicate the results of the pairwise analysis of estimated marginal means following the linear mixed effects model performed on playback phases and the associated p-value (Significance code: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘NS: not significant’ 1).

Table 2

Comparison of adult females' and pups' activity budgets between the pre-playback and the playback phases. Stars indicate the significance of the linear mixed effects model (Significance code: 0 '****' 0.001 '***' 0.01 '**' 0.05 'NS' 1). An increase of the activity during the playback (PRE < PB) is indicated in dark grey and a decrease (PRE > PB) in light grey. The intensity of the variation is expressed in percentage of time spent in this activity for both females and pups, except for the sea side/medium level where a significant interaction was found and thus results are given separately for pups and adult females.

Car motor noise	Sleep	Awake	Vigilance	Nursing	Agonistic interaction	Nuzzling	Locomotion
Low (N _{fem} = 41, N _{pup} = 10)	** PRE > PB - 17.0%	** PRE < PB + 13.8%	*** PRE < PB + 17.6%	PRE > PB	NS	NS	*** PRE < PB + 4.6%
Medium (N _{fem} = 36, N _{pup} = 12)	** PRE > PB - 18.0%	NS	*** PRE < PB + 14.8%	PRE > PB	NS	NS	* PRE < PB + 2.3%
High (N _{fem} = 39, N _{pup} = 5)	*** PRE > PB - 17.4%	NS	*** PRE < PB +13.6%	NS	NS	NS	NS
Boat motor noise	Sleep	Awake	Vigilance	Nursing	Agonistic interaction	Nuzzling	Locomotion
Low (N _{fem} = 30, N _{pup} = 5)	*** PRE > PB - 45.0%	*** PRE < PB + 24.8%	*** PRE < PB + 19.1%	NS	NS	NS	** PRE < PB + 2.6%
Medium (N _{fem} = 26, N _{pup} = 12)	*** PRE > PB - 24.8%	* PRE < PB + 15.8%	Phase x SocCat * Fem: + 26.6% Pup: + 7.6%	** PRE > PB - 15.4%	NA	NA	* PRE < PB + 3.3%
High (N _{fem} = 15, N _{pup} = 12)	*** PRE > PB - 34.3%	*** PRE < PB + 26.3%	*** PRE < PB +31.2%	*** PRE > PB - 31.8%	NS	* PRE < PB + 1.5%	*** PRE < PB + 2.1%

noise (+26.6%) compared to pups (+7.6%). Low level playbacks from land side appeared to induce time budget modifications for more activities compared to higher levels, however degree of behavioural modification is comparable among levels (see 'sleep' and 'vigilance' in Table 2). For boat noise playbacks, results were relatively consistent among intensity levels (Table 2).

3.4. Behavioural modification following noise exposure

In total 164 individuals (101 for car noise and 63 for boat noise) were followed both during the 10 min of pre-playback and the 10 min of post-playback. As before, yearlings and subadult males were poorly represented (13 individuals out of the 164) and thus removed from analysis. The final dataset included a total of 151 individuals: 92 for car noise (79 females and 13 pups) and 59 for boat noise (44 females and 15 pups). Linear mixed effects models performed for each set up (car or boat motor noise and low, medium or high level) revealed no significant change in seal's activity budget between pre- and post-playback periods, except in one case: a 11.2% decrease in the nursing time in medium-level sea-side experiments (equivalent decreases for females and pups). In all other configurations, there was no differences in the time budget between pre- and post-playback periods.

4. Discussion

In this study we experimentally assessed the behavioural response of Cape fur seals on land to the broadcasting of airborne noises from two common human sources in their environment (i.e. car and boat motor noise) from the direction the seals would normally experience it. In pinniped breeding colonies, one of the most severe consequences caused by a disturbance (natural or anthropogenic) is animal stampedes during the peak breeding season. These events lead to the disruption of the group's structure (harems, territories), a resulting increase in the energy expenditure of the animals which are already weakened during this period, but also to an increase of pups' mortality by separating mother-pup pairs or by trampling pups (Birtles et al., 2001; Mattlin, 1978). Unlike studies showing that human presence can cause stampedes on

colonies (Andersen et al., 2012; Barton et al., 1998; Burleigh et al., 2008; Holst et al., 2011), we did not observe such reactions during our noise playback experiments at Pelican Point. However, we observed that a significant number of animals that left the noise exposure area during the playback experiment (Fig. 4) settled down a few metres further, outside the focal group (either on the side or the back of the group).

Avoidance of the noise broadcast area was the same regardless of the intensity level of noise broadcast and regardless of the stimulus (car motor noise broadcast from the land side or boat motor noise broadcast from the sea side). It suggests that a low- or high level of car or boat motor noise was disruptive and elicited a physical movement of seals on land. Even if these reactions are less energy-consuming than a stampede, it inevitably leads to a disruption of seals' baseline behaviour such as nursing or resting, disruption of social interactions and it can lead to the temporary separation of a pup from its mother, resulting in a loss of energy to reunite, and stress (Riedman, 1990). Some experiments showed stronger animal escapes during playback, especially during land side car noise playbacks at a low intensity level (Fig. 4). This is likely due to individual variations in temperament, with seals being more nervous and fearful in these particular groups (Harding et al., 2019). Indeed, the stress expressed by one individual of the group can be spread to other individuals of the group. Such allelomimetic behaviour (or behaviour synchronization) has been shown in group-living species (rodents, sheep, kangaroos, etc.), and is a way to increase collective vigilance and awareness of a danger (Briefer, 2018; Hare et al., 2014; McDougall and Ruckstuhl, 2018; Pays et al., 2009). In addition, even though we could only focus on the morning hours, these experiments revealed that the avoidance reaction of seals to motor noise did not seem to vary with the time of day. This behaviour may not be influenced by the number of boats or cars the animals have experienced earlier in the morning. Further investigations would be interesting to perform throughout the day but so far this suggests a potential lack of habituation of these animals to this type of disturbance, despite both sounds being common in their environment.

The reaction of Cape fur seals' to the 2-min noise exposures were variable among individuals: responses were distributed across the four categories of the ethological scale but a large proportion of the seals

were reported to insistently look towards the noise source, to change of posture and to show signs of alertness for both car and boat motor noise experiments (predicted probabilities from the CLMM for score '2' close or higher than 0.4, Fig. 5). The variability of responses among individuals can be explained by both intrinsic and extrinsic factors. Indeed, factors such as body size, condition, sex, personality (i.e., intrinsic characteristics) or environmental context, repeated measures and multiple stressors (i.e., extrinsic factors) were reported to affect the response of animals to anthropogenic noise (Ellison et al., 2012; Gomez et al., 2016; Harding et al., 2019). In our experiments, we did not notice any obvious link between the reaction of seals' and their age or sex, but some individuals seemed more fearful than others, likely associated to different individual experience with human activities or innate personality differences. It would be interesting to determine which biological, environmental or behavioural factors can affect their responsiveness to a disturbance. In comparison, Australian fur seals showed more homogeneous reactions to boat motor noise (Tripovich et al., 2012). Compared to car-noise playbacks, experiments conducted from the sea side with boat motor noise resulted in generally stronger responses, with more strong reactions such as retreat or escape from the source noise and fewer individuals with mild responses like reaction or only looking towards the loudspeaker. This suggests that, at equal noise levels, seals may consider boat noise heard from the sea more threatening than land-based car noise. This can be explained by a phenomenon of familiarisation: seals may be less used to hearing such amplitudes from the sea side and therefore have stronger reactions. Seals might perceive the noise from the seaside more threatening than from the landside as they cannot escape in the water knowing the threat comes from the seaside.

The third part of the study, comparing the activity budget of adult females and pups before noise exposure (control phase) and during noise exposure, showed much more homogeneous results among groups and individuals. Besides some variations, we found similar results between the three levels of amplitude (low, medium and high) and between the two set-ups: sea-side and land-side experiments. We found a significant increase in energetically costly behaviours: time spent awake, vigilance and locomotion for both females and pups, to the detriment of vital activities such as resting and nursing that decreased considerably during the playback phases. We found no significant statistical differences in terms of time budget between females and pups and we did notice a general reaction pattern in mother-young pairs. The start of the playback generally resulted in the cessation of nursing because the pup was looking towards the source of the noise or because the mother changed posture, i.e. standing up. Generally, pups tended to move first (either for fear of the noise or because stopping suckling encouraged them to move around), causing the females to also move to follow their young. The increase in vigilance in females could thus be linked to the direct disturbance caused by the noise but could also sometimes be due to the displacement of her pup that moved away from the noise. Increased vigilance and locomotion were also indirectly related to conspecifics' movement within the group and to resulting conflicts for space. Similar findings were reported in Australian fur seals with individuals being more alert, spending more time engaged in agonistic interactions and resting significantly less during noise exposure (Tripovich 2012). A modification of the activity budget due to exposure to anthropogenic noise has been observed in other marine species such as killer whales *Orcinus orca* (Williams et al., 2006), the harbour porpoise *Phocoena phocoena* (Pirodda et al., 2014), the Florida manatee *Trichechus manatus* (Miksis-Olds et al., 2005) or the European spiny lobster *Palinurus elephas* (Filiciotto et al., 2014).

We have shown evidence of an effect of a noise disturbance on Cape fur seals. Moreover, our findings are probably an underestimate of the real intensity of the disturbance. Indeed, the time budgets reported here came from only individuals present during the entire observation period (22 min). The most sensitive animals left the observation area during the exposure and thus their activities could not be monitored. So, we studied seals that are likely the least bothered or the least anxious individuals in

the face of this environmental disturbance.

Even if anthropogenic noise does not cause *en masse* fleeing of animals, we showed that their natural activities are modified and the acoustic disturbance could result in animals dedicating less time to biologically important behaviours e.g. feeding and/or resting. Nevertheless, the comparison of the activity budget between the pre- and the post-playback phases revealed that animals returned to their normal activities as soon as the noise exposure ended and thus the disturbance appeared to be limited to the duration of the noise exposure only. Such rapid behavioural recovery was also reported for seals exposed to noise from military and aeronautical exercises (Holst et al., 2005; Stewart, 1981, 1993) or exposed to human presence through tourist activities (Engelhard et al., 2002; Kovacs and Innes, 1990). In line with what has been discussed earlier, it should be noted that these observations could not be carried out on individuals who left the study area during the experiment, and therefore the assessments of the behavioural recovery of some individuals - potentially the most fearful - could not be included.

Our experimental approach might have induced some variabilities in the behavioural responses of tested seals. Within the focal group, seals were not exposed to the exact same noise level, so the animals on the forefront received higher levels of noise compared to those from the back or from the side (more distant to the noise source). So, it is likely that we are underestimating the impact of noise on these seals. Another feature to consider is that seals might react more strongly when facing the physical presence of an approaching car or boat as in addition to the sound component (i.e., engine noise) they are also exposed to the visual component. However, in our experimental design, we were aiming to measure only the acoustic component of such disturbance, and we could assess that such acoustic disturbance is impacting seals' behaviour. Finally, we exposed seals to an engine noise recorded in the near-field (within 50 cm) which may have been subject to acoustic interference patterns and consequently sound different to engine noise recorded at greater distances in the far-field. As a result, the motor noise played back to seals may have been different to what they would normally experience and could have resulted in different behavioural responses to those seen during natural settings.

This study is among the first to show the impact of anthropogenic airborne motor noise on the behaviour of a pinniped species. Such disturbances cause a significant avoidance phenomenon in Cape fur seals, increasing energetically costly activities such movements and decreasing resting and the nursing of new-born pups. Despite the animals' responses being limited to the period of disturbance and their rapid recovery post disturbance (at least from a behavioural point of view), the noise pollution generated by the presence of these vehicles could potentially represent an indirect threat to the condition of the fur seals' health and the survival of the young. In addition, exposure to noise pollution may cause other indirect and non-visible effects on animals such as stress-related changes in their body chemistry and physiology (Erbe et al., 2018; Wright et al., 2007). Finally, since Pelican Point is a site highly frequented for tourist and recreational activities, these disturbances are numerous and are repeated throughout the day, resulting in a potential cumulative effect. It would be interesting to pursue this study and explore the effect of repeated noise disturbances on groups of Cape fur seals. There could be a potential tolerance phenomenon where animals may be less likely to respond to the noise stimulus, or on the contrary a sensitization effect which would lead to a worsening of their reactions over time (Bejder et al., 2009). For these reasons, it is important that boats (tour boats and recreational boats) as well as cars respect an approach distance and speed limit that will minimise the noise near the colony and thus mitigate their impacts on the Cape fur seal population at this site.

Author contributions

IC and MM designed the study protocol and analyses. IC, TG and SHE organised the fieldwork logistics. MM conducted the experiments and

collected the data. MM performed the analyses. MM and IC drafted the manuscript, and all authors revised the manuscript.

Funding

The research was supported by CNRS and Sea Search Research and Education — Namibian Dolphin Project. This project has received financial support from the CNRS through the MITI interdisciplinary programs.

CRediT authorship contribution statement

Mathilde Martin: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **Tess Gridley:** Conceptualization, Writing – review & editing. **Simon Harvey Elwen:** Conceptualization, Writing – review & editing. **Isabelle Charrier:** Conceptualization, Methodology, Writing – original draft, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We acknowledge the Namibian Ministry of Fisheries and Marine Resources and the Namibian Chamber of Environment for their support of this research. Special thanks to Naude Dreyer, Kevin van Schalkwyk and Craig Gibson for their knowledge on the species, logistical support in the field and their enthusiasm for the project.

References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267. <https://doi.org/10.1017/S0376892999000302>.
- Andersen, S.M., Teilmann, J., Dietz, R., Schmidt, N.M., Miller, L.A., 2012. Behavioural responses of harbour seals to human-induced disturbances. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 22, 113–121. <https://doi.org/10.1002/aqc.1244>.
- Back, J.J., Hoskins, A.J., Kirkwood, R., Arnould, J.P.Y., 2018. Behavioral responses of Australian fur seals to boat approaches at a breeding colony. *Nat. Conserv.* 31, 35–52. <https://doi.org/10.3897/natureconservation.31.26263>.
- Barton, K., Booth, K.L., Ward, J.C., Simmons, D.G., Fairweather, J.R., 1998. Visitor and New Zealand fur Seal interactions along the Kaikoura Coast.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* 395, 177–185. <https://doi.org/10.3354/meps07979>.
- Birtles, A., Valentine, P., Curnock, M., 2001. Tourism Based on Free-Ranging Marine Wildlife: Opportunities and Responsibilities.
- Blickley, J.L., Patricelli, G.L., 2010. Impacts of anthropogenic noise on wildlife: research priorities for the development of standards and mitigation. *J. Int. Wildl. Law Policy* 13, 274–292. <https://doi.org/10.1080/13880292.2010.524564>.
- Boren, L.J., Gemmill, N.J., Barton, K.J., 2002. Tourist disturbance on New Zealand Fur seals. *Aust. Mammal.* 24, 85–96.
- Born, E.W., Wiig, Ø., Olsen, M.T., 2021. Anthropogenic impacts on the Atlantic walrus. *Atl. Walrus* 263–308. <https://doi.org/10.1016/B978-0-12-817430-2.00013-3>.
- Briefer, E.F., 2018. Vocal contagion of emotions in non-human animals. *Proc. R. Soc. B Biol. Sci.* 285 <https://doi.org/10.1098/rspb.2017.2783>.
- Burleigh, A., Lynch, T., Rogers, T., 2008. Best practice techniques for monitoring the fur seal haul-out site at steamers head, NSW, Australia. *Aust. Zool.* 34, 233–245. <https://doi.org/10.7882/fs.2008.027>.
- Buxton, R.T., McKenna, M.F., Mennitt, D., Frstrup, K., Crooks, K., Angeloni, L., Wittmeyer, G., 2017. Noise pollution is pervasive in U.S. protected areas. *Science* 356, 531–533.
- Campagna, C., Harcourt, R.G., 2021. *Ethology and Behavioral Ecology of Otariids and the Odobenid*. Springer Nature, Switzerland.
- Campbell, R., Knowles, T., O'Connor, S., 2011. The Economics of Seal Hunting and Seal Watching in Namibia. *A Rep. Hum. Soc. Int. World Soc. Prot. Anim. Bont Voor Dieren Respect*.
- Champagne, C.D., Crocker, D.E., Fowler, M., Houser, D.S., 2012. Fasting physiology of the pinnipeds: the challenges of fasting while maintaining high energy expenditure and nutrient delivery for lactation. In: McCue, M. (Ed.), *Comparative Physiology of Fasting, Starvation, and Food Limitation*, pp. 309–336. <https://doi.org/10.1007/978-3-642-290565>.
- Christensen, R.H.B., 2019. Ordinal - regression models for ordinal data. R Pack. Vers. 2019.12-10 <https://CRAN.R-project.org/package=ordinal>.
- David, J.H.M., Rand, R.W., 1986. Attendance behavior of south African Fur seals. In: Gentry, R.L., Kooyma, G.L. (Eds.), *Fur Seals: Maternal Strategies on Land and at Sea*, pp. 126–141. <https://doi.org/10.1515/9781400854691>.
- Demarchi, M.W., Holst, M., Robichaud, D., Waters, M., MacGillivray, A.O., 2012. Responses of Steller Sea lions (*Eumetopias jubatus*) to in-air blast noise from military explosions. *Aquat. Mamm.* 38, 279.
- Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguilluz, V.M., Erbe, C., Gordon, T.A.C., Halpern, B.S., Harding, H.R., Havlik, M.N., Meekan, M., Merchant, N.D., Miksis-Olds, J., Parsons, M., Predragovic, M., Radford, A.N., Radford, C.A., Simpson, S.D., Slabbekoorn, H., Staatterman, E.R., Van Opzeeland, I. C., Winderen, J., Zhang, X., Juanes, F., 2021. The soundscape of the Anthropocene Ocean. *Science* 371. <https://doi.org/10.1126/science.aba4658>.
- Ellison, W.T., Southall, B.L., Clark, C.W., Frankel, A.S., 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conserv. Biol.* 26, 21–28. <https://doi.org/10.1111/j.1523-1739.2011.01803.x>.
- Engelhard, G.H., Baarspul, A.N.J., Broekman, M., Creuwels, J.C.S., Reijnders, P.J.H., 2002. Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. *Can. J. Zool.* 80, 1876–1886. <https://doi.org/10.1139/z02-174>.
- Erbe, C., Dunlop, R., Dolman, S., 2018. Effects of Noise on Marine Mammals. https://doi.org/10.1007/978-1-4939-8574-6_10.
- Filiciotto, F., Vazzana, M., Celi, M., Maccarrone, V., Ceraulo, M., Buffa, G., Di Stefano, V., Mazzola, S., Buscaino, G., 2014. Behavioural and Biochemical Stress Responses of *Palinurus elephas* after Exposure to Boat Noise Pollution in Tank. <https://doi.org/10.1016/j.marpolbul.2014.05.029>.
- Fournet, M.E.H., Silvestri, M., Clark, C.W., Klinck, H., Rice, A.N., 2021. Limited vocal compensation for elevated ambient noise in bearded seals: implications for an industrializing Arctic Ocean. *Proc. R. Soc. B Biol. Sci.* 288 <https://doi.org/10.1098/rspb.2020.2712>.
- Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Gentry, R.L., Kooyma, G.L., 2014. *Fur Seal: Maternal Strategies on Land and at Sea*. Princeton.
- Gomez, C., Lawson, J.W., Wright, A.J., Buren, A., Tollit, D., Lesage, V., 2016. A systematic review on the behavioural responses of wild marine mammals to noise: the disparity between science and policy. *Can. J. Zool.* 94, 801–819.
- Halliday, W.D., Pine, M.K., Insley, S.J., 2020. Underwater noise and arctic marine mammals: review and policy recommendations. *Environ. Rev.* 28, 438–448. <https://doi.org/10.1139/er-2019-0033>.
- Harding, H.R., Gordon, T.A.C., Eastcott, E., Simpson, S.D., Radford, A.N., 2019. Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. *Behav. Ecol.* 30, 1501–1511. <https://doi.org/10.1093/beheco/arz114>.
- Hare, J.F., Campbell, K.L., Senkiw, R.W., 2014. Catch the wave: prairie dogs assess neighbours' awareness using contagious displays. *Proc. R. Soc. B Biol. Sci.* 281 <https://doi.org/10.1098/rspb.2013.2153>.
- Harris, R.E., Miller, G.W., Richardson, W.J., 2001. Seal responses to airgun sounds during summer seismic surveys in the Alaskan Beaufort Sea. *Mar. Mammal Sci.* 17, 795–812. <https://doi.org/10.1111/j.1748-7692.2001.tb01299.x>.
- Hastie, G.D., Russell, D.J.F., Lepper, P., Elliott, J., Wilson, B., Benjamins, S., Thompson, D., 2018. Harbour seals avoid tidal turbine noise: implications for collision risk. *J. Appl. Ecol.* 55, 684–693. <https://doi.org/10.1111/1365-2664.12981>.
- Holst, M., Lawson, J.W., Richardson, W.J., Schwartz, S.J., Smith, G., 2005. Pinniped responses during navy missile launches at San Nicolas Island, California. In: Garcelon, D.K., Schwemm, C.A. (Eds.), *Proceedings of the Sixth California Islands Symposium*, Ventura, California, December 1–3, 2003. Institute of Wildlife Studies, Arcata, CA, pp. 477–484.
- Holst, M., Greene, C.R., Richardson, W.J., McDonald, T.L., Bay, K., Schwartz, S.J., Smith, G., 2011. Responses of pinnipeds to navy missile launches at San Nicolas Island, California. *Aquat. Mamm.* 37, 139–150. <https://doi.org/10.1578/AM.37.2.2011.139>.
- Kastak, D., Mulsow, J., Ghoul, A., Reichmuth, C., 2008. Noise-induced permanent threshold shift in a harbor seal. *J. Acoust. Soc. Am.* 123, 2986. <https://doi.org/10.1121/1.2932514>.
- Kastelein, R.A., Gransier, R., Hoek, L., 2013. Comparative temporary threshold shifts in a harbor porpoise and harbor seal, and severe shift in a seal. *J. Acoust. Soc. Am.* 134, 13–16. <https://doi.org/10.1121/1.4808078>.
- Kelly, B.P., Quakenbush, L.T., Rose, J.R., 1986. Ringed-Seal Winter Ecology and Effects of Noise Disturbance. Fairbanks, Alaska.
- Kirkman, S., Oosthuizen, W.H., Meyer, M.A., Kotze, P.G.H., Roux, J.-P., Underhill, L.G., 2007. Making sense of censuses and dealing with missing data: trends in pup counts of Cape Fur seal *Arctocephalus pusillus* for the period 1972–2004. *Afr. J. Mar. Sci.* 29, 161–176.
- Kirkwood, R., Boren, L., Shaughnessy, P., Szeteren, D., Mawson, P., Huckstadt, L., Hofmeyr, G.J.G., Oosthuizen, H., Schiavini, A., Campagna, C., Berris, M., 2003. Pinniped-focused tourism in the southern hemisphere: a review of the industry. In: *Marine Mammals: Fisheries, Tourism and Management Issues*, pp. 257–276.
- Kovacs, K.M., Innes, S., 1990. The impact of tourism on harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence, Canada. *Appl. Anim. Behav. Sci.* 26, 15–26. [https://doi.org/10.1016/0168-1591\(90\)90083-P](https://doi.org/10.1016/0168-1591(90)90083-P).

- Lenth, R.V., 2021. Emmeans: estimated marginal means, aka least-squares means. R Pack. Vers. 1.6.2-1 <https://CRAN.R-project.org/package=emmeans>.
- Matthlin, R., 1978. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). *N. Z. J. Ecol.* 1, 138–144.
- McDougall, P.L., Ruckstuhl, K.E., 2018. Vigilance behaviour is more contagious when chewing stops: examining the characteristics of contagious vigilance in bighorn sheep. *Behav. Ecol. Sociobiol.* 72, 1–10. <https://doi.org/10.1007/s00265-018-2536-0>.
- Mikkelsen, L., Johnson, M., Wisniewska, D.M., van Neer, A., Siebert, U., Madsen, P.T., Teilmann, J., 2019. Long-term sound and movement recording tags to study natural behavior and reaction to ship noise of seals. *Ecol. Evol.* 9, 2588–2601. <https://doi.org/10.1002/ece3.4923>.
- Miksis-Olds, J.L., Donaghay, P.L., Miller, J.H., Tyack, P.L., 2005. Environmental noise levels affect the activity budget of the Florida manatee. *J. Acoust. Soc. Am.* 118, 1910. <https://doi.org/10.1121/1.4780209>.
- Newsome, D., Rodger, K., 2008. Impacts of tourism on pinnipeds and implications for tourism management. In: Higham, J.E.S., Lück, M. (Eds.), *Marine Wildlife and Tourism Management: Insights from the Natural and Social Sciences*, pp. 182–205.
- Pavez, G., Muñoz, L., Barilari, F., Sepúlveda, M., 2015. Variation in behavioral responses of the south American sea lion to tourism disturbance: implications for tourism management. *Mar. Mammal Sci.* 31, 427–439. <https://doi.org/10.1111/mms.12159>.
- Pays, O., Goulard, M., Blomberg, S.P., Goldizen, A.W., Sirot, E., Jarman, P.J., 2009. The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behav. Ecol.* 20, 469–477. <https://doi.org/10.1093/beheco/arp019>.
- Pirota, E., Brookes, K.L., Graham, I.M., Thompson, P.M., 2014. Variation in harbour porpoise activity in response to seismic survey noise. *Biol. Lett.* 10 <https://doi.org/10.1098/rsbl.2013.1090>.
- Rand, R.W., 1955. Reproduction in the female cape Fur seal, *Arctocephalus pusillus* (Schreber). *Proc. Zool. Soc. London* 124, 717–740. <https://doi.org/10.1111/j.1469-7998.1955.tb07812.x>.
- Reichmuth, C., Sills, J.M., Mulsow, J., Ghoul, A., 2019. Long-term evidence of noise-induced permanent threshold shift in a harbor seal (*Phoca vitulina*). *J. Acoust. Soc. Am.* 146, 2552. <https://doi.org/10.1121/1.5129379>.
- Riedman, M., 1990. *The Pinnipeds: Seals, Sea Lions, and Walruses*, vol. 12. Univ of California Press.
- Russell, D.J.F., Hastie, G.D., Thompson, D., Janik, V.M., Hammond, P.S., Scott-Hayward, L.A.S., Matthiopoulos, J., Jones, E.L., McConnell, B.J., 2016. Avoidance of wind farms by harbour seals is limited to pile driving activities. *J. Appl. Ecol.* 53, 1642–1652. <https://doi.org/10.1111/1365-2664.12678>.
- Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Frstrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S., Wittemyer, G., 2015. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* <https://doi.org/10.1111/brv.12207>.
- Shaughnessy, P.D., Nicholls, A.O., Briggs, S.V., 2008. Do tour boats affect fur seals at Montague Island, New South Wales? *Tour. Mar. Environ.* 5, 15–27. <https://doi.org/10.3727/154427308785855260>.
- Southall, B.L., Bowles, A.E., Ellison, W.T., Finneran, J.J., Gentry Jr., R.L., Kastak, D., Ketten, D.R., Miller, J.H., Nachtigall, P.E., Richardson, W.J., Thomas, J.A., Tyack, P.L., Greenejr, C.R., Kastak, D., Ketten, D.R., Miller, J.H., Nachtigall, P.E., Richardson, W.J., Thomas, J.A., Tyack, P.L., 2007. Aquatic mammals noise exposure criteria. *Aquat. Mamm.* <https://doi.org/10.1578/AM.33.4.2007.411>.
- Stewart, B.S., 1981. Behavioural response of northern elephant seals and California Sea lions on san Nicolas Island, California to loud impulse noise. *J. Acoust. Soc. Am.* 70 <https://doi.org/10.1121/1.2019078>.
- Stewart, B.S., 1993. Behavioral and hearing responses of pinnipeds to rocket launch noise and sonic bloom. *J. Acoust. Soc. Am.* 94 <https://doi.org/10.1121/1.407787>.
- Stewart, B.S., Francine, J.K., Thorson, P.H., 1994. Taurus Launch at Vandenberg Air Force Base, 13 March 1994; Sound Levels and Behavioral Responses of Harbour Seals (*Phoca vitulina richardsi*) et Purisma Point and Rocky Point (HSWRI Technical Report 94–252). San Diego.
- Sueur, J., Aubin, T., Simonis, C., 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* 18, 213–226.
- Tripovich, J.S., Hall-Aspland, S., Charrier, I., Arnould, J.P.Y., 2012. The behavioural response of australian fur seals to motor boat noise. *PLoS One* 7, 3–9. <https://doi.org/10.1371/journal.pone.0037228>.
- Williams, R., Lusseau, D., Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol. Conserv.* 133, 301–311. <https://doi.org/10.1016/j.biocon.2006.06.010>.
- Wright, A.J., Baldwin, A.L., Bateson, M., Beale, C.M., Clark, C., Deak, T., Edwards, E.F., Hatch, L.T., Studds, G.E., Bank, S., Martineau, D., Notarbartolo-di-sciana, G., Martin, V., 2007. Do Marine mammals experience stress related to anthropogenic noise? *Int. J. Comp. Psychol.* 20, 274–316.