1 **Can fear conditioning repel California sea lions from fishing activities?**

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9

10 **Abstract**

11 Marine mammal interactions with fisheries create conflicts that can threaten human safety,

12 economic interests, and marine mammal survival. A deterrent that capitalizes on learning

13 mechanisms, like fear conditioning, may enhance success while simultaneously balancing

14 welfare concerns and reduce noise pollution. During fear conditioning, individuals learn the cues

15 that precede the dangerous stimuli, and respond by avoiding the painful situations. We tested the

16 efficacy of fear conditioning using acoustic stimuli for reducing California sea lion (*Zalophus*

17 *californianus*) interactions from two fishing contexts in California, USA; bait barges and

18 recreational fishing vessels. We performed conditioning trials on 24 individual sea lions

19 interacting with bait barges. We tested for acquisition of conditioned fear by pairing a neutral

20 tone with a startle stimulus. Avoidance was strongest in response to the startle stimulus alone,

21 but low when paired with a neutral tone. From actively fishing vessels we tested for fear

22 conditioning by exposing sea lions to a neutral tone followed by a startle pulse, a startle pulse

23 alone, or a no sound control. We conducted playbacks from 146 (including 48 no sound control)

24   stops over two summer fishing seasons (2013, 2014). The startle stimulus decreased surfacing

25   frequency, reduced bait foraging and increased surfacing distance from the vessel while the

26   conditioned stimulus only caused a mild reduction in surfacing frequency with no other

27   behavioral change. Exposing animals to a pair of a conditioned stimulus with a startle pulse did

28   not achieve the intended management outcome. Rather, it generated evidence (in two study

29   contexts) of immediate learning that led to the reduction of the unconditioned response. Taken

30   together, our results suggest that for fear conditioning to be applied as a non-lethal deterrent,

31   careful consideration has to be given to individual behavior, the unconditioned/conditioned

32   responses, and the overall management goals.

33

34   **Introduction**

35   As part of rapid anthropogenic environmental change, wildlife are increasingly turning to

36   human-derived resources such as fish from fishing lines or nets (Zollett & Read, 2006),

37   domesticated livestock (Muhly & Musiani, 2009) or garbage cans (Baruch-Mordo *et al.*, 2013).

38   Animals exploiting these resources create human-wildlife conflicts, ultimately threatening

39   human safety, economic interests, and their own survival (Woodroffe *et al.,* 2005). In the marine

40   environment, marine mammal depredation, or the removal of fish from lines or nets, creates

41   scientific, management, and conservation concerns that include socio-economic losses upon

42   fisheries (Hamer *et al.,* 2012), increased marine mammal entanglements, and potential (and

43   realized) retaliatory actions by fisherman (Powell & Wells, 2011; Read, 2008). As a consequence

44   of these conflicts, there is increasing demand for effective non-lethal mitigation techniques, such

45   as effective deterrents to reduce conflicts (Berrow *et al.,* 2008; Forrest *et al.,* 2009; Gordon &

46   Northridge, 2002; Götz & Janik, 2015, 2016).

47   Deterrents use aversive stimuli to prevent animals from acquiring human resources (Ramp *et*

48   *al.*, 2011). Deterrent stimuli use a variety of mechanisms to elicit defensive responses in animals

49   (Götz & Janik, 2010; Schakner & Blumstein, 2013). A range of different presumably aversive

50   stimuli, such as intense acoustic signals, can elicit avoidance in marine mammals (Berrow *et al.*,

51   2008; Brandt *et al.*, 2013; Cosgrove *et al.*, 2009). However, the use of such intense acoustic

52   signals in marine environments to prevent depredation is controversial. There are concerns about

53   their overall efficacy, ethical and conservation concerns over potential hearing damage, and

54   ecological impacts on non-target wildlife (Gordon & Northridge, 2002; Götz & Janik, 2013).

55   Focusing deterrents on species-specific sensory capabilities and individual learning mechanisms

56   can potentially limit the effects on non-target species, as well as reduce an individual's exposure

57   to painful stimuli (Götz & Janik, 2013). Most species can learn the cues, context, or conditions

58   that predict threatening situations (e.g., predator attack). This suggests that a deterrent which

59   capitalizes on learning mechanisms may enhance success while simultaneously balancing

60   welfare concerns and potential deleterious impacts on non-target species if the aversive stimulus

61   does not elicit avoidance responses in non-target species.

62   *Pavlovian fear conditioning* is a form of associative learning in which individuals are

63   exposed to an aversive, unconditioned stimulus (US) that is paired with an innocuous

64   conditioned stimulus (CS) (Fanselow & Ponnusamy, 2008; Fanselow, 1984). While exposure to

65   the unconditioned stimulus alone generally generates unconditioned fear reactions, conditioned

66   responses to a CS after conditioning are different from unconditioned response to the US itself

67   (Blanchard & Blanchard, 1969; Fanselow, 1980; Hollis *et al.*, 1997). For instance, rats'

68   unconditioned response to aversive electric shock (US) involves a burst of motor activity

69   (Fanselow, 1982). In contrast, rats exposed to a stimulus that predicts shock or threat (CS such as

70   context or experimenter) react by fleeing, engaging in hyper-vigilance, or exhibiting generalized

71   avoidance (Blanchard, 1997; Bolles & Collier, 1976; Fanselow, 1980). Conditioned responses

72   involve behaviors like vigilance or avoidance designed to circumvent threat that can also be the

73   target responses for an effective deterrent (Hollis *et al.,* 1997). To use this in deterrents, a painful

74   or aversive deterrent stimulus designed to elicit an unconditioned response is needed as a US. If

75   effectively conditioned with a paired CS, individuals will have learned that the CS indicates an

76   impending US stimulus so that they can learn to avoid the US stimulus entirely. Employing fear

77   conditioning to create deterrents might be a very effective way to reduce human-wildlife

78   conflicts in a relatively humane way, especially if the conditioned response to the target CS is

79   avoidance (Greggor *et al.*, 2014; Mazur, 2010; Rossler *et al.,* 2012; Schakner *et al.,* 2014).

80   The acoustic startle reflex is a response to a fast onset of an acoustic stimulus that results in

81   eyelid closure, contraction of neck and skeletal muscles, and sympathetic activation (Koch,

82   1999). It also disrupts ongoing behavioral patterns, and reduces sensory and cognitive

83   functioning (Graham, 1979). In a captive setting, Janik & Götz (2011) demonstrated that

84   repeated startle stimuli elicited flight responses in grey seals (*Halichoerus grypus*) even when the

85   seals were highly motivated to feed and in the presence of food (Götz & Janik, 2011). In field

86   trials on harbour seals (*Phoca vitulina*) and grey seals, startle sounds have been used successfully

87   to reduce seal approaches and seal depredation on salmon farms (Götz & Janik, 2015, 2016).

88   These results suggested that a startle pulse could be used as an aversive, unconditioned stimulus.

89   This had also previously been shown in the laboratory, when grey seals were successfully fear-

90   conditioned with a startle stimulus as a US and a non-startling tone as a CS (Götz & Janik, 2011).

91   We used a fear conditioning approach with acoustic deterrents by pairing a tone, the CS, with

92   an acoustic startle stimulus, the US, on free-living California sea lions (*Zalophus californianus*)

93   that were interacting with commercial fishing activities in southern California. By doing so, we

94   evaluated the efficacy of fear conditioning in contexts in which it had not previously been

95   studied.

96   California sea lion depredation of commercial passenger fishing vessels and bait receivers—

97   barges and docks where live bait is sold to recreational fishers (hereafter bait barges) off the west

98   coast of the United States has been observed for decades and has increased as pinniped

99   populations have increased dramatically since the 1970's (Fletcher, 2008; Keledjian & Mesnick,

100   2013; Lowry & Maravilla-Chavez, 2005). Our objective was to test the efficacy of fear

101   conditioning in reducing sea lion interactions from these two commercial fishing contexts; bait

102   barges and fishing vessels. We tested whether: (1) individual sea lions interacting with bait

103   barges can be fear conditioned using aversive acoustic stimuli and whether fear-conditioned

104   individuals' responses differ from those of non-conditioned individuals and (2) fear conditioning

105   reduces interactions between sea lions and commercial passenger fishing vessels in southern

106   California.

107

108   **Materials and methods**

109   **Study site**

110   We conducted two sets of fear conditioning trials. The first focused on California sea lions

111   hauled out on bait barges in Southern California's Mission Bay. The second focused on sea lions

112   interacting with commercial passenger fishing vessels off Southern California. These vessels

113   were based in San Diego Bay, Mission Bay, Dana Point, San Pedro, and Marina Del Rey.

114

115   **Playback equipment and stimuli**

116   We broadcast acoustic stimuli through a Lubell 9162T underwater loudspeaker (Lubell Labs Inc.,

117   Columbus, Ohio), using a Vibe 292 power Amplifier (Lanzar Inc.), from a Tascam DR40 player.

118   The loudspeaker was calibrated using a variety of test signals at broadband source levels.

119   Stimuli were adjusted digitally using Adobe Audition (Adobe® Systems, Mountain View, CA,

120   USA) to create the desired source level. The Conditioned Stimulus (CS) was a 6 s long, 120 dB

121   re 1 μPa sine wave tone (shaped with a 1.5 s long fade in to be non-startling), with a frequency

122   range of 1-2 kHz (Figure 1). The Unconditioned Stimulus (US), the startle pulse, was centered

123   around 10-11 kHz with a bandwidth from 2 kHz to 18kHz. The pulse was synthesized from

124   white noise in Adobe Audition 2.0 software with a band-pass filter and an envelope gain function.

125   The stimulus was played at a source level of 190 dB re 1 μPa rms, had a duration of 200 ms, and

126   a rise time of 2 ms (figure 1). During pairings, the US was played 2 seconds after the CS.

127

128   Insert Figure 1 about here

129

130   **Experimental design**

131   *Conditioning trials on bait barges*

132   Two observers were stationed at the end of the bait barge to control the acoustic apparatus and

133   perform focal follows. Individual sea lions were marked with non-toxic paint pellets. After

134   marking, a focal individual was flushed into the water by walking towards it. Each individual

135   was randomly assigned to a paired startle-pulse or control treatment. For the paired group,

136   treatment consisted of 6 trials of CS/US training followed by a test phase of 6 trials of the CS

137   alone (CS-) (Figure 2). Individuals in the unpaired control group were presented with the same

138   total number of CS and US sounds (6 control-CS and 6 control-US) as the paired group in their

6

139   training phase, but in a predetermined random order so there was no consistent association

140   between the CS and US (Figure 2). Thus, the control animals were exposed to 6 isolated CS

141   presentations and 6 isolated US presentations. Following a 2 min pre-trial observation period,

142   trials commenced when the focal individual surfaced within 20 m of the speaker. The stimulus

143   was played as soon as the animal put its head underwater after being detected. Each trial

144   consisted of a sound exposure followed by observation of the subject's response (surface time

145   and distance to barge measured using a laser rangefinder). The subsequent surfacing of the

146   animal within a 20 m radius of the deterrent initiated the next trial, again playing the stimulus as

147   soon as the head was underwater after surfacing. This continued until all trials were completed

148   for the focal animal's treatment.

149

150   *Bait barge conditioning trials analysis*

151   To study factors that predicted response during observation, we fitted generalized linear mixed

152   effects models (GLMMs) with distance fled (in m) and time spent outside of a 20 m radius of the

153   transducer (in min) as response variables, using a gamma error distribution and (log-link

154   function). For all statistical analyses, we used R 2.14 (R Development Core Team, 2014) using

155   the package lme4 (Bates *et al.*, 2011). We used a two-step (Zuur *et al.*, 2009) model selection

156   procedure using the Akaike Information Criterion for small sample sizes (AICc). In a first step

157   we determined the optimal random effects combination with the fully populated fixed effects. In

158   a second step we determined the optimal fixed effects combination while using the previously

159   determined random effects. Fixed effects that we considered included treatment (factor levels:

160   CS/US training, CS- testing, Control US-Alone and Control CS-alone), trial number, and sex, as

161   well as the interaction between trial number and treatment. We tested the following random

162 effect combinations (here shown in R notation); random intercept term for individual (1 | ID) as

163 well as random slope terms for treatment x individual (treatment | ID) and trial number (Trial |

164 ID) within individual.

165   The fixed and random effects combination retained in the final selected model are shown in

166 supplementary table 1. We calculated 95% confidence intervals using the 'confint' function

167 (method "Wald") in lme4. We validated model assumptions by examining the distribution of

168 residuals and quantile-quantile plots. Table S1 lists the information on the random and fixed

169 effects included in the full model and distributions. All model parameter coefficients and CIs are

170 shown on the scale of the response variable.

171

172   Insert Figure 2 about here

173

174 *Conditioning trials on fishing boats*

175 Each commercial passenger fishing vessel (CPFV) fishing trip had multiple fishing stops. At

176 each stop, the deterrent apparatus was deployed at the stern of the fishing vessel where fishing

177 was concentrated. The acoustic stimuli were broadcast only when sea lions were observed within

178 50 m of the vessel. Three conditions were randomly selected for playback: Paired stimuli

179 (CS/US), startle-pulse alone (US), or control with no sound.

180   Two observers, one stationed on the observation deck and one on the stern performed

181 behavioral observations and counts of the number of sea lions within 50 m of the vessel while

182 scanning for other marine mammals > 50 m away. Surface distances from vessel were measured

183 with a laser range finder. The observers focused on quantifying the following behavioral

184 variables: bait foraging (the amount of time sea lions were within 30 m of the stern actively

185   taking bait from fishing lines or chum while swimming back and forth), surface take (when sea

186   lions removed a hooked fish as evidenced by movement on the fishing line indicating that a fish

187   was no longer hooked, and a sea lion surfaced immediately with a fish), surfacing behavior

188   (number and distance of surfacings), and the number of sea lion-vessel interactions (number of

189   sea lions and time spent within 50 m of vessel).

190

191   *Analysis of conditioning trials on fishing boats*

192   To study the factors that influenced sea lion surfacing behavior during playback, we fitted a

193   GLMM (Poisson error distribution, log link) with surfacing frequency as a response variable and

194   a GLM (Gamma error distribution, log link) with surfacing distance as a response variable. For

195   all fishing boat analyses, we first used the AICc value to select whether to use GLM or GLMM,

196   then we used the same two-step procedure mentioned above to find the optimal fixed and

197   random effect model structure. Predictor variables included were treatment (factor levels: control,

198   CS/US pairing, US-alone) and time spent fishing. Location and the fishing stop number were

199   included as random effects for all GLMMs. To study how the startle pulse influenced sea lion

200   bait foraging, we fitted a GLM with bait foraging presence as the binomial response variable and

201   predictor variables were treatment and time spent fishing. Bait foraging occurred when sea lions

202   were stern foraging for at least 50% time fishing at a single stop (absence defined as a sea lion

203   bait foraging for less than 50% time fishing at a stop).

204

205   **Results**

206   **Conditioning trials on bait barges**

207   Conditioning trials took place from September through November 2014. A total of 24 individual

208   California sea lions were marked and used for playback (12 treatment, 12 control). The only

209   factor to significantly predict the distance and time spent away in response to playback was the

210   US when played alone in the control group (Table 1; Figure 2). Individual sea lions surfaced 7.7

211   times farther and spent nearly 8 times more time away from the bait dock in response to the US-

212   alone (table 1, Figure 2) than in response to the control CS. There was a trend that seals came

213   closer in later trials. In response to CS/US paired playback, individuals surfaced 2.2 times farther

214   away but did not spend any more time away from the transducer compared to control individuals.

215   The interaction between trial number and CS/US treatment was significant for both distance and

216   time spent away, suggesting that responses diminished with each successive trial (CS/US

217   pairings) compared to control individuals. The interaction between CS-Testing x Trial and US x

218   Trial was significant for distance, indicating somewhat diminished responses in later trials for

219   treatment compared to control individuals.

220   Insert Figure 3 about here

221

222   **Conditioning trials on fishing boats**

223   We monitored 226 fishing stops across five locations in southern California during two summer

224   fishing seasons (May-September 2013, 2014). Fishing time at a stop ranged from 0.08 h to 1.9 h

225   with a mean of 0.73 h ($\pm$45 h SD). Over the two seasons of observations, interactions with sea

226   lions occurred during 62% of the 226 fishing stops. Playbacks were performed on 98 fishing

227   stops; in addition, we had 48 control (no sound) observations. Surface takes occurred too

228   infrequently to be included in analyses.

10

229   Compared to no-sound control treatment, playback of the startle pulse (US-alone) caused sea

230   lions to surface 2.7 times farther from the vessel and reduced surfacing frequency by 23% (Table

231   2). The paired playback caused a 26% decrease in surfacing but had no effect on distance

232   surfaced compared to control treatments (Table 2). In addition more surfacings were detected

233   during stops with longer fishing times (Table 2).

234   The US-alone treatment reduced the presence of sea lion bait foraging behavior causing an

235   83% reduction in the number of events when bait foraging was present (more than 50% of the

236   time). There was no significant effect of the paired playback on bait foraging behavior (Table 3).

237

238   Insert Figure 4 around here

239

240   **Discussion**

241   The purpose of our study was to investigate whether individual sea lions could be fear

242   conditioned using aversive acoustic stimuli and whether fear conditioning reduces interactions

243   between sea lions and commercial passenger fishing vessels in southern California.

244   From bait docks, playback of startle pulses evoked strong, unconditioned behavioral

245   responses in California sea lions that included rapid flight and increased surfacing distances.

246   These results are consistent with earlier studies that showed avoidance responses to startling

247   stimuli in grey seals (Götz & Janik, 2011) and harbor seals (Götz & Janik, 2015, 2016). The

248   pairing of a neutral tone with the startling pulse produced conditioned responses in individual sea

249   lions interacting with bait barges. However, this response was not as strong compared to the

250   startle pulse alone, and it diminished with successive CS/US pairings. Thus, we found evidence

251   for prominent behavioral responses to the unconditioned stimulus, and moderate to weak

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252 responses to the pairing of CS and US, as well as in response to CS (after training). From the

253 vessels, sea lions clearly responded to the startle pulse by increasing the distance from the boat

254 and by decreasing their time spent bait foraging, while showing minor responsiveness to pairing.

255 It appears the presence of the CS effectively removed the ability of the deterrent (the US) to

256 reduce the behavior we aimed to reduce—bait foraging.

257   According to adaptive-evolutionary perspectives on learning theory, the nature of the

258 conditioned response is determined by the unconditioned stimulus (Fanselow & Lester, 1988;

259 Timberlake, 1994). Learned responses are tailored to the particular US. For instance, response to

260 sickening food involves taste aversion (Garcia *et al.,* 1955), whereas responses to CS preceding

261 tactile pain, like a shock, include the avoidance of the context where pain occurred. For our study,

262 the unconditioned stimulus was a startle-eliciting acoustic pulse. We found hat the behavioral

263 responses to the startle pulse included avoidance of the site of sound exposure, as observed in

264 captive experiments (Finneran *et al.,* 2003; Götz & Janik, 2011). However, once conditioned

265 with a paired CS, individuals showed weaker responses to the US, eventually diminishing any

266 responsiveness with successive trials. A possible explanation for this is that the animals

267 developed strategies to reduce hearing sensitivity that could not be observed behaviorally. In

268 some cetacean species for instance, the Pavlovian response to a warning signal preceding intense

269 acoustic stimuli reduces hearing sensitivity (Nachtigall & Supin, 2014, 2013), a possibility that

270 has not been explored with pinnipeds. In contrast to previous studies, we used a relatively long

271 CS tone that may have provided the animals with a relatively long warning period. Thus, the

272 specific duration of the CS might have helped sea lions develop successful avoidance strategies.

273   For the purpose of reducing pinniped/fisheries conflict, our startle pulse changed the

274 behavior of sea lions interacting with fishing vessels but the deterrence range was limited

275   because the average distance of surfacing during playback was still within the 50 m of boats. It

276   may be that individuals surfaced further out to avoid being near the sound source while stern

277   foraging. However, we found bait foraging to be reduced by 83%. The increased surfacing

278   distance elicited in response to the startle pulse may be useful in other commercial fisheries (e.g.,

279   bottom set gillnets), or on fish farms where predators need to spend a significant amount of time

280   underwater, close to the fishing apparatus to obtain prey (e.g., by manipulating nets).

281   In some cases, the startle deterrent did not influence sea lion behavior. This also happened

282   with some of the grey seals in a previous study, possibly due to elevated hearing thresholds in the

283   subjects (Götz & Janik, 2011). Identifying the specific mechanisms underlying the lack of

284   response (habituation, increased motivation, higher hearing thresholds, or indeed a high turnover

285   of animals) requires further investigation. Generally speaking, one problem with otariids (which

286   include California sea lions) is that they have less sensitive underwater hearing than most phocid

287   seals (which include grey seals) limiting the applicability of acoustic startle devices

288   (Schusterman, 1981). The lack of the ability to mark individual sea lions foraging in the open

289   ocean remains a major limitation of our and other studies that require individual identification

290   (e.g., studies of habituation to repeated exposure of stimuli).

291   Our observations suggest that the conditioned response to acoustic stimuli failed to create the

292   desired management goal (avoidance) in this particular fishery. However, the unconditioned

293   stimulus we used on its own holds potential because the startle pulse elicited strong responses.

294   The addition of the CS, introduced to minimize the overall impact on the animal, and indeed may

295   prevent the development of contextual fear by providing time for an individual to engage in other

296   responses. Thus, while we were able to induce mild fear conditioning in individual Californian

297   sea lions interacting with commercial fishing activities, we were unable to create the desired

298 avoidance necessary to mitigate the predation problem in the tested industries by using a CS/US

299 pairing.

300   Taken together, the pollution of an effective acoustic US with a warning CS reduced the

301 efficacy of the US for controlling sea lions interacting with recreational fishing activities in our

302 study. For the fear conditioning method to have promise for development of non-lethal deterrents

303 in other contexts, careful consideration has to be given to the behavior of individuals, the

304 unconditioned/conditioned responses, and the overall management goal when designing these

305 acoustic deterrents.

306

307 **Acknowledgments**

314

315 **Appendix A. Supplementary material**

316 A table specifying specific models and transformations used can be found in the online version.

317

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427 **Table 1**

428 Generalized linear mixed effects models for individual California sea lion responses (time spent

429 away and distance fled) during conditioning trials on bait barges. Model coefficients for fixed

430 effects are presented on the scale of the response variable. Significant ($p < 0.05$) variables are

431 highlighted in bold.

	model	Model Coefficient	95% CI	*P-value*
(intercept)	time	1.96	1.17, 3.28	**0.01**
	distance	10.11	6.4, 15.95	**6.4×10^{-29}**
Treatment: US-Alone	time	7.92	4.47, 14.00	**1.2×10^{-12}**
	distance	7.74	3.59, 16.65	**6.9×10^{-7}**
Treatment: CS/US training	time	1.60	0.79, 3.27	0.37
	distance	2.32	1.20, 4.37	**0.02**
Treatment: CS- Testing	time	0.73	0.36, 1.47	0.37

	distance	1.71	0.93, 3.14	0.08
Trial number	time	1.16	1.03,1.30	**0.014**
	distance	1.22	1.08,1.37	**0.016**
US-Alone × Trial number	time	0.88	0.75,1.03	0.10
	distance	0.87	0.78,0.97	**0.02**
CS/US × Trial number	time	0.82	0.71,0.95	**0.001**
	distance	0.80	0.69, 0.93	**0.02**
CS-Testing × Trial number	time	0.92	0.80,1.06	0.216
	distance	0.77	0.66, 0.89	**0.03**

432

433 **Table 2**

434   Generalized linear mixed effects models for sea lion surfacing behavior (surfacing frequency--surf.frequency and distance) during

435 playback from active fishing vessels. Model coefficients presented on the scale of the response variable. Significant (p < 0.05)

436 variables are highlighted in bold. 'nr' indicates the variable was not retained in the model selection process.

	model	Model Coefficient	95% CI	*P-value*
(intercept)	Surf. frequency	22.1	14.2, 34.2	**4.4×10^{-44}**
	Distance	19.1	13.6, 27.1	**6.4×10^{-9}**
Treatment: US-Alone	Surf. frequency	0.77	0.71, 0.83	**2.6×10^{-11}**
	Distance	2.70	1.99, 3.62	**1.3×10^{-10}**
Treatment: CS/US training	Surf. frequency	0.74	0.67, 0.80	**2.3×10^{-9}**
	Distance	1.06	0.75, 1.50	0.72
Time spent fishing	Surf. frequency	1.08	1.02, 1.10	**5.0×10^{-3}**
	Distance	nr	nr	nr
Stop N	Surf. frequency	nr	nr	nr
	Distance	0.88	0.78, 0.99	0.051

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441   **Table 3**

442   Influence of startle pulse on sea lion foraging behavior during active fishing.

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	Model: Presence of Bait foraging		
Variable	*Coefficient*	*CI (95%)*	*P*
(Intercept)	5.40	2.27, 15.9	**5.0×10^{-4}**
Treatment: US-alone	0.27	0.08, 0.72	**0.015**
Treatment: CS/US pairing	6.30	0.94, 124.5	0.10

444   **Figure Legends**

445   **Fig. 1.** Conditioned Stimulus (CS) and Unconditioned Stimulus (US) playback sounds.

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447   **Fig. 2.** Reinforcement schedules for individuals in paired playback or control treatments from

448   bait docks. Red dotted lines refer to US and black solid lines represent CS.

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450   **Fig. 3** Boxplot for sea lion responses (time spent away from bait barge) during bait barge trials.

451   Boxes show median (line within the box) and upper (25%) and lower (75%) quartiles, whiskers

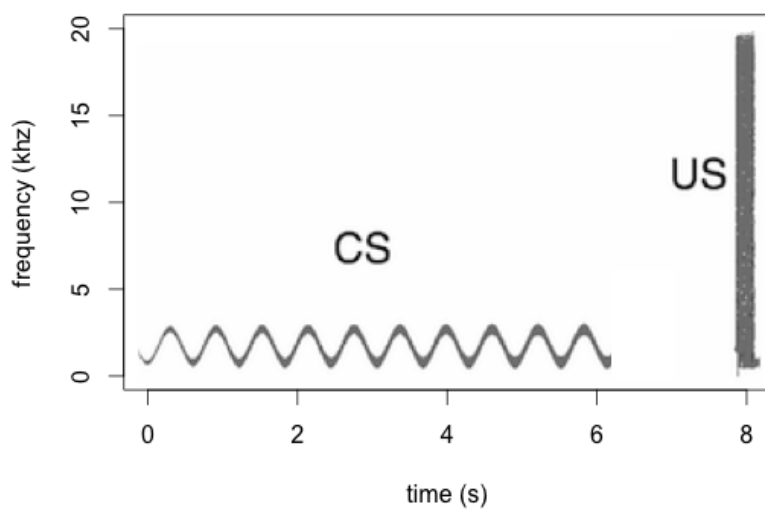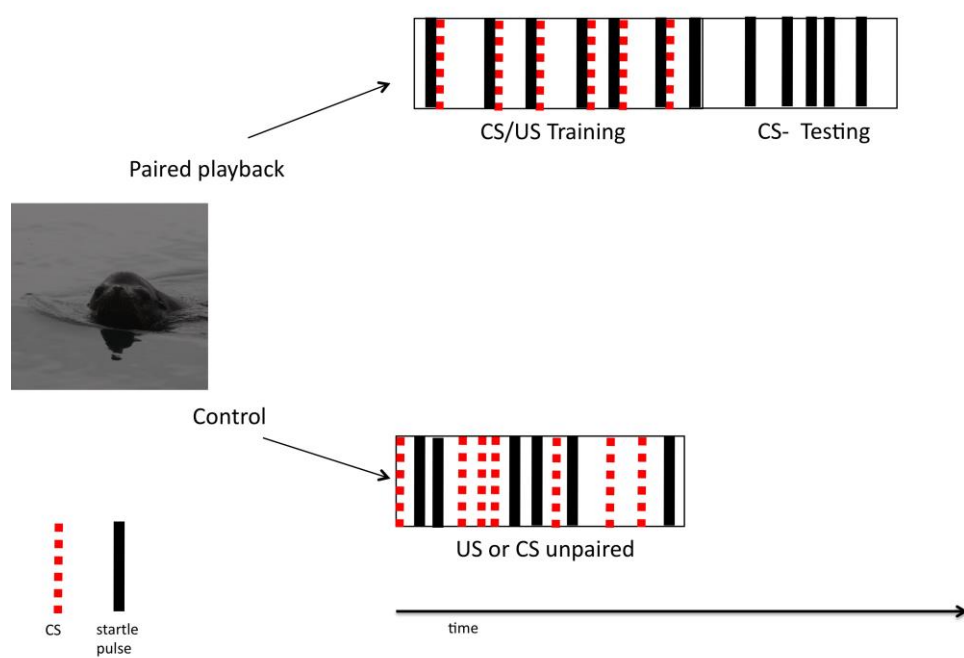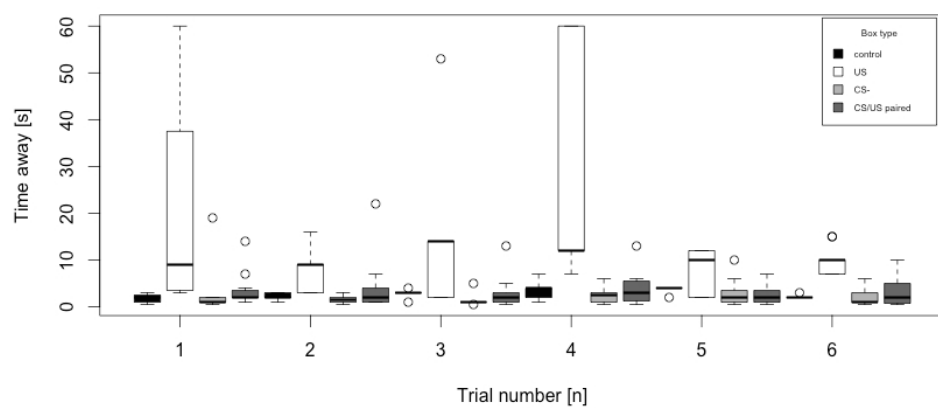452   indicate outermost data points within a 1.5 interquartile range, and circles are outliers.

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454   **Fig. 1**

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473   **Fig. 3**

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477   **Appendix A. Full generalized linear (mixed) models with random and fixed effects that**

478   **were evaluated during model selection**

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Dependent variable	Factors	Random Factors	Model
Conditioning trials on bait barges			
Time away from dock	Sex, trial, treatment	(1| ID), (treatment | ID), (Trial | ID)	Gamma distribution with log-link function
Distance fled from dock	Sex, trial, treatment	(1| ID), (treatment | ID), (Trial | ID)	Gamma distribution with log-link function
Conditioning trials on fishing boats			
Bait Foraging (GLM)	treatment, time spent fishing	n/a	Binomial
Surfacing Frequency	treatment, time spent fishing	(1|stop), (1|Site)	Poisson distribution with log-link function
Surfacing Distance (GLM)	treatment, time spent fishing, stop	n/a	Gamma distribution with log-link function

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