

1 **Good vibrations by the beach boys: Magnitude of substrate vibrations is a**  
2 **reliable indicator of male grey seal size.**

3

4 Running Title: Ground vibrations contain information on male seal size

5

6 **ABSTRACT**

7 Communication via substrate vibrations can convey information on conspecific presence, individual  
8 quality, group cohesion, and/or allow for predator avoidance. While studies have identified that various  
9 species use this modality, few studies on mammalian taxa have investigated if the information contained  
10 in substrate vibrations is a reliable indicator of resource holding potential (RHP). The grey seal  
11 (*Halichoerus grypus*) breeding colony at Donna Nook, UK, is part of a limited geographic region where  
12 the Body Slap (BS) behaviour is performed during male-male conflicts. This behaviour is thought to have  
13 a mechanical component. We examined if the magnitude of the BS substrate vibrations contained reliable  
14 information on male mass and size as measures of RHP, and if reliability varied across environmental  
15 conditions. To test this, we deployed seismometers during the breeding season that recorded continuous  
16 seismic data over a frequency bandwidth 0.03Hz-500Hz. Locations and times of BS events performed by  
17 individual males were recorded, matched with the seismic data, and a distance corrected magnitude was  
18 calculated for each event. Our results demonstrate the BS generates a stereotyped seismic signature  
19 measurable up to 126.3 m away. We found a positive correlation between the maximum and mean  
20 magnitudes of the substrate-borne vibrations and a male's length. Dampness of the sand substrate had no  
21 effect on magnitude. Results of this study confirm that the maximum magnitude substrate vibrations  
22 generated by the Body Slap behaviour is an indicator of male size and that the substrate-borne vibrations  
23 are reliable across varying environmental conditions.

24

25 **Indexing Words:** *Halichoerus grypus*, male conflict, pinniped, seismic, signalling, substrate vibrations,

26

## 27 INTRODUCTION

28 Resource holding potential (RHP) is a representation of an individual's ability to win in a contest,  
29 and as such, is often positively correlated with size, mass or ornamentation (Carlini et al., 2006; Insley &  
30 Holt, 2011; Smith, 1979, Sneddon, Huntingford, & Taylor, 1997; Vannoni & McElligott, 2008).  
31 Signalling during agonistic interactions has been favoured by selection to convey information regarding  
32 these correlates of RHP, which opponents can use in assessment to avoid costly escalations (Arnott &  
33 Elwood, 2009; Smith, 1979). Such signals are particularly common in polygynous systems with intense  
34 male-male competition; for example, roaring in male red deer (*Cervus elaphus*) (Clutton-Brock & Albon,  
35 1979) or vocalizations by northern elephant seal bulls (*Mirounga angustirostris*) (Sanvito, Galimberti, &  
36 Miller, 2007b). While the literature investigating air-borne acoustic and visual displays as indicators of  
37 male or female RHP is extensive (Arnott & Elwood, 2009; Clutton-Brock & Albon, 1979; Sanvito,  
38 Galimberti, & Miller, 2007b; Vannoni & McElligott, 2008), only a few studies have extended these  
39 questions to signals that generate substrate-borne vibrations (Elias et al., 2008; Rivero et al., 2000). The  
40 lack of studies is particularly evident in mammalian systems. Interest in mammalian use of substrate  
41 vibrations as a mode of communication has risen in recent years (Hill, 2009; O'Connell-Rodwell, 2007),  
42 but has generally focused on the use of vibrations to convey information about the presence of  
43 conspecifics (Brownell & Farley, 1979; Randall & Matocq, 1997; Shipley, Stewart, & Bass, 1992), group  
44 cohesion and spacing (O'Connell-Rodwell, 2007) or predator avoidance (Randall, 2001). Some studies  
45 have suggested links (Shipley, Stewart, & Bass, 1992), but few have explicitly investigated the use of the  
46 characteristics of substrate-borne vibrations as advertisement of male RHP in mammalian systems.

47 Substrate vibrations generated by animal signalling are extensively documented across numerous  
48 animal taxa; conservative estimates suggest that in the order Insecta alone, a total of 195,000 species use  
49 this mode of communication (Hill, 2009). In comparison, the number of mammalian species known to use  
50 this form of communication is estimated at 32 species across 11 families (Hill, 2009). These signals can  
51 be generated via direct contact: stridulation (Gordon & Uetz, 2011), tremulation (Caldwell et al., 2010) or  
52 percussive drumming (Elias et al., 2008; Randall & Matocq 1997); or through vocalizations strong

53 enough to excite substrate-borne vibrations (Hill, 2009; O'Connell-Rodwell, 2007; Shipley, Stewart, &  
54 Bass, 1992). Previous work has identified that the substrate-vibration components of signals can be used  
55 in various forms of communication: stridulations and tremulations can advertise quality during conflict  
56 and mate choice, while foot drumming and substrate coupled vocalizations have been linked with  
57 conspecific avoidance and group cohesion (Elias et al., 2008; Hill, 2009). In this study, we investigate a  
58 specific behaviour performed by male grey seals (*Halichoerus grypus*) during the breeding season and  
59 investigate if the substrate vibrations generated convey reliable information regarding male RHP that  
60 could be used in contest assessment by receivers.

61         Wild, breeding male grey seals are ideal model species for this investigation. Grey seals in the  
62 UK have individually unique and stable natural markings and site fidelity, which allows for individual-  
63 based observations within and between breeding seasons (Anderson & Fedak 1985; Boyd, Lockie, &  
64 Hewer, 1962; Hiby & Lovell 1990; Pomeroy, Twiss, & Redman, 2000; Twiss, Pomeroy, & Anderson,  
65 1994). Parturition and mating occurs yearly in the autumn or winter in the UK, and seals breed across a  
66 variety of substrates (e.g. sand, rocky-intertidal, grass) depending on colony locality. The breeding season  
67 lasts for approximately 8 weeks. Females are ashore for 18-20d during which they give birth to a single  
68 pup, mate (oestrus is roughly on day 16 post-partum), and wean; this results in a turnover of females and  
69 variation in local densities throughout the breeding season (Anderson, Burton, & Summers, 1975; Boness  
70 & James 1979). Males maximize mating success by remaining among groups of females for as long as  
71 possible by forming loose territories and exhibit a range of aggressive behaviours (Boness & James 1979;  
72 Twiss, 1991; Twiss, Anderson, & Monaghan, 1998). Aggressive interactions occur between males  
73 throughout the season as territories shift, new males arrive and as access to females in oestrus changes  
74 (Boness & James 1979; Twiss, 1991; Twiss, Pomeroy, & Anderson, 1994). Inter-male aggression  
75 typically takes the form of ritualized displays, but some interactions will escalate to physical fights  
76 comprised mainly of wrestling (Boness, 1984; Twiss, 1991). The known correlates for RHP for grey seals  
77 and other closely related pinnipeds are length and mass (Anderson & Fedak, 1985; Carlini et al., 2006);

78 although, some studies have suggested that for grey seals, intermediate values of these traits are the best  
79 correlate of RHP (Lidgard et al., 2005).

80         The male grey seal agonistic behavioural repertoire consists primarily of threat behaviours such  
81 as the Open-Mouth Threat, body positioning and Roll (Lawson, 1993; Miller & Boness, 1979; Twiss,  
82 1991). Recently a geographically isolated addition to the repertoire was noted: the Body Slap (BS), which  
83 is used during the breeding season in male-male conflict and male-female interactions at some beach  
84 breeding colonies in the UK (Bishop et al., 2014). In the performance of the BS, males lie prone, push  
85 their ventral surface off the ground with their flippers and then let their chest and stomach fall back to the  
86 substrate (Bishop et al., 2014, Video 1). A Body Slap event typically consists of 2 to 3 repetitions of this  
87 general motor pattern in immediate sequence (Bishop et al., 2014, Video 1). The display generates a  
88 distinct slapping noise as contact is made with the ground (Video 1); the arching of the back potentially  
89 serves to display lateral area; and vibrations can be felt through the substrate by observers (AB, SDT pers.  
90 obs.) suggesting that the display likely serves as a multi-modal form of non-vocal communication (Miller,  
91 1991).

92         Investigations into multi-modal signals have shown that when substrate-borne vibrations are  
93 present, they often serve as a mechanism for complementing acoustic or visual displays (Elias et al.,  
94 2005; Hebets & Uetz, 1999; Shipley, Stewart, & Bass, 1992; Stratton & Uetz 1983). For northern  
95 elephant seals, playback experiments demonstrated that males responded more strongly to stimuli with  
96 substrate-borne vibrations and air-borne acoustic components than air-borne acoustic alone (Shipley,  
97 Stewart, & Bass, 1992). Similar findings were demonstrated in insect systems (Elias et al., 2005; Hebets  
98 & Uetz 1999; Stratton & Uetz, 1983). There are also cases where acoustic, visual or chemical modes were  
99 thought to be the primary component of a communication signal, but upon further inspection the  
100 substrate-borne vibration component was found to be the most important (Gibson & Uetz, 2008; Hebets  
101 et al., 2013; Torr, Heritage, & Wilson, 2004). While the BS does have an air-borne acoustic component,  
102 grey seals generally do not have stereotypical vocal displays, with the exception of a 'yodel call' on Sable  
103 Island (Boness & James, 1979). Their other agonistic behaviours have been described as visual displays

104 (Lawson, 1993; Miller & Boness, 1979; Twiss, 1991), but while little work has been done on night-time  
105 activity budgets for breeding pinnipeds (Anderson, 1978; Culloch et al., 2014), elephant seal behaviours  
106 that generate substrate-borne vibrations were found to persist through the night (Shiple, Stewart, & Bass,  
107 1992), lending support to the hypothesis that the visual component of these displays may not be the  
108 primary mode of communication.

109         Therefore, for this study we chose to investigate the substrate-borne vibrations of the BS and ask:  
110 are the characteristics of the substrate-borne vibrations of a BS an indicator of male RHP, and do the  
111 characteristics of individuals' displays vary across environmental conditions? To test this, we compared  
112 both the maximum magnitude of the substrate-borne vibrations a male produced while Body Slapping and  
113 the mean magnitude across all his Body Slap events, with his length, mass and dominance in order to  
114 determine which of the two measures of the substrate vibrations was more reliable in predicting known  
115 correlates to RHP (Anderson & Fedak, 1985; Carlini et al., 2006; Lidgard et al., 2005). As any air-borne  
116 acoustic components of the BS would arguably vary by wind direction, air temperature, and surface  
117 dampness of the substrate (Hill, 2009), we also examined the effects of environmental variability on the  
118 reliability of the substrate-borne vibrations by testing to see if individuals' magnitudes varied with surface  
119 saturation of the substrate due to tidal fluctuations or rain on the beach breeding site.

120

## 121 **METHODS**

### 122 *Field Site*

123         Data were collected on breeding male grey seals at the Donna Nook breeding colony on the North  
124 Lincolnshire coast, eastern England (53.47°N, 0.15°E). The colony produces approximately 1,500 pups  
125 annually and is managed as part of the Lincolnshire Wildlife Trust's wildlife refuge system and also spans  
126 the Ministry of Defence's (MOD) Royal Air Force (RAF) training range (Bishop et al. 2014). Field  
127 observations were conducted across the autumn breeding season in 2013 (27 October – 12 December)  
128 during all daylight hours for an average of 8h 48min daily. The breeding colony was split into two study  
129 sites to cover the range of topography: the PUB (53.476°N, 0.155°E) and RAF (53.474°N, 0.155°E) sites.

130 All observations for this study were conducted at the RAF site, characterized as tidal sand flats. While  
131 some colonies have restricted, or few, access points from the sea to the breeding grounds (e.g. North  
132 Rona; Twiss, 1991), Donna Nook is characterized by open access along the entire beach front. Males in  
133 the study area were identified daily via unique pelage markings or *post-hoc* from high resolution pictures  
134 taken with a Canon EOS 30D or 40D with a 100-400mm lens (Bishop et al., 2014; Twiss, Pomeroy, &  
135 Anderson, 1994) at distances ranging from 10 – 180 m, yielding a total of 105 males identified.

136

### 137 *Seismometer Deployment and Behavioural Data Collection*

138 We deployed 2 Guralp 6TD seismometers (Guralp Systems Ltd) from 30 October to 23  
139 November 2013. The seismometers were both buried at 53.47491 N, 0.15503 E, at a depth of 1 m.  
140 Continuous seismic data were recorded over 24 h encompassing a frequency bandwidth of 0.03Hz-500Hz  
141 (Brisbourne, 2012). Velocity was measured in 3 axes (X, Y and Z); however, for the purpose of this study  
142 we chose to follow the methods of previous work on northern elephant seals (Shiple, Stewart, & Bass,  
143 1992) and focus on the vertical movement axis only. During daylight hours, field observers recorded BS  
144 events, noting ID of male and time of event to the second (h:m:s). An event was defined as a bout of  
145 displaying, usually comprised of 2 repetitions of the motor pattern, but the range varied from 1 - 6  
146 repetitions (Bishop et al., 2014). Events were labeled as being performed on ‘wet’ or ‘dry’ sand; wet sand  
147 being any sand exposed to tidal inundation within the past 12 h or with visibly pooled water. Locations of  
148 events were mapped onto aerial photographs of the study area using a Nikon laser 550 rangefinder (6x21),  
149 with accuracy of 0.5 m up to 100m and  $\pm 1$ m at >100m distance, along with horizon reference points.  
150 Maps were digitized and distance (km) of each BS event to the seismometer was calculated using ArcMap  
151 10 (ESRI, 2011).

152

### 153 *Post-processing Seismic Data*

154 Post deployment, we matched the time of an observed event to the seismic record of vertical  
155 velocity traces using *Scream!* v4.5 (Guralp Systems Ltd). The unfiltered peak to peak amplitudes (nm/s)

156 of the displays were extracted. To minimize potential false positive matches, only displays that were at  
 157 least double in amplitude relative to the background were considered positive matches (Shipley, Stewart,  
 158 & Bass, 1992). As males performed BSs at different distances from the seismometer, in order to compare  
 159 their relative magnitudes, the amplitudes had to be distance corrected. The seismometer measures  
 160 amplitudes as velocity in nm/s ( $v$ ); however the distance correction formula required this measure to first  
 161 be converted into vertical displacement in nm ( $A$ ) using the formula

$$162 \quad A = \left( \frac{[v]}{f * 2\pi} \right) \quad (1)$$

163 where  $v$  is the vertical velocity in nm/s of an event, and  $f$  is the frequency in Hz. Frequency analysis of the  
 164 displays indicated that the bulk of the energy contained in these signals lay within the 20Hz band. To  
 165 ensure that all calculations were carried out using the same formula, we used this frequency to convert  
 166 peak-peak velocity amplitudes to displacement.

167 Magnitude values, which could be compared relative to each other, were then calculated using  
 168 Booth's (2007) distance correction equation generated specifically for seismic activity in the UK (Booth,  
 169 2007)

$$170 \quad \text{Magnitude} = (1 * \text{LOG}_{10}(A)) + (1.11 * \text{LOG}_{10}(D)) + (0.00189 * D) - 2.09 \quad (2)$$

171 where  $A$  was the displacement amplitude of the display in nm and  $D$  was the distance in km an event was  
 172 from the seismometer (see Booth, 2007 for derivation of constants). The maximum magnitude generated  
 173 per male, mean magnitude per male (for males with 4 or more events), and the variation in magnitude  
 174 (standard error around the mean for males with 4 or more events) were calculated and used in further  
 175 analyses.

176

### 177 *Photogrammetric Measures of Morphological Features*

178 We selected to use standard length (cm) and lateral area (proxy for mass) as our morphological  
 179 measures of male RHP. For male grey seals, the links between male mass and RHP suggests that mid-  
 180 sized males have highest mating success, likely due to tradeoffs between mass and maneuverability

181 (Lidgard et al., 2005; Twiss, 1991). Lidgard et al., (2005) also found a positive relationship between  
 182 standard length and length of stay, the latter of which is a known positive correlate of mating success for  
 183 males adopting the primary strategy of ‘residency’ (Twiss, 1991). Finally, Anderson and Fedak (1985)  
 184 found that larger males lost fewer male-male encounters than smaller males by mass, again suggesting  
 185 that size is positively associated with RHP.

186         Seals cannot be handled at Donna Nook, so to determine morphological features associated with  
 187 RHP, we adopted a photogrammetric estimation technique similar to that used by Jacquet (2006) and  
 188 McFadden, Worthy, & Lacher (2006). Standardized photographs at a fixed height of 1m above the ground  
 189 were taken of known males lying prone and perpendicular to the photographer using a Canon EOS 40D  
 190 digital SLR with 100-400mm Canon Lens (Fig. 1a). Distance to the male in the photograph was  
 191 determined using a Nikon Laser Range Finder 550 with +/- 0.5m accuracy. Multiple photographs were  
 192 taken of individual males throughout the season. Each photograph was assessed for quality across the  
 193 following criteria: where the male’s neck was fully extended, the angle of offset from perpendicular was  
 194 minimal, and the tail was visible (Jacquet, 2006; McFadden, Worthy, & Lacher, 2006). Distance  
 195 correction calibration formulae (Eq 3) for each of the four zoom levels used (100, 200, 300, 400mm) were  
 196 generated following the methods of Jacquet (2006). We calculated the formula for the linear relationship  
 197 describing how the ratio of the known length of an object in cm ( $SL$ ) to the width in pixels of that object  
 198 in a photograph ( $P$ ) changes as distance from the camera increases ( $D$ ) (Jacquet, 2006). In the example  
 199 formula (Eq 3), at 400mm zoom, the 0.0015 was derived from the slope of the regression line and 0.0038  
 200 represents the intercept. The  $R^2$  values for the best fit lines for each zoom level were all 0.99. These  
 201 formulae were then used to calculate nose to tail standard lengths ( $SL$ ) for each male from photographs.

$$202 \quad SL = [(0.0015 * D) + 0.0038] * P \quad (3)$$

203         McFadden, Worthy, & Lacher, (2006) found that for weaned monk seals (*Monachus*  
 204 *schauinslandi*) values of lateral area (LA), girth perimeter (GP) and lateral perimeter (LP) calculated from  
 205 photographs were highly correlated with measured values for body mass. Also, for northern elephant seals  
 206 (Haley, Deutsch, & LeBoeuf, 1991) and southern elephant seals (*Mirounga leonina*) (Bell, Hindell, &



207 Burton, 1997) lateral area was a strong predictor of body mass. To estimate mass from our photographs,  
 208 we selected to calculate the LA of the seal using methods similar to McFadden, Worthy & Lacher (2006).  
 209 A digitized outline of the seal, including hind-flippers, was generated in ArcMap 10 and the area of the  
 210 polygon was calculated in pixels<sup>2</sup> (Fig 1b). Using quadratic versions of the distance correction calibration  
 211 formulae used to estimate SL (Eq 3), where  $D$  was again distance to the seal, and  $P$  was the area of the  
 212 seal in pixels squared from the photograph, we then estimated LA in cm<sup>2</sup> (Eq 4).

$$213 \quad LA = [(0.000002 * D^2) + (0.00004 * D) - (0.0013)] * P^2 \quad (4)$$

214 Our final dataset included measurements for 70 of 105 males. No quantification of accuracy  
 215 between actual morphometric and photogrammetric values was possible due to handling restrictions.  
 216 However, the range of generated lengths, 166.1 to 240.3 cm ( $\pm 0.5 - 10.9$  cm SE per male), were well  
 217 within the range of known grey seal sizes (Lidgard et al., 2005; Twiss, 1991; Twiss et al., 2000). To  
 218 account for the remaining uncertainty resulting from off-angle positioning or lack of neck-extension, both  
 219 of which would under-estimate length or area, we only used the photograph resulting in the maximum SL  
 220 and the photograph with the maximum LA for each male in our analysis.

221

### 222 *Dominance and Local Density*

223 In addition to morphometric measures, we calculated a daily dominance score for each male to  
 224 compare to the values generated in the seismic record. Dominance has also been positively linked to  
 225 mating success (Twiss, 1991; Twiss, Anderson, & Monaghan, 1998) and individual dominance scores can  
 226 vary throughout the season in response to turnover of males and females. We selected to use the  
 227 dominance calculation of Elo scores (Neumann et al., 2011) as this method allows for calculation of  
 228 dominance scores sequentially through time. Only males who were present on the colony for at least 2  
 229 days and were involved in a minimum of 10 aggressive interactions were included for this analysis  
 230 (Bishop et al., 2014; Twiss, Anderson, & Monaghan, 1998). For each male, the mean Elo score on the day  
 231 of a BS event (Elo) was calculated using records of his wins, losses and draws up to that date in the

232 season (see: Neumann et al., 2011 for further details of calculation). The mean Elo score across the entire  
233 study period was also calculated per male. Lastly, to account for unequal density of males within the  
234 study site, we mapped male positions on the colony hourly and calculated the average nearest neighbor  
235 distance (DNM) per day for each male using ArcMap 10 (ESRI, 2011).

236

### 237 *Statistical Analysis*

238 Our objective was to determine if maximum magnitude or an average magnitude was the most  
239 reliable indicator of male RHP. To do this, we used generalised linear models comparing the maximum  
240 magnitude a male generated ( $N = 26$  males) against his maximum standard length (MSL), maximum  
241 lateral area (MLA), Elo on the day of maximum magnitude, mean distance to nearest neighbor (DNM) on  
242 the day of maximum magnitude and the substrate type on which the maximum was performed (1 = wet  
243 sand; 0 = dry sand). Because lateral area as a proxy for mass would be expected to decrease through time  
244 due to fasting (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss, 1991) there was a potential  
245 temporal disconnect between the date of maximum seismic magnitude and the date of the  
246 photogrammetric MLA. Twiss (1991) found individual variation in mass loss was not correlated with  
247 dominance, age, arrival weight or other metrics; therefore, to account for mass loss over time we included  
248 a variable of the difference between the date of the maximum magnitude generated by a male and the date  
249 when the photograph of his MLA was taken (DayDIFF), which ranged from 0 – 23 d. MSL does not  
250 change throughout the course of a breeding season so no temporal measure was included for this variable.  
251 Similar models were run with the response variable set as either the mean magnitude per male ( $N = 22$   
252 males) or standard error of the mean magnitude per male ( $N = 22$  males). In the models examining mean  
253 magnitude and standard error, the predictor variables of mean dominance and mean nearest neighbor  
254 distance were calculated across the entirety of each male's stay, and the mean substrate type across all  
255 displays per male was used instead of a single value. To account for temporal disconnects in these  
256 models, the number of days over which the mean was calculated (DayMEAN) and the difference in days  
257 between the first BS event and the date of MLA were included in the models (DayDIFF). Models for all

258 analyses were run in R 2.13.2 (R Development Core Team, 2011). Final model selection followed AIC  
259 minimization criteria, where all models within  $\Delta 6$  AIC are retained, and any models within this set that  
260 are more complex versions of their nested counterparts, but with higher  $\Delta$ AIC values, are excluded  
261 (Richards, 2008).

262 While the last two models account for mean substrate type, this was across males and not within  
263 individual IDs. To test if surface substrate dampness enhances or degrades the magnitude of the vibrations  
264 of an individual's display, for males that we observed displaying on both wet and dry sand we also tested  
265 for differences in mean and maximum magnitude of a display by substrate. Due to the small sample size  
266 ( $N = 11$  males), we used small-sample randomization tests designed for two-repeated measures on small  
267 group or single-case blocks (Todman & Dugard, 2001).

268

## 269 **RESULTS**

### 270 *Seismic signature of the Body Slap*

271 The Body Slap generated a stereotyped seismic trace with raw amplitudes ranging from 10 752  
272 nm/s to 475 136 nm/s, and after distance corrections, magnitudes ranged from  $-1.62$  to  $-0.14$  (Figure 2a).  
273 Frequency was broadband and ranged from 10-80Hz. Other male behavioural events were observed *ad lib*  
274 and matched to the seismic record for comparison, including male locomotion (Figure 2b). BS displays  
275 were measurable up to 126.3 m from the source; of the observed BS events in the field, 94.3% were  
276 positively matched in the seismic record up to 70m distance, but proportion matched dropped to 71.7%  
277 from 80-100m and to 37% on average beyond 100m (Figure 3). We recorded events for 39 individual  
278 males (within-male sample sizes ranging from 1-255 events, median for males with  $>4$  events = 22.5) for  
279 a total of 470 observed events comprised of 990 individual slaps matched in the seismic trace. Similar to  
280 findings of Bishop et al. (2014), 9.45% of events consisted of a single slap, 61.5% consisted of 2 slaps,  
281 and 28.9% consisted of  $>3$  repetitions. Inter-repetition intervals were typically 1s apart and separately  
282 distinguishable (Figure 2a).

283

284 ***BS contains information on male size***

285 MSL and DayDIFF were retained in the best model ( $\Delta AIC = 0$ ) for predicting maximum  
286 magnitude; however, the model with only MSL had a  $\Delta AIC$  of 0.21 suggesting this variable on its own is  
287 a strong predictor of maximum magnitude (Table 1). In both models, MSL shared a significantly positive  
288 relationship with maximum magnitude a male produced (Figure 4a; Table 1). The best model predicting  
289 mean magnitude retained MSL and DNM as predictive parameters. MLA and Elo were each retained in 2  
290 models but both with greater  $\Delta AIC$  values and small effect sizes (Table 1). The relationship between  
291 MSL and mean magnitude was weaker than that seen between MSL and maximum magnitude (Figure 4b;  
292 Table 1). DNM shared a statistically significant negative relationship with mean magnitude, suggesting  
293 mean magnitude decreases as density of competitors decreases (Figure 4c; Table 1). A total of 7 models  
294 were retained by the selection criteria for predicting mean magnitude, each with varying parameters  
295 (Table 1). DNM was retained in the top 4 models, and was retained in more models than any other  
296 parameter (Table 1). We fit a further 3 models to test if the relationship between mean magnitude and  
297 DNM was the result of larger or more dominant males occupying areas of greater conspecific density  
298 (Table 2), but found no evidence of MSL, MLA or Elo correlating with DNM (Table 2). Finally,  
299 variability in magnitude per male was best predicted by only the null model, suggesting that none of the  
300 variables were good predictors of variability in magnitude.

301

302 ***BS displays on wet and dry sand***

303 The maximum magnitude of displays for males who had events recorded on both wet and dry  
304 substrates was not different across substrate type (2-tailed:  $t = 0.069$ , 1000 permutations,  $P = 0.432$ ).  
305 Similarly, no difference was found comparing the mean magnitude of displays for males who had events  
306 recorded on both wet and dry substrates (2-tailed:  $t = 0.008$ , 1000 permutations,  $P = 0.919$ ).

307

308 **DISCUSSION**

309           Our findings confirm that male grey seals generate substrate-borne vibrations associated with a  
310 specific, stereotyped display. Furthermore, while the frequency of the percussive display was broadband,  
311 the maximum generated magnitudes of this display were reliable indicators of male size. Previously, the  
312 rates of percussive displays of the BS were linked to success in agonistic interactions (Bishop et al., 2014)  
313 and this study suggests that the magnitude of the BS contains information regarding RHP that could be  
314 used by opponents in assessment. The results of this study also indicate that, while the breeding colonies  
315 at which the BS has been observed are all open-access beach sites with variable surface water pooling due  
316 to tidal and rain fluctuations, individuals' maximum and mean magnitudes were not significantly different  
317 across wet or dry surface sand conditions.

318           In a polygynous mating system, selection should favour signals of male RHP to maximize  
319 information transfer and minimize the costs of agonistic interactions (Arnott & Elwood, 2009; Smith,  
320 1979). Since percussive, vibratory signal energy depends on both mass and available muscular power  
321 (Markl, 1983), one would expect maximum magnitudes to highly correlate with size (*e.g.* mass) and  
322 strength (*e.g.* height a male can achieve in 'push-up'). Our results support this relationship in that we  
323 found that of our predictor variables, standard length significantly correlated with the magnitude of the  
324 substrate vibrations in the best model. Interestingly, our proxy for mass (MLA) and dominance (Elo) were  
325 retained in models for mean magnitude, but these models did not perform as well and the effects were  
326 expressed by very low coefficients. In male grey seal agonistic encounters, wrestling is the primary form  
327 of physical contact (Boness & James, 1979) and previous studies investigating mating success in male  
328 grey seals have suggested length and mass are selected for in two separate processes: length provides  
329 maneuverability for fighting agility, while mass provides ability to fast for longer periods and maximize  
330 mating success through length of stay (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss, 1991). In  
331 this system, it seems likely stabilizing selection has favoured males with intermediate masses and males  
332 of longer standard lengths to maximize the tradeoffs between maneuverability and prolonged residency  
333 (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss 1991). In the closely related northern elephant  
334 seals, length was also positively correlated with dominance (Carlini et al., 2006). Other examples of mass

335 not being the best predictor of RHP have been found in species that rely on maneuverability, and often  
336 these cases are found in aquatic habitats. Standard length in male sword-tails (*Xiphophorus cortezi*) was  
337 the strongest predictor of RHP (Moretz, 2003). We found that length strongly correlated with maximum  
338 magnitude, which if longer males are able to achieve greater heights during the display, could provide  
339 information on male maneuverability. However, there was still some unexplained variation which may  
340 provide information on other characteristics of the performer. For example, inter-individual variation in  
341 musculature, possibly associated with length or mass, could subsequently produce greater magnitudes.  
342 Alternatively, previous work has found winners on average performed the BS at greater rates than losers  
343 (Bishop et al., 2014) and rate of percussive displays has been shown to signal stamina in other animal  
344 systems (Briffa, Elwood, & Russ, 2003); therefore it might be interesting in future work to consider the  
345 potential tradeoffs between the physical constraints of generating substrate vibrations (maneuverability  
346 and musculature) and the physiological constraints (available energy for repeat displays) to determine  
347 what other potential information might be available in the Body Slap display.

348         Compared to other vibratory signals, communication via percussive behaviours which generate  
349 broadband substrate vibrations has been considered highly adaptive to conditions requiring  
350 communication over long distances, sensory-limited environments (*e.g.* caves, subterranean), or for  
351 home-ranges that span a variety of environmental conditions (Aicher & Tautz 1990; Elias, Mason, &  
352 Hoy, 2004; Hebets et al., 2008; Hill, 2009; O'Connell-Rodwell, Hart, & Amason, 2001; Randall &  
353 Matocq, 1997). In regards to vibrations in sand, early research has demonstrated that even soft, desert  
354 sand substrate can carry vibrations such as those used by the predatory desert scorpion (*Paruroctonus*  
355 *mesaensis*) to orient to and determine the distance to prey (Brownell, 1977; Brownell & Farley, 1979).  
356 Aicher & Tautz (1990) tested for difference in signals across dry and wet beach sand, and found that dry  
357 sand appeared to reduce the velocity of vibrations simulated from fiddler crab (*Uca pugilator*) percussive  
358 behaviours, but this was for signals in the frequency range of 340-370Hz. In the present study, we found  
359 that individuals' maximum and mean magnitudes did not vary across surface saturation of the substrate.  
360 This might be explained by the environment at the site for this study, Donna Nook, and at similar sites

361 where the BS behaviour has been observed. The site is characterized by expansive, uniform tidal flats of  
362 packed sand that experience a high variability in the levels of surface water; however, the underlying  
363 substrate likely remains fairly well saturated throughout the tidal cycle. Seals were not observed  
364 performing in the soft, dune sand. Therefore, while the variation in surface substrate dampness and visible  
365 pooling of water would arguably alter the airborne acoustic characteristics, there is no evidence that  
366 surface dampness has an effect on the magnitude of the substrate vibrations across the substrates occupied  
367 by seals. Another potential component of the BS display which might act as a signal, the visual  
368 component, would also be limited by the visual range of grey seals on land, which is particularly  
369 attenuated at low-light conditions (Schusterman, 1981), and the grey seals' low line of sight being  
370 obscured by other seals. Furthermore, there was evidence of BS traces in the seismic record during the  
371 nighttime; although, observational confirmation of these was not possible. If the visual component is used  
372 at all, it is likely to be most effective at very short range and only during daylight (Culloch et al. 2014).  
373 These findings suggest the possible adaptive significance of using the substrate-borne vibration  
374 component of the percussive BS display as a way to transmit information in a variable environment.

375         According to operational sex-ratio theory, the intensity and/or frequency of aggressive behaviours  
376 are predicted to increase relative to number of competitors or male density (deJong et al., 2013; Weir,  
377 Grant, & Hutchings, 2011) and this has been demonstrated in numerous studies, mainly in controlled  
378 conditions (Quinn, Adkinson, & Ward, 1996; Smith, 2007). As the grey seal breeding season progresses,  
379 sex-ratios shift from male biased to female biased and local densities of both sexes increase (Boness &  
380 James, 1979; Twiss, Anderson, & Monaghan, 1998). In our study, we found mean magnitude of the BS  
381 display increased with relative male density, but maximum magnitude did not. This could suggest that  
382 longer males occupy areas of greater densities, but we found no evidence of male length, lateral area or  
383 dominance correlating to mean neighbour distances. Alternatively, local competitor density might  
384 influence the amount of effort put into a display. Males that can maintain position in high density female  
385 areas have been shown to have greater mating success (Twiss, Pomeroy, & Anderson, 1994); therefore,  
386 males in patches of higher female, and subsequently higher male, densities might consistently display

387 closer to their maximum because the costs of losing access to females outweighs the energetic costs of  
388 displaying at their physical limits. This corresponds with previous work that suggests, for male grey seals,  
389 not losing a position on the breeding grounds was more important than physically besting an opponent  
390 (Anderson & Fedak, 1985; Twiss, 1991). Similar mechanisms for maximizing mating opportunities while  
391 minimizing costs can be seen in the Natterjack Toad (*B. calamita*) mating system, where males escalate  
392 the intensity of their signalling as female densities increase by switching from stationary calling to active  
393 movement and clasping (Arak, 1983). Agonistic displays by male mosquitofish (*Gambusia affinis*) to  
394 other males increased as competitor density increased, and were greatest when male and female density  
395 were high (Smith, 2007). This study provides some evidence that characteristics of the substrate-borne  
396 vibrations of the BS might be tailored to local competitor densities, but further examination is needed to  
397 determine how flexible males are in their displays in regards to matching local conditions.

398         Male northern elephant seals vocalize during contests and multiple components of this signal  
399 contain information regarding male RHP (Insley & Holt, 2011; Sandegren, 1976; Sanvito, Galimberti, &  
400 Miller, 2007a; Sanvito, Galimberti, & Miller, 2007b; Shipley, Hines, & Buchwald, 1981; Thomas et al.,  
401 1988). Similarly, in intra-sexual interactions in sexually dimorphic species, vocalization components such  
402 as formant frequencies have been found to correlate with male size (Reby & McComb, 2003; Vannoni &  
403 McElligott, 2008). Determining if components contain information associated with RHP is the first step  
404 to understanding the potential usage of a behavioural display by a receiver. Our results have demonstrated  
405 a positive relationship between the magnitude of the BS's substrate-borne vibrations and proxies for RHP,  
406 but how the receiver responds to the information in the BS still requires further examination and is likely  
407 context dependent. For example, a recent playback study indicated that while calls of male elephant seals  
408 contain information regarding RHP, recipients did not appear to respond to information regarding size  
409 from the signal (Casey et al., 2012; Casey et al., 2013). Instead, researchers found that males recognize  
410 the individual pattern associated with a dominant or subordinate male (Casey et al., 2012; Casey et al.,  
411 2013). As the proportion of males returning between years in the elephant seal system is relatively high  
412 (~50%, LeBoeuf, 1974), there might be selection for 'remembering' individual signals and the dominance



413 rank of the sender within and between years. While grey seals are closely related to elephant seals, in the  
414 grey seal system, male return is lower in comparison (31.4% Donna Nook, Bishop n.d.) and the BS is  
415 highly stereotyped, suggesting that it is unlikely a similar recognition mechanism is in effect. Still, further  
416 work utilizing playback manipulations (*e.g.* observations of receivers' response when presented with a  
417 range of substrate-borne vibration magnitudes) could be done to investigate the honesty of the  
418 information in the BS display and if active or passive receivers are deriving the information regarding size  
419 from the BS substrate vibrations and basing decisions on that information.

420         In summary, our results demonstrate that the substrate-borne vibrations of a male-male agonistic  
421 behaviour in a classically polygynous mammal contain information of the performer's RHP, and that the  
422 information on size is reliable in a variable environment. Given the BS is a behaviour that has only been  
423 noted within the past 30 years and is at present geographically isolated (Bishop et al., 2014), it is  
424 interesting to consider the evolutionary history of this species. Grey seals in the UK have experienced  
425 increased terrestrialization of breeding colonies since the last glaciation. At present, grey seals breed on a  
426 variety of substrates; however, the BS display has only been observed at colonies with flat sandy beaches  
427 (Bishop et al., 2014). Other colonies across their range exhibit similar substrate types and conditions but  
428 observers have not reported usage of this behaviour. Furthermore, the usage of this behaviour appears to  
429 have evolved in a reasonably short period of time. An exciting aspect of these findings therefore is that  
430 while it is likely the BS originated as an extension of the locomotor pattern (Bishop et al., 2014), it is  
431 possible the substrate and local environmental conditions at Donna Nook and nearby colonies promoted  
432 the use of this behaviour.

433

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- 619

620 **FIGURE LEGENDS**

621

622 **Figure 1.** Example of photogrammetric positioning and digitizing of image to calculate: (a) nose to tail  
623 standard length (SL; 1 point unit = 1 pixel) and (b) lateral area (LA) for an individual male.

624

625 **Figure 2:** Oscillogram (top) and spectrogram (bottom) recorded at 0.03-500Hz. (a) 3 BS events (3  
626 repetitions at 7:02:31; 2 repetitions at 7:02:50; 2 repetitions at 7:03:09). Distance from source = 50 m.

627 All three events presented between 10-80Hz with highest energy at 20-40Hz.; (b) Male locomotion at  
628 7:49:30. Distance from source = 40 m.

629

630 **Figure 3:** Proportion of BS events positively matched in the seismic record to the number observed in the  
631 field across distance (10m bins). Labels represent number of events observed in field. Detectability  
632 dropped off after 80m from source and maximum distance detected was 126.3 m.

633

634 **Figure 4:** Results of best models. Correlations for maximum (a) and mean magnitude (b) indicated a  
635 positive relationship with maximum standard length. Mean magnitude also shared a negative relationship  
636 with mean nearest neighbor distance (c). See Table 1 for coefficient estimates.



637 **Table 1:** Model outputs of signal information analyses. Displayed models include all retained models within 6  $\Delta$ AIC, ignoring more complicated  
 638 versions of nested models that had higher  $\Delta$ AIC (Richards 2008). Values for predictor variables represent coefficient estimates; significant  
 639 variables are in bold.  
 640

Seismic Component	AICc	$\Delta$ AICc	N	INT	MSL	MLA	Elo	DNM	SUB	DayDIFF	DayMEAN
<i>*Maximum Magnitude</i>											
Model 1	0.8	0	26	<b>-3.32</b>	<b>0.013</b>					-0.009	
Model 2	1.0	0.21	26	<b>-3.43</b>	<b>0.013</b>						
<i>†Mean Magnitude</i>											
Model 1	-21.11	0	22	<b>-1.50</b>	<b>0.005</b>						<b>-0.020</b>
Model 2	-19.84	1.27	22	<b>-1.34</b>			0.0007				<b>-0.018</b>
Model 3	-19.34	1.77	22	<b>-0.85</b>		4E-05					<b>-0.019</b>
Model 4	-19.15	1.97	22	<b>-0.50</b>							<b>-0.023</b>
Model 5	-17.72	3.39	22	<b>-1.97</b>			<b>0.0010</b>				
Model 6	-17.30	3.81	22	<b>-2.03</b>	<b>0.005</b>						
Model 7	-17.21	3.90	22	<b>-1.33</b>		<b>5E-05</b>					
<i>†SE Magnitude</i>											
Model 1	-125.0	0	22	<b>0.032</b>							

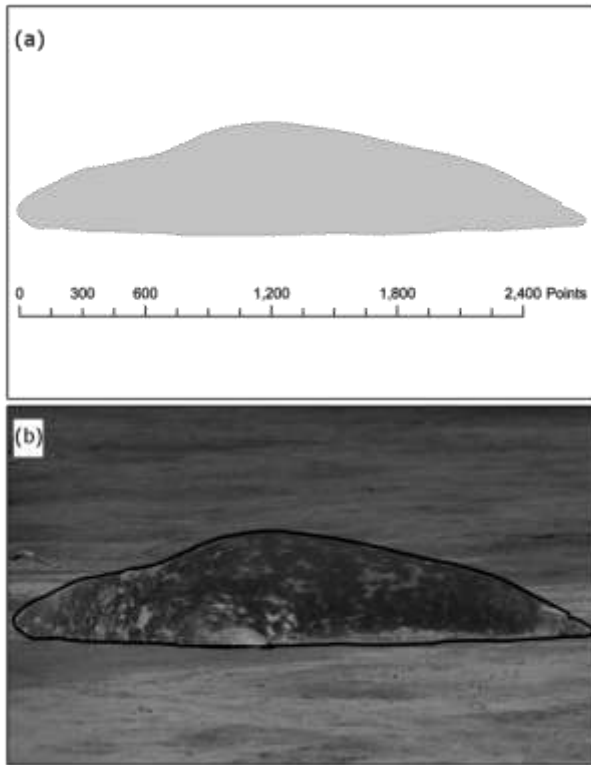
641 \* MSL = maximum standard length (cm); MLA = maximum lateral area (cm<sup>2</sup>); Elo=mean dominance score up to and including the day of maximum magnitude;  
 642 DNM = mean distance to nearest neighbor on day of maximum magnitude; SUB = substrate (1=wet; 0=dry); DayDIFF = difference in dates between maximum  
 643 magnitude and maximum LA measure.

644 † MSL, MLA (same as above). Elo= mean dominance score for whole season; DNM = mean distance to nearest neighbor for whole season, SUB = mean  
 645 substrate across all BS events; DayDIFF = difference in dates between first BS event and maximum LA measure; DayMEAN = number of days mean seismic  
 646 magnitude was calculated across.

647 **Table 2:** Generalised linear model (GLM) testing for relationship between: 1) MSL and DNM, 2) MLA  
 648 and DNM, and 3) Elo and DNM. The Null models were the best for all three response variables (bold;  
 649 Richards 2008).  
 650

Model ( $N = 22$ )	AICc	$\Delta$ AICc
1) MSL ~ DNM	184.0	2.24
<b>MSL ~ 1</b>	<b>181.7</b>	<b>0</b>
2) MLA ~ DNM	380.8	0.78
<b>MLS ~ 1</b>	<b>380.0</b>	<b>0</b>
3) Elo ~ DNM	257.4	0.81
<b>Elo ~ 1</b>	<b>256.6</b>	<b>0</b>

651 \* *MSL* = maximum standard length (cm); *MLA* = maximum lateral area (cm<sup>2</sup>); *Elo* = mean dominance score for  
 652 whole season; *DNM* = mean distance to nearest neighbor for whole season.  
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655 Figure 1

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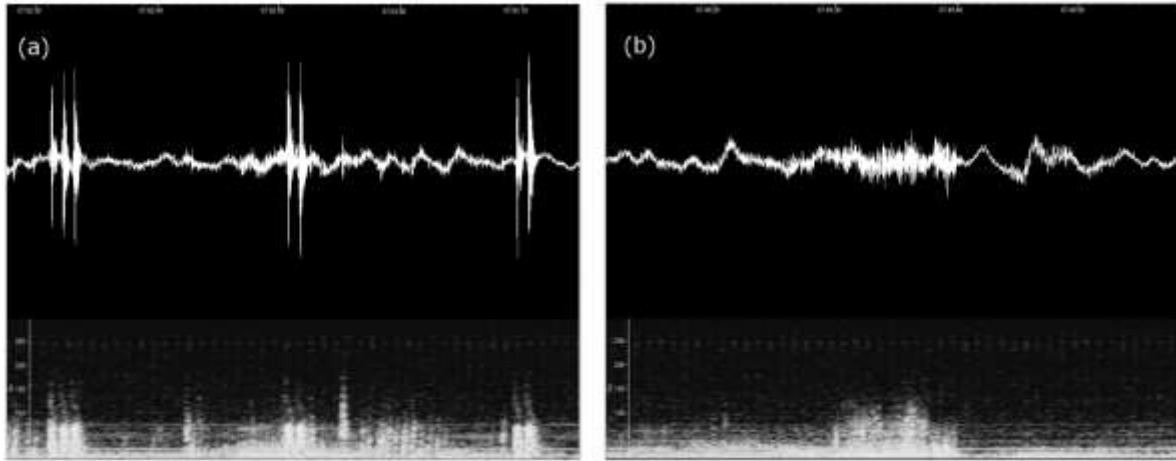
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669 Figure 2

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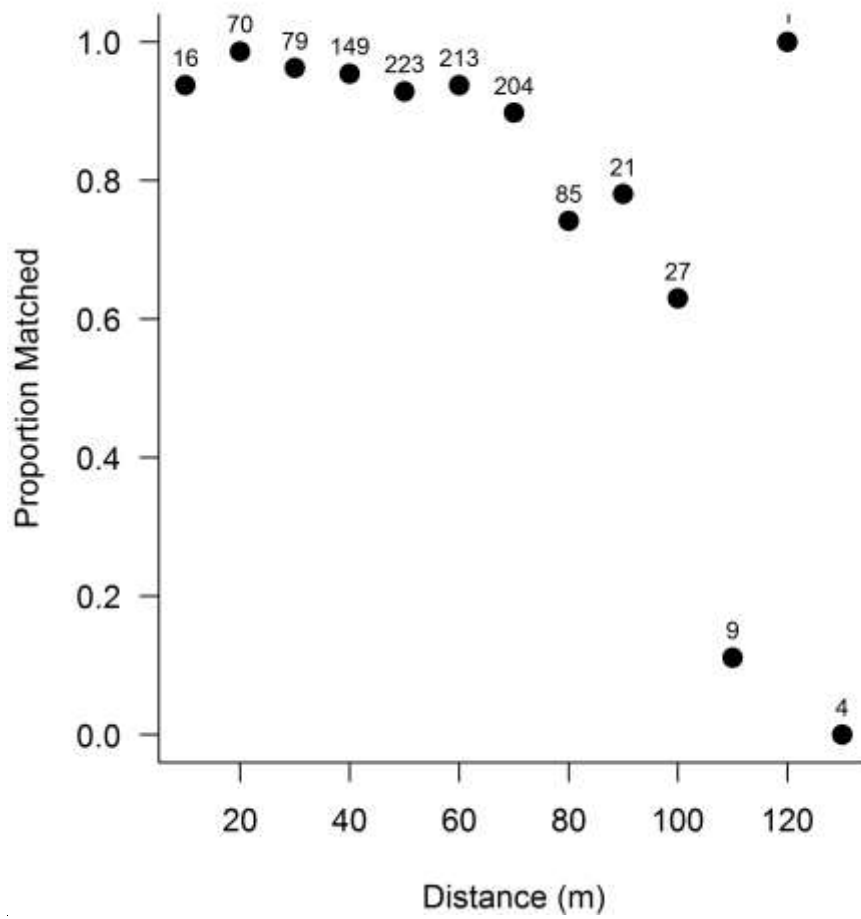
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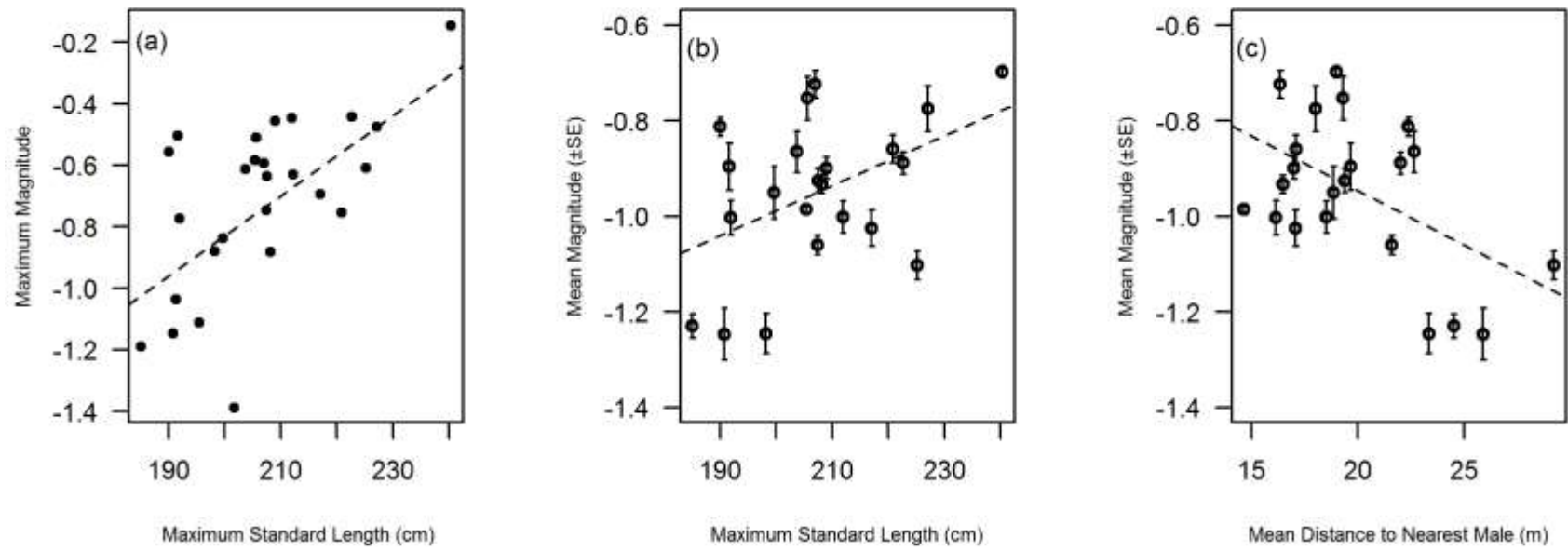
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680 Figure 3



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682 Figure 4

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