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

Running Title: Ground vibrations contain information on male seal size

ABSTRACT

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

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

INTRODUCTION

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

Substrate vibrations generated by animal signalling are extensively documented across numerous animal taxa; conservative estimates suggest that in the order Insecta alone, a total of 195,000 species use this mode of communication (Hill, 2009). In comparison, the number of mammalian species known to use this form of communication is estimated at 32 species across 11 families (Hill, 2009). These signals can be generated via direct contact: stridulation (Gordon & Uetz, 2011), tremulation (Caldwell et al., 2010) or percussive drumming (Elias et al., 2008; Randall & Matocq 1997); or through vocalizations strong enough to excite substrate-borne vibrations (Hill, 2009; O’Connell-Rodwell, 2007; Shipley, Stewart, & Bass, 1992). Previous work has identified that the substrate-vibration components of signals can be used in various forms of communication: stridulations and tremulations can advertise quality during conflict and mate choice, while foot drumming and substrate coupled vocalizations have been linked with conspecific avoidance and group cohesion (Elias et al., 2008; Hill, 2009). In this study, we investigate a specific behaviour performed by male grey seals (*Halichoerus grypus*) during the breeding season and investigate if the substrate vibrations generated convey reliable information regarding male RHP that could be used in contest assessment by receivers.

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

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

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

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

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

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

METHODS

Field Site

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

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

Seismometer Deployment and Behavioural Data Collection

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

Post-processing Seismic Data

Post deployment, we matched the time of an observed event to the seismic record of vertical velocity traces using *Scream!* v4.5 (Guralp Systems Ltd). The unfiltered peak to peak amplitudes (nm/s) of the displays were extracted. To minimize potential false positive matches, only displays that were at least double in amplitude relative to the background were considered positive matches (Shipley, Stewart, & Bass, 1992). As males performed BSs at different distances from the seismometer, in order to compare their relative magnitudes, the amplitudes had to be distance corrected. The seismometer measures amplitudes as velocity in nm/s (*v*); however the distance correction formula required this measure to first be converted into vertical displacement in nm (*A*) using the formula

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

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

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

$$Magnitude = \left(1 * LOG10(A)\right) + \left(1.11 * LOG10(D)\right) + (0.00189 * D) - 2.09 \qquad \textbf{(2)}$$

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

Photogrammetric Measures of Morphological Features

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

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

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

$$SL = [(0.0015 * D) + 0.0038] * P \tag{3}$$

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

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

$$LA = \left[(0.000002 * D^2) + (0.00004 * D) - (0.0013)\right] * P^2 \qquad \textbf{(4)}$$

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

Dominance and Local Density

In addition to morphometric measures, we calculated a daily dominance score for each male to compare to the values generated in the seismic record. Dominance has also been positively linked to mating success (Twiss, 1991; Twiss, Anderson, & Monaghan, 1998) and individual dominance scores can vary throughout the season in response to turnover of males and females. We selected to use the dominance calculation of Elo scores (Neumann et al., 2011) as this method allows for calculation of dominance scores sequentially through time. Only males who were present on the colony for at least 2 days and were involved in a minimum of 10 aggressive interactions were included for this analysis (Bishop et al., 2014; Twiss, Anderson, & Monaghan, 1998). For each male, the mean Elo score on the day of a BS event (Elo) was calculated using records of his wins, losses and draws up to that date in the season (see: Neumann et al., 2011 for further details of calculation). The mean Elo score across the entire study period was also calculated per male. Lastly, to account for unequal density of males within the study site, we mapped male positions on the colony hourly and calculated the average nearest neighbor distance (DNM) per day for each male using ArcMap 10 (ESRI, 2011).

Statistical Analysis

Our objective was to determine if maximum magnitude or an average magnitude was the most reliable indicator of male RHP. To do this, we used generalised linear models comparing the maximum magnitude a male generated (N = 26 males) against his maximum standard length (MSL), maximum lateral area (MLA), Elo on the day of maximum magnitude, mean distance to nearest neighbor (DNM) on the day of maximum magnitude and the substrate type on which the maximum was performed (1 = wet sand; 0 = dry sand). Because lateral area as a proxy for mass would be expected to decrease through time due to fasting (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss, 1991) there was a potential temporal disconnect between the date of maximum seismic magnitude and the date of the photogrammetric MLA. Twiss (1991) found individual variation in mass loss was not correlated with dominance, age, arrival weight or other metrics; therefore, to account for mass loss over time we included a variable of the difference between the date of the maximum magnitude generated by a male and the date when the photograph of his MLA was taken (DayDIFF), which ranged from 0 – 23 d. MSL does not change throughout the course of a breeding season so no temporal measure was included for this variable. Similar models were run with the response variable set as either the mean magnitude per male (N = 22 males) or standard error of the mean magnitude per male (N = 22 males). In the models examining mean magnitude and standard error, the predictor variables of mean dominance and mean nearest neighbor distance were calculated across the entirely of each male's stay, and the mean substrate type across all displays per male was used instead of a single value. To account for temporal disconnects in these models, the number of days over which the mean was calculated (DayMEAN) and the difference in days between the first BS event and the date of MLA were included in the models (DayDIFF). Models for all analyses were run in R 2.13.2 (R Development Core Team, 2011). Final model selection followed AIC minimization criteria, where all models within Δ6 AIC are retained, and any models within this set that are more complex versions of their nested counterparts, but with higher ΔAIC values, are excluded (Richards, 2008).

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

RESULTS

Seismic signature of the Body Slap

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

BS contains information on male size

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

BS displays on wet and dry sand

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

DISCUSSION

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

In a polygynous mating system, selection should favour signals of male RHP to maximize information transfer and minimize the costs of agonistic interactions (Arnott & Elwood, 2009; Smith, 1979). Since percussive, vibratory signal energy depends on both mass and available muscular power (Markl, 1983), one would expect maximum magnitudes to highly correlate with size (*e.g.* mass) and strength (*e.g.* height a male can achieve in 'push-up'). Our results support this relationship in that we found that of our predictor variables, standard length significantly correlated with the magnitude of the substrate vibrations in the best model. Interestingly, our proxy for mass (MLA) and dominance (Elo) were retained in models for mean magnitude, but these models did not perform as well and the effects were expressed by very low coefficients. In male grey seal agonistic encounters, wrestling is the primary form of physical contact (Boness & James, 1979) and previous studies investigating mating success in male grey seals have suggested length and mass are selected for in two separate processes: length provides maneuverability for fighting agility, while mass provides ability to fast for longer periods and maximize mating success through length of stay (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss, 1991). In this system, it seems likely stabilizing selection has favoured males with intermediate masses and males of longer standard lengths to maximize the tradeoffs between maneuverability and prolonged residency (Anderson & Fedak, 1985; Lidgard et al., 2005; Twiss 1991). In the closely related northern elephant seals, length was also positively correlated with dominance (Carlini et al., 2006). Other examples of mass not being the best predictor of RHP have been found in species that rely on maneuverability, and often these cases are found in aquatic habitats. Standard length in male sword-tails (*Xiphophorus cortezi*) was the strongest predictor of RHP (Moretz, 2003). We found that length strongly correlated with maximum magnitude, which if longer males are able to achieve greater heights during the display, could provide information on male maneuverability. However, there was still some unexplained variation which may provide information on other characteristics of the performer. For example, inter-individual variation in musculature, possibly associated with length or mass, could subsequently produce greater magnitudes. Alternatively, previous work has found winners on average performed the BS at greater rates than losers (Bishop et al., 2014) and rate of percussive displays has been shown to signal stamina in other animal systems (Briffa, Elwood, & Russ, 2003); therefore it might be interesting in future work to consider the potential tradeoffs between the physical constraints of generating substrate vibrations (maneuverability and musculature) and the physiological constraints (available energy for repeat displays) to determine what other potential information might be available in the Body Slap display.

Compared to other vibratory signals, communication via percussive behaviours which generate broadband substrate vibrations has been considered highly adaptive to conditions requiring communication over long distances, sensory-limited environments (*e.g.* caves, subterranean), or for home-ranges that span a variety of environmental conditions (Aicher & Tautz 1990; Elias, Mason, & Hoy, 2004; Hebets et al., 2008; Hill, 2009; O’Connell-Rodwell, Hart, & Amason, 2001; Randall & Matocq, 1997). In regards to vibrations in sand, early research has demonstrated that even soft, desert sand substrate can carry vibrations such as those used by the predatory desert scorpion (*Paruroctonus mesaensis*) to orient to and determine the distance to prey (Brownell, 1977; Brownell & Farley, 1979). Aicher & Tautz (1990) tested for difference in signals across dry and wet beach sand, and found that dry sand appeared to reduce the velocity of vibrations simulated from fiddler crab (*Uca pugilator*) percussive behaviours, but this was for signals in the frequency range of 340-370Hz. In the present study, we found that individuals’ maximum and mean magnitudes did not vary across surface saturation of the substrate. This might be explained by the environment at the site for this study, Donna Nook, and at similar sites where the BS behaviour has been observed. The site is characterized by expansive, uniform tidal flats of packed sand that experience a high variability in the levels of surface water; however, the underlying substrate likely remains fairly well saturated throughout the tidal cycle. Seals were not observed performing in the soft, dune sand. Therefore, while the variation in surface substrate dampness and visible pooling of water would arguably alter the airborne acoustic characteristics, there is no evidence that surface dampness has an effect on the magnitude of the substrate vibrations across the substrates occupied by seals. Another potential component of the BS display which might act as a signal, the visual component, would also be limited by the visual range of grey seals on land, which is particularly attenuated at low-light conditions (Schusterman, 1981), and the grey seals' low line of sight being obscured by other seals. Furthermore, there was evidence of BS traces in the seismic record during the nighttime; although, observational confirmation of these was not possible. If the visual component is used at all, it is likely to be most effective at very short range and only during daylight (Culloch et al. 2014). These findings suggest the possible adaptive significance of using the substrate-borne vibration component of the percussive BS display as a way to transmit information in a variable environment.

According to operational sex-ratio theory, the intensity and/or frequency of aggressive behaviours are predicted to increase relative to number of competitors or male density (deJong et al., 2013; Weir, Grant, & Hutchings, 2011) and this has been demonstrated in numerous studies, mainly in controlled conditions (Quinn, Adkinson, & Ward, 1996; Smith, 2007). As the grey seal breeding season progresses, sex-ratios shift from male biased to female biased and local densities of both sexes increase (Boness & James, 1979; Twiss, Anderson, & Monaghan, 1998). In our study, we found mean magnitude of the BS display increased with relative male density, but maximum magnitude did not. This could suggest that longer males occupy areas of greater densities, but we found no evidence of male length, lateral area or dominance correlating to mean neighbour distances. Alternatively, local competitor density might influence the amount of effort put into a display. Males that can maintain position in high density female areas have been shown to have greater mating success (Twiss, Pomeroy, & Anderson, 1994); therefore, males in patches of higher female, and subsequently higher male, densities might consistently display closer to their maximum because the costs of losing access to females outweighs the energetic costs of displaying at their physical limits. This corresponds with previous work that suggests, for male grey seals, not losing a position on the breeding grounds was more important that physically besting an opponent (Anderson & Fedak, 1985; Twiss, 1991). Similar mechanisms for maximizing mating opportunities while minimizing costs can be seen in the Natterjack Toad (*B. calamita*) mating system, where males escalate the intensity of their signalling as female densities increase by switching from stationary calling to active movement and clasping (Arak, 1983). Agonistic displays by male mosquitofish (*Gambusia affinis*) to other males increased as competitor density increased, and were greatest when male and female density were high (Smith, 2007). This study provides some evidence that characteristics of the substrate-borne vibrations of the BS might be tailored to local competitor densities, but further examination is needed to determine how flexible males are in their displays in regards to matching local conditions.

Male northern elephant seals vocalize during contests and multiple components of this signal contain information regarding male RHP (Insley & Holt, 2011; Sandegren, 1976; Sanvito, Galimberti, & Miller, 2007a; Sanvito, Galimberti, & Miller, 2007b; Shipley, Hines, & Buchwald, 1981; Thomas et al., 1988). Similarly, in intra-sexual interactions in sexually dimorphic species, vocalization components such as formant frequencies have been found to correlate with male size (Reby & McComb, 2003; Vannoni & McElligott, 2008). Determining if components contain information associated with RHP is the first step to understanding the potential usage of a behavioural display by a receiver. Our results have demonstrated a positive relationship between the magnitude of the BS's substrate-borne vibrations and proxies for RHP, but how the receiver responds to the information in the BS still requires further examination and is likely context dependent. For example, a recent playback study indicated that while calls of male elephant seals contain information regarding RHP, recipients did not appear to respond to information regarding size from the signal (Casey et al., 2012; Casey et al., 2013). Instead, researchers found that males recognize the individual pattern associated with a dominant or subordinate male (Casey et al., 2012; Casey et al., 2013). As the proportion of males returning between years in the elephant seal system is relatively high (~50%, LeBoeuf, 1974), there might be selection for 'remembering' individual signals and the dominance rank of the sender within and between years. While grey seals are closely related to elephant seals, in the grey seal system, male return is lower in comparison (31.4% Donna Nook, Bishop n.d.) and the BS is highly stereotyped, suggesting that it is unlikely a similar recognition mechanism is in effect. Still, further work utilizing playback manipulations (*e.g.* observations of receivers' response when presented with a range of substrate-borne vibration magnitudes) could be done to investigate the honesty of the information in the BS display and if active or passive receivers are deriving the information regarding size from the BS substrate vibrations and basing decisions on that information.

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

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FIGURE LEGENDS

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

Figure 2: Oscillogram (top) and spectrogram (bottom) recorded at 0.03-500Hz. (a) 3 BS events (3 repetitions at 7:02:31; 2 repetitions at 7:02:50; 2 repetitions at 7:03:09). Distance from source = 50 m. All three events presented between 10-80Hz with highest energy at 20-40Hz.; (b) Male locomotion at 7:49:30. Distance from source = 40 m.

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

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

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

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

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

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

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

Model (*N* = 22)	AICc	ΔAICc
1) MSL ~ DNM	184.0	2.24
MSL ~ 1	**181.7**	**0**
2) MLA ~ DNM	380.8	0.78
MLS ~ 1	**380.0**	**0**
3) Elo ~ DNM	257.4	0.81
Elo ~ 1	**256.6**	**0**

** MSL = maximum standard length (cm); MLA = maximum lateral area (cm^2); Elo = mean dominance score for whole season; DNM = mean distance to nearest neighbor for whole season.*

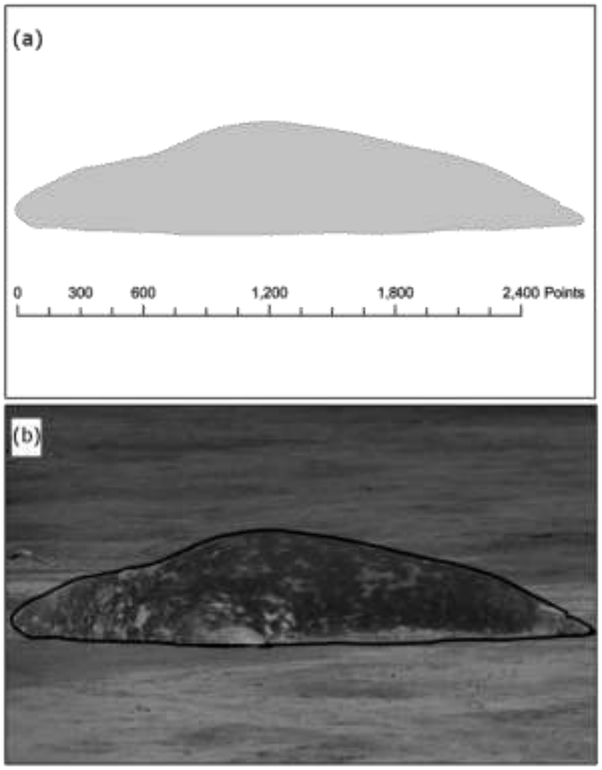


Figure 1

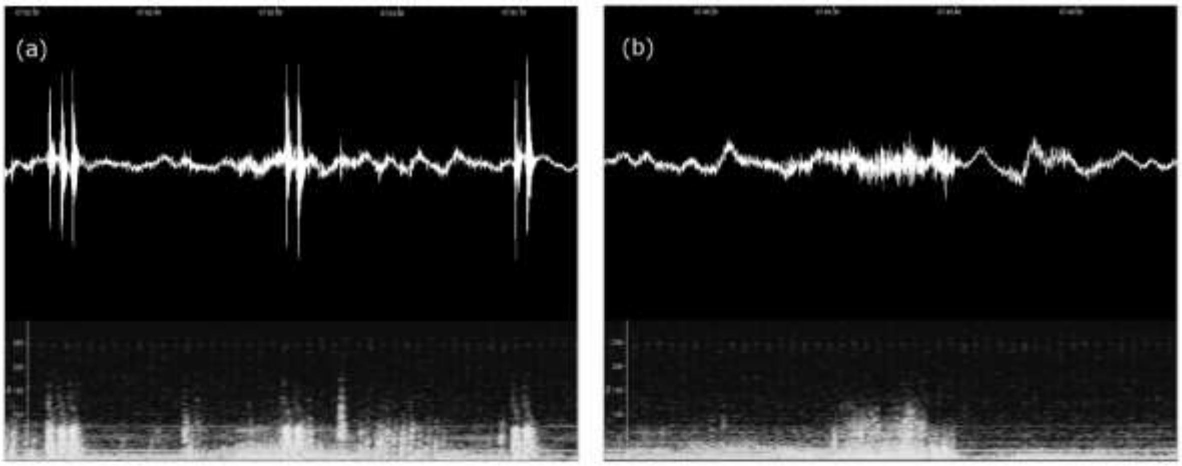
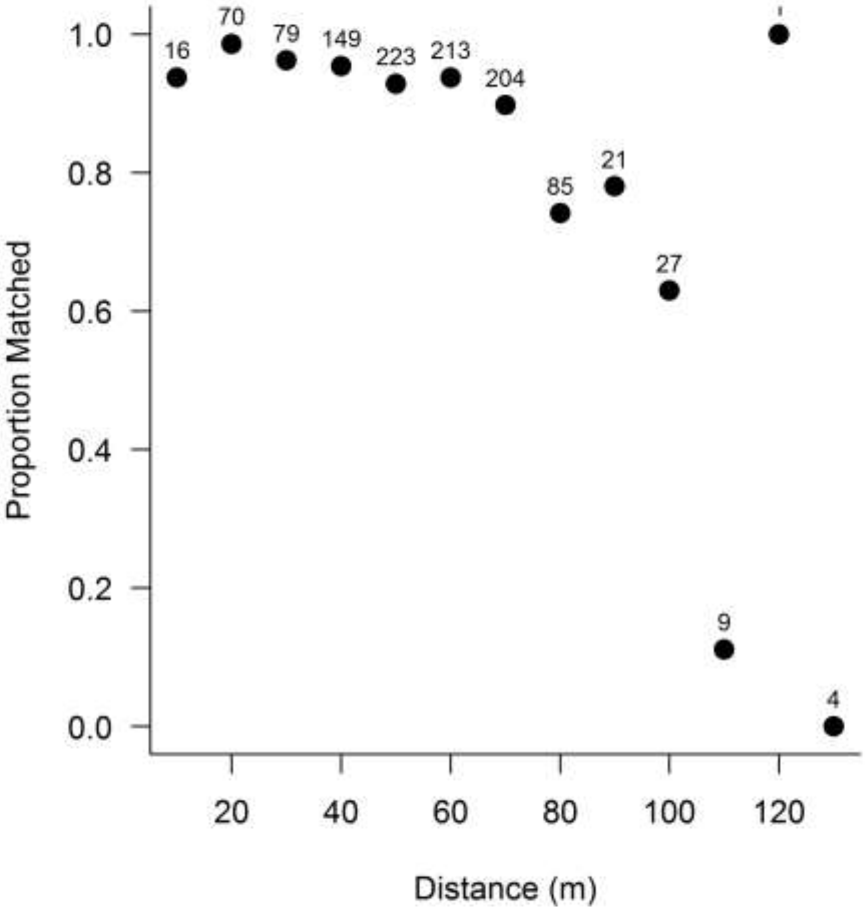


Figure 2


16
70
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Proportion Matched
20
40
60
80
100
120
Distance (m)

Figure 3

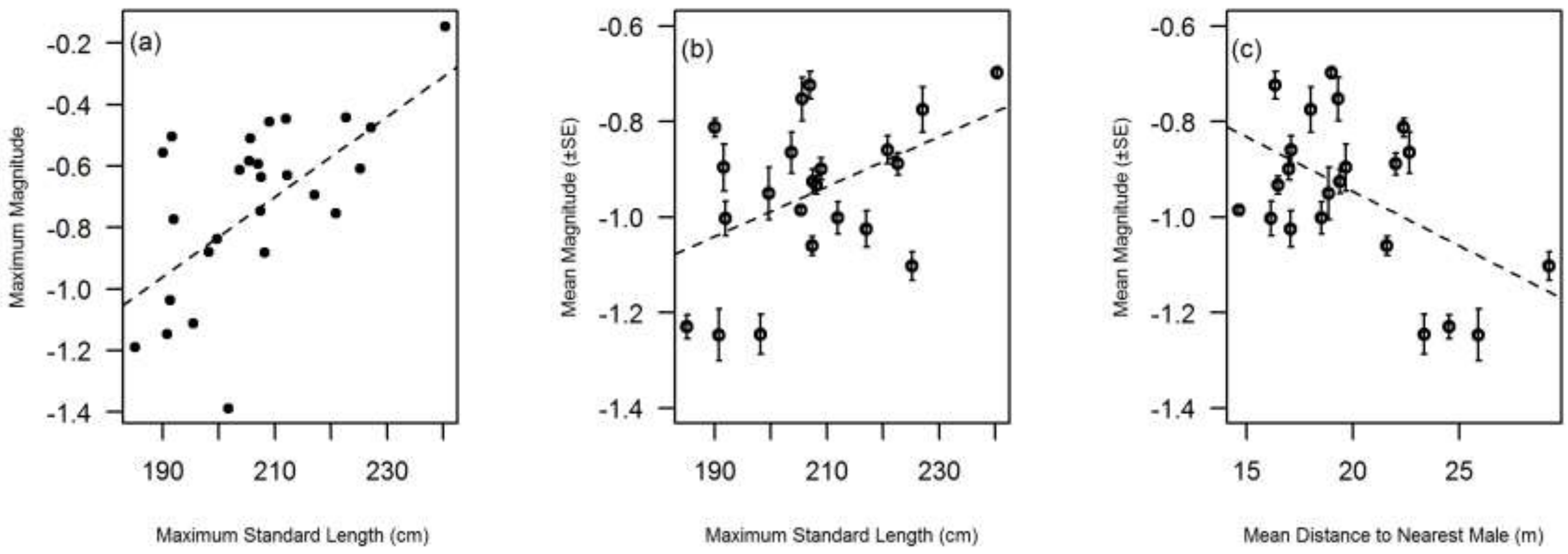
(a)
Maximum Magnitude
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
190
210
230
Maximum Standard Length (cm)
(b)
Mean Magnitude (±SE)
-0.6
-0.8
-1.0
-1.2
-1.4
190
210
230
Maximum Standard Length (cm)
(c)
Mean Magnitude (±SE)
-0.6
-0.8
-1.0
-1.2
-1.4
15
20
25
Mean Distance to Nearest Male (m)

Figure 4