



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



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Communication via substrate vibrations can convey information on conspecific presence, individual quality, group cohesion and/or allow for predator avoidance. Although studies have identified that various species use this modality, few studies on mammalian taxa have investigated whether 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, U.K., is part of a limited geographical region where the Body Slap (BS) behaviour is performed during male–male conflicts. This behaviour is thought to have a mechanical component. We examined whether the magnitude of the BS substrate vibrations contained reliable information on male mass and size as measures of RHP, and whether reliability varied across environmental conditions. To test this, we deployed seismometers during the breeding season that recorded continuous seismic data over a frequency bandwidth of 0.03–500 Hz. 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 BS behaviour is an indicator of male size and that the substrate-borne vibrations are reliable across varying environmental conditions.

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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, Poljak, Daneri, Marquez, & Negrete, 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). Although the literature investigating airborne acoustic and visual displays as indicators of male or female

RHP is extensive (Arnott & Elwood, 2009; Clutton-Brock & Albon, 1979; Sanvito et al., 2007b; Vannoni & McElligott, 2008), only a few studies have extended these questions to signals that generate substrate-borne vibrations (Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Rivero, Alatalo, Kotiaho, Mappes, & Parri, 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 et al., 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 signalling are extensively documented across numerous animal taxa; conservative estimates suggest that in the order Insecta alone, a total of 195 000 species

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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, Johnston, McDaniel, & Warkentin, 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 et al., 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 investigated a specific behaviour performed by male grey seals, *Halichoerus grypus*, during the breeding season and investigated whether 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 U.K. 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 occur yearly in the autumn or winter in the U.K., 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 18–20 days during which they give birth to a single pup, mate (oestrus is roughly on day 16 postpartum) and wean the pup; 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 et al., 1994). Intermale aggression typically takes the form of ritualized displays, but some interactions will escalate to physical fights comprising mainly 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, Boness, Bowen, & McMillan, 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 U.K. (Bishop, Lidstone-Scott, Pomeroy, & Twiss, 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; see Supplementary Video 1). A BS event typically consists of two to three repetitions of this general motor pattern in immediate sequence (Bishop et al., 2014; Supplementary Video 1). The display generates a distinct slapping noise as contact is made with the ground (Supplementary Video 1); the arching of the back potentially serves to display the lateral area and vibrations can be felt through the substrate by observers

(A. M. Bishop & S. Twiss, personal observations) suggesting that the display probably serves as a multimodal form of nonvocal communication (Miller, 1991).

Supplementary video related to this article can be found at <http://dx.doi.org/10.1016/j.anbehav.2014.11.008>.

Investigations into multimodal signals have shown that when substrate-borne vibrations are present, they often serve as a mechanism for complementing acoustic or visual displays (Elias, Hebets, Hoy, & Mason, 2005; Hebets & Uetz, 1999; Shipley et al., 1992; Stratton & Uetz, 1983). For northern elephant seals, playback experiments demonstrated that males responded more strongly to stimuli with substrate-borne vibrations and airborne acoustic components than airborne acoustic components alone (Shipley et al., 1992). Similar findings were demonstrated in insect systems (Elias et al., 2005; Hebets & Uetz, 1999; Stratton & Uetz, 1983). There are also cases in which 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, Vink, Sullivan-Beckers, & Rosenthal, 2013; Torr, Heritage, & Wilson, 2004). Although the BS does have an airborne acoustic component, grey seals generally do not have stereotypical vocal displays, with the exception of a 'yodel call' on Sable Island, Nova Scotia, Canada (Boness & James, 1979). Their other agonistic behaviours have been described as visual displays (Lawson, 1993; Miller & Boness, 1979; Twiss, 1991), but although little work has been done on night-time activity budgets for breeding pinnipeds (Anderson, 1978; Culloch, Pomeroy, & Twiss, 2014), elephant seal behaviours that generate substrate-borne vibrations were found to persist through the night (Shipley et al., 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 BS 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 airborne 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 whether 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 1500 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 8 h 48 min daily. The

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