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Play Behavior of Wild Grey Seals (*Halichoerus grypus*): Effects of Haulout Group Size and Composition

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Abstract

Burghardt's Surplus Resource Theory of Play states that long periods of immaturity and parental care are among the most important conditions for play to occur among young individuals. Grey seals (*Halichoerus grypus*) are polygynous, sexually dimorphic marine mammals. Young individuals are known to be social and playful—especially males, who do not take an overt part in breeding colonies until they are at least 8 y old. However, unlike most other social species, the lactation period of grey seals is short, with abrupt weaning, and no parental provisioning is provided afterward. We hypothesized that haulout group size of grey seals should have a positive effect on their social play because it provides indirect protection of young playful individuals. Social play behavior of a haulout group of grey seals of various ages and both sexes was observed during the nonbreeding season in Abertay Sands, Scotland. Adult individuals made up approximately 80% of the haulout group, and males were predominant. There was a moderate positive relationship ($R = 0.46$, $p < 0.0001$) between social contacts (number of play interactions between two individuals) and group size. The majority of play interactions were observed during the second hour of group formation when young individuals started to join the group. Group size is an important factor that increases vigilance, provides indirect protection for young individuals, and helps them acquire the necessary skills and physical condition for the breeding season.

Key Words: grey seal, *Halichoerus grypus*, social play, haul out, group effect

Introduction

Grey seals (*Halichoerus grypus*) are gregarious, polygynous, sexually dimorphic mammals (Boness & James, 1979). Male grey seals become physiologically mature at approximately 3 to 5 y of age as do females, but most males do not take an overt part in breeding colony matings until they are at least 8 y old. This delay in reproductive activity is likely because young mature males must gain mass and social experience to be able to compete with other adult males (Boness & James, 1979; Harcourt et al., 2007).

In many land mammals (e.g., wolves [*Canis lupus*; Bekoff, 1974], rats [*Rattus* sp.; Pellis & Pellis, 1998], spotted hyenas [*Crocuta crocuta*; Drea et al., 1996], and brown bears [*Ursus arctos*; Fagen & Fagen, 2004]), as well as in many other polygynous pinniped species (e.g., South American fur seals [*Arctocephalus australis*; Harcourt, 1991b], Galapagos fur seals [*Arctocephalus galapagoensis*; Arnold & Trillmich, 1985], Steller sea lions [*Eumetopias jubatus*; Gentry, 1974], and elephant seals [*Mirounga angustirostris*; Reiter et al., 1978]), play has an important role in the behavioral development of juveniles. Typically, there are three categories of play: (1) solitary locomotor-rotational, (2) object, and (3) social play. While it is assumed that the first two are more related to the development of motor-neural skills and help to improve movement and coordination, social play is related to more complex group activities (Graham & Burghardt, 2010). Animals play because it is a rewarding and pleasurable activity (Vanderschuren et al., 1995; Balcombe, 2009; Trezza et al., 2010; Vanderschuren, 2010), which also is initiated by a stress-free environment with sufficient energy resources (Arnold & Trillmich, 1985; Almeida et al., 1996; Almeida & Araujo, 2001) or boredom (Graham & Burghardt, 2010) and necessary for the growth of specific prefrontal brain areas during critical developmental periods (Bell et al., 2010). These factors affecting social play are also known as proximal causes of play.

Social play interactions are also thought to facilitate social integration of young individuals because play helps them practice and dynamically assess their physical capabilities under nonstressful conditions, develop fighting skills, and form dyadic or group relationships (Fagen, 1981; Burghardt, 2005). Adult rats deprived of social play (mainly play fighting) during their infancy become hyperdefensive during social contact: they are not able to exhibit proper submissive behaviors towards dominant males or coordinate movements with other mates, are overly stressed, and escalate aggression (Hol et al., 1999; Pellis et al., 2010). Improper behavior towards conspecifics does not allow maintaining of stable relationships within a group and might have implications for reproductive success.

In his Surplus Resource Theory of Play, Burghardt described several conditions/surplus resources such as ecological (i.e., favorable environmental conditions with intense competition among rivals), socio-psychological (i.e., need for stimulation and a complex adult behavior in the future), energetic (i.e., possibility to thermoregulate and easily recover from vigorous activity), and ontogenetic (i.e., long juvenile period) that might be necessary for play to occur. Social play is a costly behavior for young individuals not only due to high metabolic rates but also because young individuals are less vigilant during play activities and become more vulnerable to predators or might suffer accidental injuries. An extreme example given by Harcourt (1991a) showed that 22 of 26 South American fur seal pups that were caught and killed by southern sea lions (*Otaria byronia*) had been involved in social play. Playing pups were distracted, moved away from their mothers, or ignored fleeing group members. Since play behavior made up only about 6% of their total time budget, it was a very costly behavior in terms of surviving. In this case, the lactating female South American fur seals alternate periods of suckling the pup with periods of feeding at sea; thus, there are times when pups are left onshore unattended. Therefore, prolonged parental provisioning of young individuals (which leads to an extended juvenile period) is an important prerequisite for play behavior in mammals that helps to reduce their survival costs (see Burghardt, 2005). However, in cases where parental provisioning is limited or terminates early, other group members could act as an "alarm signal" when necessary and provide direct or indirect protection. Indeed, in many groups of mammals, play behavior is positively related to group size (Burghardt, 2005). Juveniles of gregarious ungulates and primates tend to play more frequently and with longer durations when group size is larger (Baldwin & Baldwin, 1974; Berger, 1979).

However, in grey seals, a short 17- to 21-d lactation period is followed by abrupt weaning, and no further parental provisioning is provided (Mellish et al., 1999; Pomeroy et al., 2000). Grey seal pups are largely immobile during lactation and spend most of their time resting, presumably to avoid loss of contact with the mother. During lactation, pup play behavior becomes more evident with age but is usually solitary and not directed towards other seals (Kovacs, 1987).

Play behavior is most easily observed while grey seals are on land. In common with other pinniped species, grey seals use remote islands or sites exposed by low tide to come ashore between foraging trips out at sea. These periods ashore, *haulouts*, often occur within a limited space such as a rocky islet or tidal sand bank. Telemetry studies indicate that grey seals tend to spend approximately 40 to 75% of their time in the water near haulout sites (McConnell et al., 1999; Sjöberg & Ball, 2000). Grey seals are also known for having strong site fidelity to their specific haulout sites during both nonbreeding (McConnell et al., 1999; Sjöberg & Ball, 2000; Karlsson et al., 2005) and breeding (Twiss et al., 1994; Pomeroy et al., 2000) seasons. When they are not breeding, grey seals haul out to molt once a year, thermoregulate, rest, and possibly digest (Riedman, 1990). It is considered that the "cost of immersion" motivates pinnipeds to haul out for rest after foraging (Watts, 1996); and if they are deterred from hauling out, they spend more time ashore subsequently than expected (Brasseur et al., 1996). Grey seals haul out to form large groups that are sometimes close to mainland beaches, where they can be vulnerable to danger because of reduced mobility on land. Thus, gregarious behavior at haulout sites may afford increased vigilance and help with the detection of potential threats (Da Silva & Terhune, 1988; Terhune & Brillant, 1996; Watts, 1996).

McConnell et al. (1999) suggested that the large amount of time spent near haulout sites, especially for young individuals, might be related to social interactions. Thus, young individuals playing in a mixed age group obtain public information from the reaction of adults to possible dangers.

Grey seals are often observed playing, but very few studies have been performed to investigate this behavior (Wilson, 1974; Hunter et al., 2002). Recent growth of the grey seal population in the North Sea has helped focus attention on understanding the structure of the population, including group behavior and the behavior of separate individuals (Thompson & Härkönen, 2008).

Here, we hypothesized that group size affects social play in nonbreeding, hauled-out young grey seals. Thus, the occurrence of play behavior should be positively correlated with group size. To test the hypothesis, nonbreeding grey seals were observed at a haulout. We investigated (1) the sex and age of playing individuals, (2) how social play behavior relates to the size (i.e., number of individuals) and composition of the group of grey seals, and (3) the temporal sequence of play during observations of haulout groups.

Methods

Study Location and Animals

The study was performed in Tentsmuir National Nature Reserve on the east coast of Scotland. The Abertay Sands are exposed at the mouth of the River Tay during the low tide (Figure 1a & 1b). The tidal sand banks were the haulout sites used by grey seals. Although a few harbor seals (*Phoca vitulina*) sometimes hauled out on the mainland beach, this was seen very rarely for grey seals.

Age and Sex Determination

Grey seals present were classified into age and sex categories according to visible features, including genital openings, body size, development of secondary sexual features, and marking dimorphism (Davies, 1949; Hewer, 1964). Sex was determined according to the genital openings (see King, 1983). If genitalia were impossible to observe, sex was assigned based on the pelage pattern. Dark shades (i.e., brown, black, and grey) form the entire background of grey seal males; the background is punctuated by darker irregular spots. Typically, female pelage has a light grey background with dark irregular patches overlaid. The most distinctive feature of mature males were secondary sexual characteristics, including a large neck and shoulders (often scarred) and a long nasal rostrum (Boness & James, 1979). Adult males are, in general, larger than adult females, reaching a body length of 250 cm and a mass of 350 kg; in contrast, females usually grow up to 200 cm long and weigh up to 250 kg (Special Commission on Seals [SCOM], 2010).

Three age groups were distinguished: (1) adults, (2) subadults, and (3) juveniles. Males with bulky and rugose necks and shoulders and with a prominent rostrum were classified as adults (*M A*). Males were considered to be subadult (*M Sub*) when they had a smaller body mass, leaner neck, and fewer scars on their neck, indicating that they had been involved in few or no fights. Females that were obviously pregnant (i.e., with a distended abdomen) and had a typical light pelage were considered to be adults (*F A*), whereas subadult females (*F Sub*) had a flatter abdomen and were slightly smaller. All small individuals without well-defined secondary sexual characteristics but with clear pelage markings were classified as juveniles (*Juv*) (King, 1983). Subadults and juveniles altogether are also referred to as *young* individuals in the text. In most cases, the sex of juveniles was not determined. If it was impossible to determine the age and sex of an animal, it was considered unknown (*Unkn*).

Observation Procedure

Behavioral observations were made from 15 June to 6 August 2009. In total, 107 h of observations were used for the analysis. Observations were made during daylight hours between 0700 and 2100 h BST. The observation time and duration depended on weather conditions and tidal conditions. No observations were made during unfavorable weather conditions when visibility was restricted by fog or when the closest group of grey seals was too far away to be observed in sufficient detail (i.e., farther than approximately 400 m).

Video recordings using a Sony Handycam (DCR-SR36, x40 optical zoom, x200 digital zoom, 40 GB internal hard drive) with voiceover were made alongside visual observations. Bushnell binoculars (8×32 mm), a telescope (x20 to 60) with a tripod, and data sheets were used for recording data. Observations were made from a wooden hide built on the top of a sand dune on the mainland overlooking the closest *haulout group* (or *group*) of grey seals, 10 m from the high water mark and 200 to 300 m from the closest haulout site A (Figure 1b).

The scan sampling method (Altmann, 1974; Martin & Bateson, 1993; Lehner, 1996) was used (1) to obtain information about haulout patterns in the study area (the number of haulouts and their position in the study area [Figure 1b]; the approximate number of individuals in each haulout); and (2) to obtain information about the sex and age structure of the haulout group of individuals and the number of playing individuals in the closest haulout. The number of grey seals visible in up to eight haulout sites was recorded every hour from the start of observations (i.e., scans). Groups of grey seals were considered separate if the distance between them was more than 20 m. (Locations of these groups are indicated by letters A through H in Figure 1b).

Detailed observations were restricted to scans from haulout site A. Scans of this haulout site were repeated at *15-min intervals*. Number of grey seals, their sex and age, and number of social play interactions were recorded along with the date and time of day. Only social play was recorded, and only dyadic interactions were seen and recorded during the social play of grey seals. It was not always possible to assess the sex and age of playing individuals during scan sampling; thus, this indicator was not used in the analysis. Observation scans started as soon as the observers entered the hide, and, thus, scans could include observations with no animals.

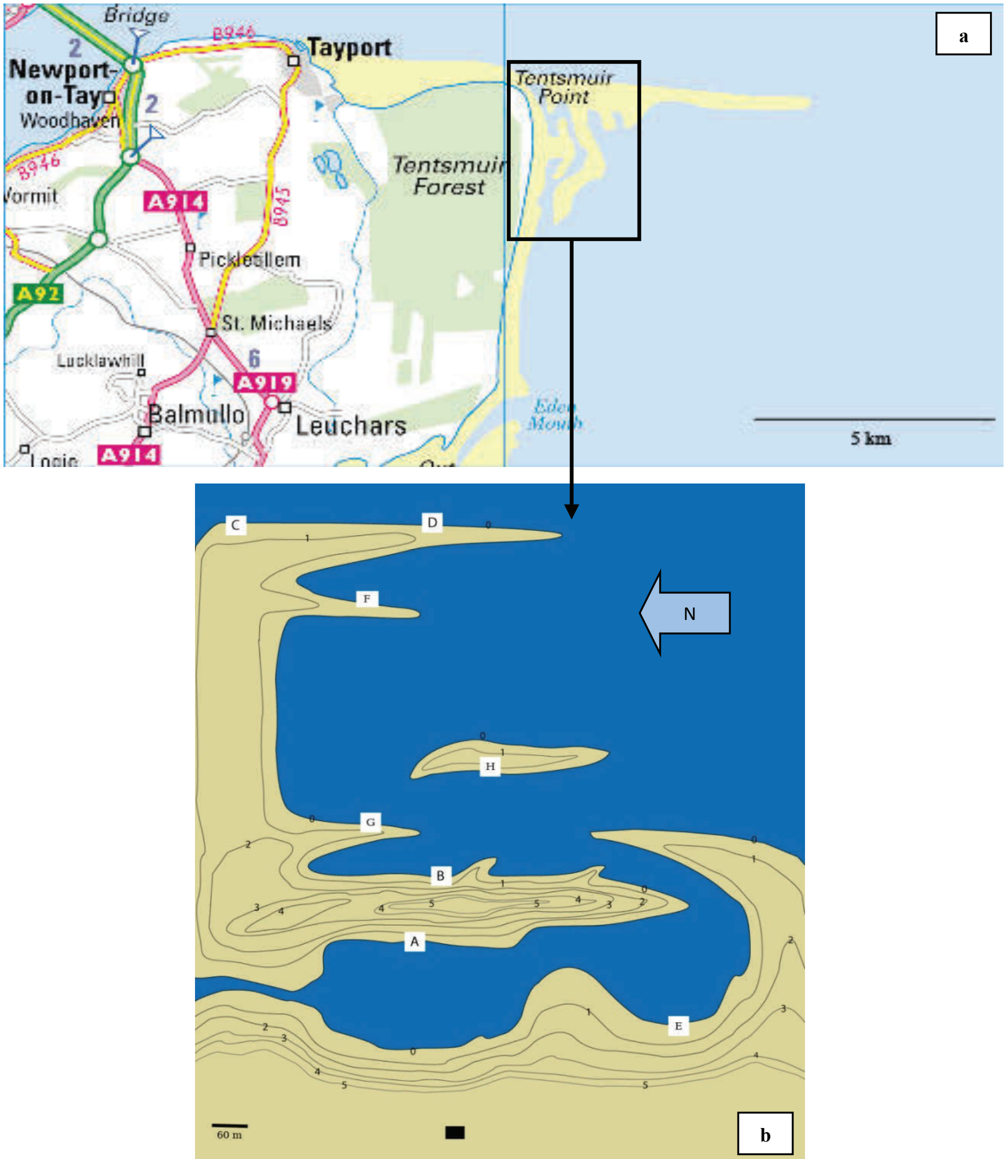

Figure 1. (a) Location of the study area (www.streetmap.co.uk); and (b) schematic overhead view of the haulout area. Annotated lines show approximate water level, and numbers denote hours before/after low tide (0) when the proportion of sand (light brown) above the water (blue) reaches its maximum. Haulout areas used by groups of grey seals (*Halichoerus grypus*) are shown (A-H). The solid black rectangle shows the approximate position of the hide from which observations were taken.

Ad libitum sampling (Altmann, 1974; Martin & Bateson, 1993) between scans was used for detailed play observations (Figure 2). It was possible to determine the sex of most of the interactants and assign them to a certain age group.

Haulout Group Formation and Temporal Frequency of Play

Water-level fluctuation was a limiting factor for group formation because haulout groups could be formed only on the sand banks that appeared during the low tide. Observation times were expressed as time relative to low tide. Water level and tidal state were registered using the Admiralty

Figure 2. Grey seal subadult males initiating social play interaction in the shallow water on the edge of a haulout group; at least two already hauled-out subadult males can be seen to the sides of the interactants (circled in white). (Photo credit: Claire Lacey)

Easy Tide website (http://easytide.ukho.gov.uk) predictions for River Tay Bar, Scotland. During the observation period, low tide (i.e., hour 0) water levels dropped to 1.38 m above datum (i.e., meters above a fixed base elevation at a local tide station to which all water level measurements are referred); at high tide, approximately ± 6.18 h from low tide, the water level rose up to 4.65 m above datum (see Figure 1b).

The beginning of the haulout group's formation was defined as the time point at which the observer could clearly see the process of *two individuals* hauling out on land. The haulout formation process was recorded in time periods (15-min scans) from the beginning of its formation (given as 0 time). These intervals were combined to 1-h periods in the analysis, and these hourly intervals are further denoted as the *haulout formation period* (HFP). The group size included individuals who hauled out and those who were playing or present in the adjacent shallows.

Statistical Analysis

Both the absolute number of play interactions (PI) in the closest haulout and the contact rate (CR), or the proportion of playing individuals in a group at a particular time, were used in the analysis. CR was calculated by the formula

$$CR_i = \frac{2 \times y_i}{N_i},$$

where y_i is the number of dyadic play interactions and N_i is the group size at a particular observation time, *i*.

Data analysis and graphs were prepared using *STATISTICA*, Version 8.0.550, with *p* values considered to be significant based on $\alpha = 0.05$. Graphs were also prepared with Microsoft Office *Excel 2010*. Nonparametric statistical analysis methods such as Friedman's ANOVA with Kendall's coefficient of significance (χ^2, Kendall's W), the Mann-Whitney U test (U), Kruskal-Wallis tests (H), and Spearman rank correlations (R) were used. Their use is further discussed in the "Results" section. Median values with quartiles (Q_1-Q_3) also are presented in the "Results" section, with the quartiles always presented in parentheses following the median value.

Results

Social Play Interactions

A total of 85 PIs out of 2,551 behavioral elements were recorded during the *ad libitum* sampling. The median duration of PIs recorded was 4.52 min (2.5 to 10.03 min), with the longest interactions extending to 47.25 min. The majority of interactions lasted less than 10 min (Figure 3).

A total of 170 individuals were involved in dyadic interactions. Most of them were submales (61.76%) and subfemales (13.53%); less frequent participants were adult males (10%) and juveniles (9.41%). There were no adult females seen interacting. There were also eight individuals whose sex and age were not identified.

The most frequent interactions were between submales (42.35%) and between subadult females and males (21.18%) (Table 1).

Scan Details

A total of 441 scans, covering 21 separate days of observations of the closest group at haulout site A, were recorded over 4 to 9 h of observations per day. Of these scans, 304 included at least two individuals hauled out, while in 137 scans only one or no animals were observed hauled out at site A.

There was a median of 61.5 (7 to 211.5) individuals in the closest haulout site A during observations and up to 720 individuals at a time. Of the total amount of observation time when grey seals were visible, 27% included social play. There was a median of 2.22% (0.99 to 3.53%) of grey seals per scan involved in PI. Up to nine dyadic interactions at a time were recorded.

Haulout sites A and B were used most commonly because these areas dried out first; however, individuals in site A would usually move away and join the group at site B approximately an hour or two before low tide. Other haulout sites were used only during the 2- to 3-h period before and after low tide as land became available (Figure 4).

The Effect of Group Size on the Contact Rate, Number of Social Interactions, and Temporal Sequence of Play

There was a moderate positive relationship between both the group size and CR (Spearman, $N = 304$, $R = 0.40$, $p < 0.0001$) and the group size and PI ($N = 304$, $R = 0.46$, $p < 0.0001$). The closest haulout site A consisted of a median of 36 (6 to 107) individuals when there were no PIs and 220 (106 to 312) individuals when there was at least one social PI (Mann-Whitney, N [CR = 0] = 225, N [CR > 0] = 79, U = 3,594, $p < 0.0001$).

It was possible to record a group formation process in haulout site A on 19 occasions. These

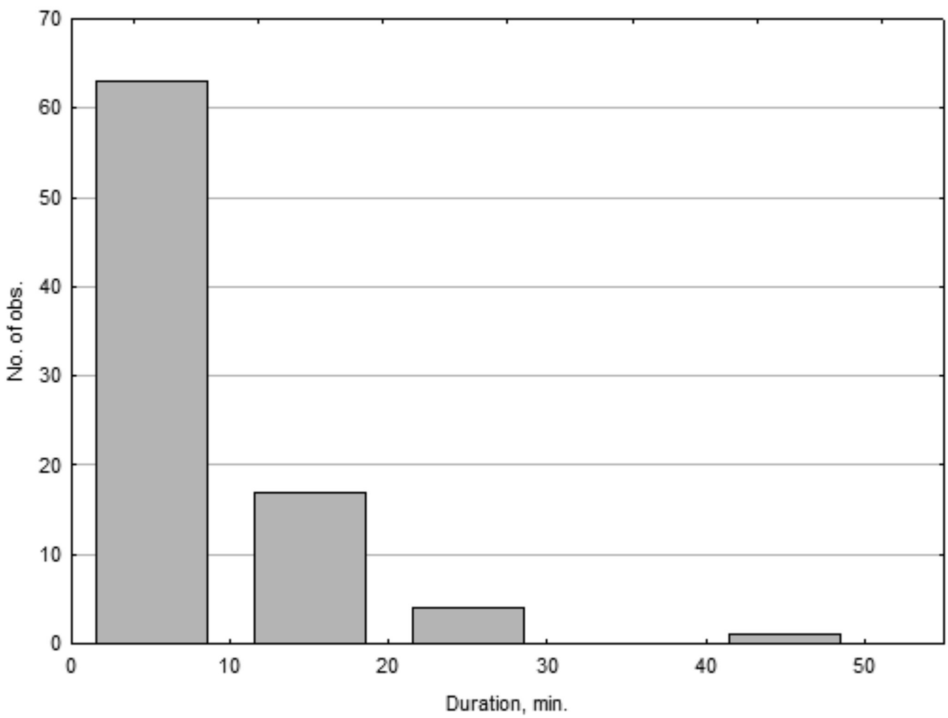

Figure 3. The frequency of various durations of social play interactions (PIs)

Table 1. Play interactions (PIs) between interactants by age and sex

Ind. 1 \ Ind. 2	Subadult male	Subadult female	Adult male	Juvenile	Unknown	Totals
Subadult male	36	18	7	4	4	69
Subadult female		0	4	0	1	5
Adult male			2	1	1	4
Juvenile				6	0	6
Unknown					1	1
Totals	36	18	13	11	7	85

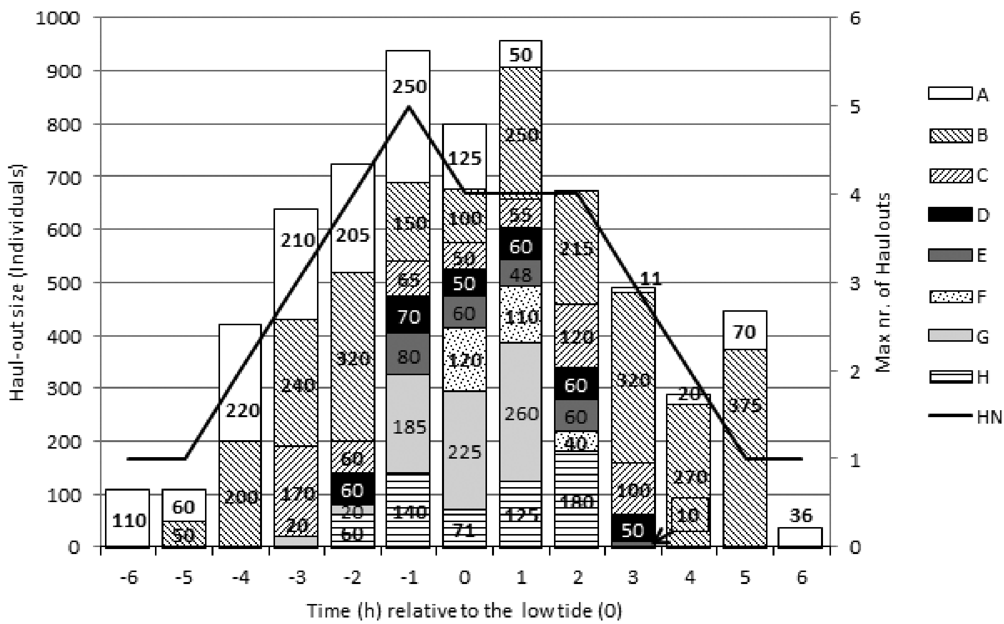

Figure 4. The median number of individuals (presented as columns on the left y-axis) present in all haulouts (A-H) and a maximum number of haulouts (HN) in the study area (represented as the dark line scaled on the right y-axis) during the study period relative to tide time (h)

occasions were identified from 201 scans taken at intervals of 15 min after at least two animals were seen hauled out on land. Groups lasted a median of 3 h (2.07 to 4.44). There was a positive relationship between group size and HFP (R = 0.5, $p < 0.0001$). Groups had a median group size of 15 (4 to 115) individuals during the first hour after the beginning of group formation, which increased to a median of 250 (60 to 340) individuals after the third hour from the beginning of group formation (Kruskal Wallis, H = 43.33, $p < 0.0001$) (Figure 5).

There was a weak relationship has been found between CR and HFP (Spearman, R = 0.17, $p = 0.018$) and between PI and HFP (R = 0.22, $p < 0.01$). Despite the low median values and no significant change in the CR (Kruskal-Wallis, H = 4.52, $p = 0.21$) during HFP (Figure 6), there was an increase in the CR during the second and third hours that decreased slightly after the third hour of HFP. Similarly, the highest PI was observed during the third hour, and the lowest during the first hour; however, this change was significant (H = 8.42, $p = 0.038$) (Figure 6).

There was a change in the number of individuals and CR in the closest haulout depending on tidal state. The highest number of individuals was

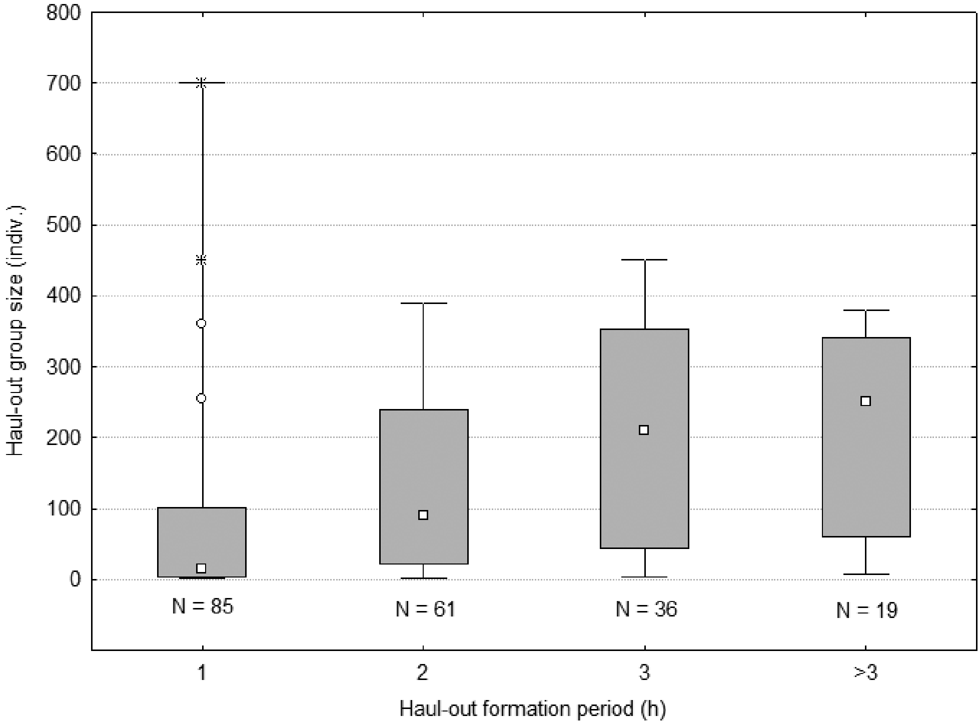

Figure 5. Change in group size (i.e., number of individuals; H = 43.33, $p < 0.0001$) during haulout formation period (HFP). Squares denote median values; boxes, Q_1-Q_2; whiskers, min-max; circles, outliers; and stars, extremes. Sample sizes are indicated below the graph.

observed 3 h before the low tide, while there were almost no individuals from 1 h before the low tide to the second hour after the low tide (Figure 7).

Group Composition and Social Play

The proportions of seals in each sex and age class in haulout groups were unequal (Friedman's ANOVA, $\chi^2 = 830.93$, $p < 0.0001$; Kendall's W = 0.68) (Figure 8). Males (i.e., subadults and adults combined) predominated and composed 60% of the group. Adults made up more than 80% of those classified.

A Mann-Whitney test was performed to determine whether there was a significant difference in the proportion of different sex-age groups when there were no interactions vs at least one interaction in the closest haulout site (Table 2). There was no difference in the proportion of males; however, the proportion of adult females decreased when interactions were recorded. The proportion of the population consisting of the demographic groups with the most playful individuals (i.e., juveniles, subadult males, and subadult females) was approximately 3% greater when play behavior was observed compared with periods of no interactions.

CRs from groups with varying proportions of young individuals (juveniles and subadults altogether) were different (Kruskal-Wallis, H [$N = 304$] = 20.28, $p < 0.001$) (Figure 9). Similar results were found regarding the relationship between PI and the proportion of young individuals in a group (H [$N = 304$] = 24.58, $p < 0.0001$) (Figure 10). The highest CRs were observed in groups in which young individuals comprised approximately 33 to 66% of the haulout group, and the group consisted of approximately 101 to 200 individuals (Figure 9); whereas the highest number of PIs was recorded when group size was between 201 and 300 individuals and consisted of 0 to 33% young individuals (Figure 10).

The increase in CR during the second hour of HFP might be explained by an increase in the proportion of young individuals (juveniles and subadults altogether) (Spearman, R = 0.31, $p < 0.0001$). There was a median of 3 individuals (0 to 16) during the first hour of HFP, which comprised 14.06% (0 to 27.08%) of the group size. During the second hour, a median of 23 (2 to 36) individuals were recorded, which comprised 16.67% (11.25 to 24%) of the group size in the closest

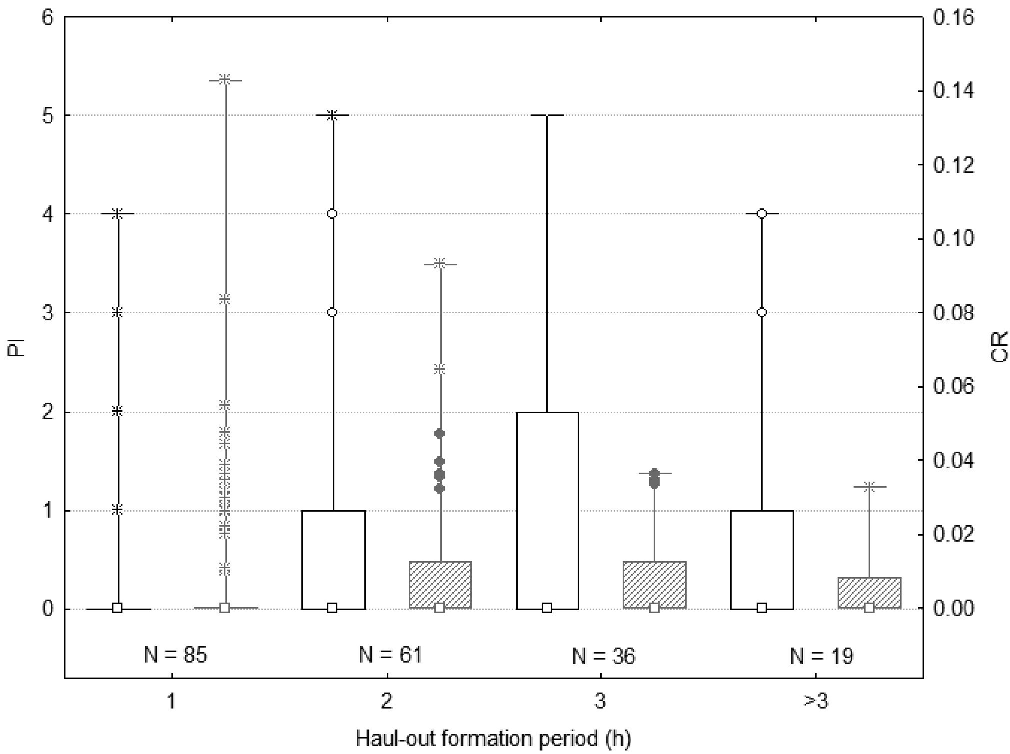

Figure 6. Change in contact rate (CR) (H = 4.52, p = 0.21) during the period of HFP. Squares denote median values; boxes, Q_1-Q_2; whiskers, min-max; circles, outliers; and stars, extremes. Sample sizes are indicated.

Table 2. Proportion (%) of different age and sex groups, expressed as median (Q_1-Q_3), for different CRs in the closest haulout group (CR = 0, N = 225 and CR > 0, N = 79). Significant differences are marked in bold (Mann-Whitney U test).

Proportion (%) of	When CR = 0 Q2 (Q1; Q3)	When CR > 0 Q2 (Q1; Q3)	U	p level	Spearman Rank Correlation Test
Adult females	**33.33 (18.27; 50)**	**28 (23.23; 34.78)**	**7,330**	**0.02**	R = -0.17 p < 0.01
Adult males	48.94 (33.33; 56.14)	49.8 (46; 54.17)	7,581	0.052	R = 0.12 p = 0.04
Subfemales	**0 (0; 4)**	**3.57 (2.33; 6.57)**	**4,820**	**< 0.0001**	R = 0.37 p < 0.0001
Submales	**8.77 (0; 16.22)**	**10.87 (8.57; 14.52)**	**6,999**	**< 0.01**	R = 0.18 p < 0.01
Juveniles	**3.59 (0; 8)**	**4.93 (3.04; 6.49)**	**7,045**	**< 0.01**	R = 0.18 p < 0.01

haulout site; this change in proportion was significant (Kruskal-Wallis, H = 12.09, p < 0.01).

The highest correlation was found between subfemales and HFP (Spearman, R = 0.4, p < 0.0001). On most occasions, there were no subfemales during the first hour, and their numbers increased to a median of 7 (2 to 17) individuals or 4.04% (2.32 to 7.21%) during the second hour

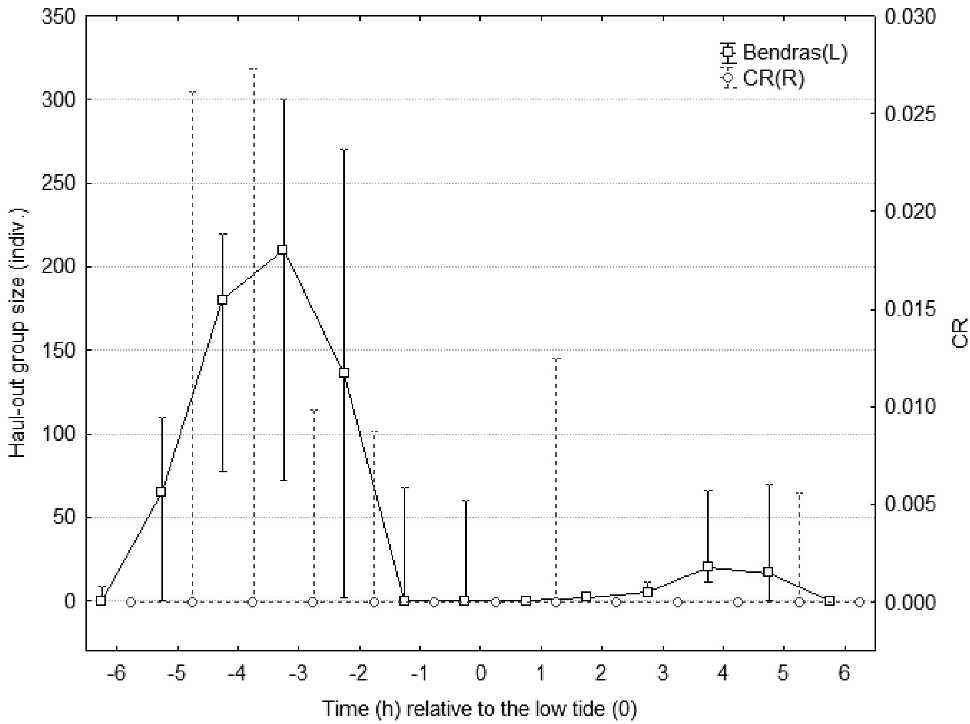

Figure 7. Change in median group size (circles) and CR (squares) at low tide (0) (whiskers denote 25th to 75th percentiles); $N = 441$.

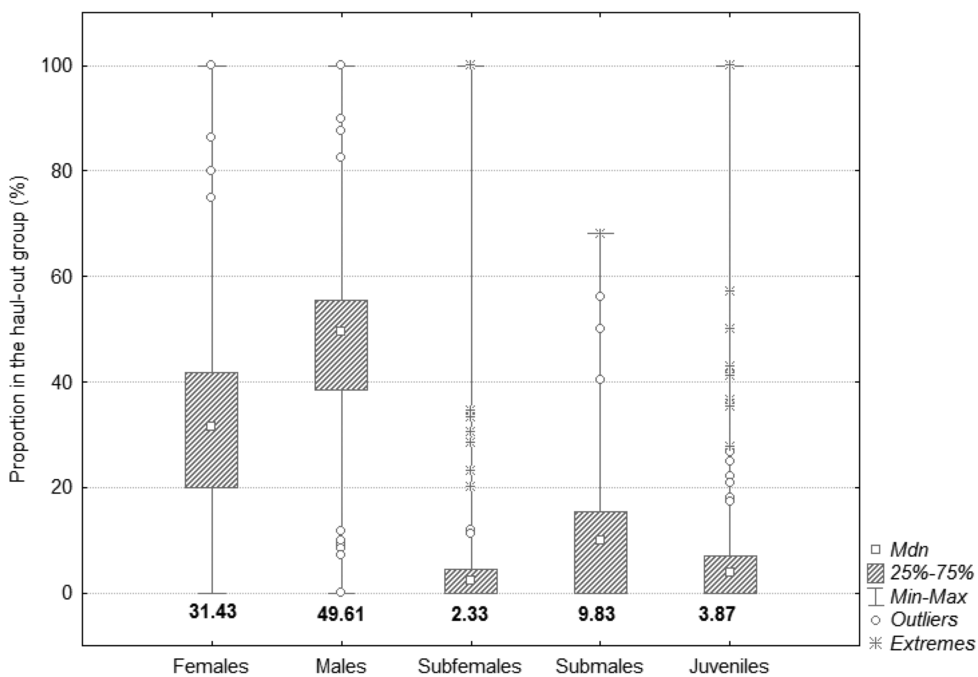

Figure 8. Age and sex ratios of grey seals in the closest haulout site A

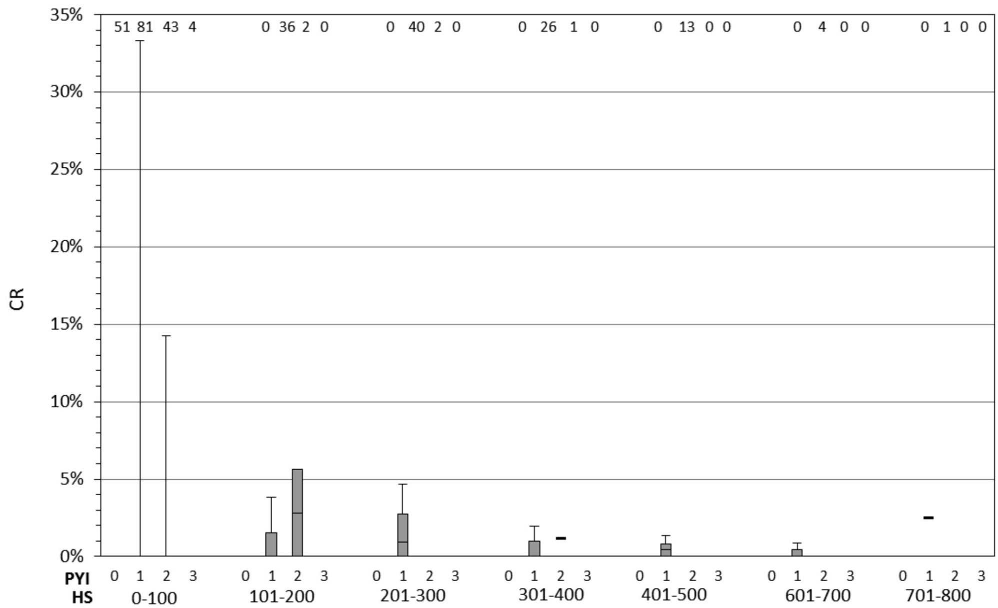

Figure 9. CRs in different haulout group sizes (HS, $N = 304$). The numbers in the PYI row beneath the chart indicate different proportions (%) of young individuals (PYI) in the closest group of grey seals: 0, 0% ($N = 51$); 1, 0 to 33% ($N = 201$); 2, 33 to 66% ($N = 48$); and 3, 66 to 100% ($N = 4$). Whiskers denote maximum values; middle lines, median values; and upper and lower columns, upper and lower quartiles.

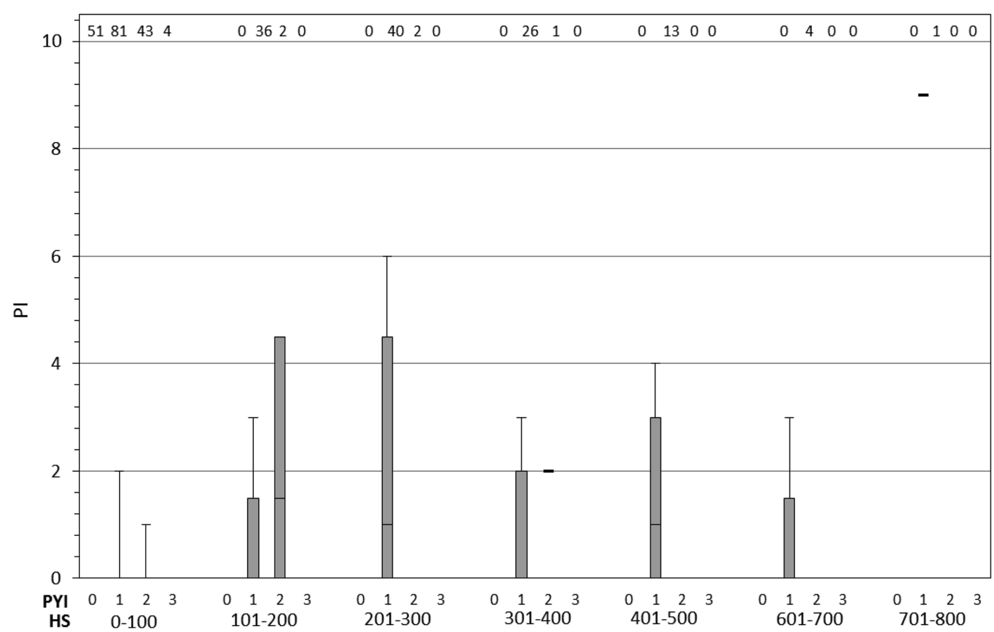

Figure 10. Number of PIs on different haulout group size (HS, $N = 304$). The numbers in the PYI row beneath the chart indicate different proportions (%) of young individuals (PYI) in the closest group of grey seals: 0, 0% ($N = 51$); 1, 0 to 33% ($N = 201$); 2, 33 to 66% ($N = 48$); and 3, 66 to 100% ($N = 4$). Whiskers denote maximum values; middle lines, median values; and upper and lower columns, upper and lower quartiles.

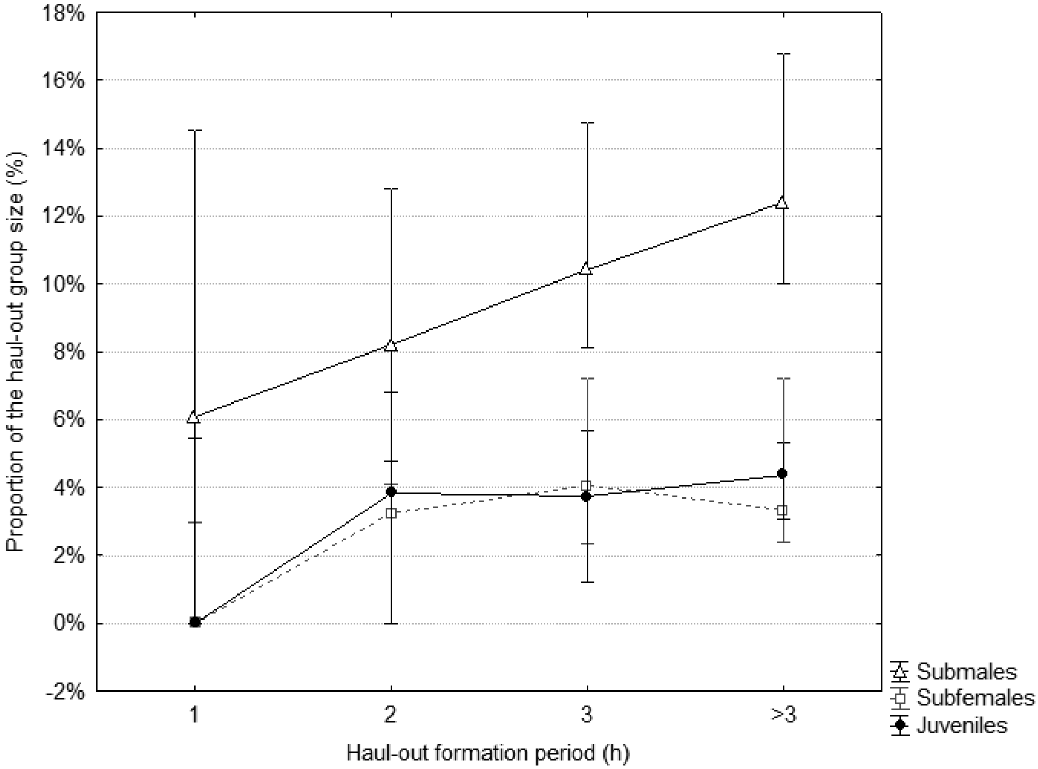

Figure 11. The change in proportion of young individuals—submales (open squares), subfemales (grey squares), and juveniles (black circles)—during the HFP. Squares/circles denote medians, and lines indicate the Q_1-Q_3 spread.

(Kruskal-Wallis, H = 25.4, $p < 0.0001$). Submales comprised the highest proportion of young individuals in the group and increased from a median of 2 (0 to 10) individuals or 6.06% (0 to 14.51%) during the first hour of HFP to a median of 31 (6 to 59) individuals or 12.40% (10 to 16.77%) after the third hour (H = 12.23, $p < 0.01$) (Figure 11). The relationship between submales and CR was weaker (R = 0.29, $p < 0.0001$).

Juveniles comprised the weakest proportion of young individuals in the group (Spearman, R = 0.25, $p < 0.001$). There was a small difference in the proportions of juveniles during HFP (H = 8.36, $p = 0.039$) (Figure 11): juveniles increased from a median of 0 (0 to 5) individuals or 0% (0 to 5.43%) during the first hour of HFP to a median of 13 (2 to 14) individuals or 4.38% (3.06 to 5.31%) after the third hour; proportions remained stable between the second and fourth hour (Figure 11).

The proportion of adult grey seals decreased (Spearman, R = -0.31, $p < 0.0001$) throughout the HFP, whereas the number of individuals in the group increased (R = 0.52, $p < 0.0001$). There was no strong correlation between HFP and either the proportion of adult females or adult males. The median proportion of adult females remained around 33% (21.43 to 50%) during HFP (Kruskal-Wallis, H = 3.32, $p = 0.34$). The proportion of adults that were male did not exhibit any change during HFP (H = 1.01, $p = 0.8$). However, the number of both adult females and males increased in the group during HFP (males: from a median of 5 [1 to 60] to 122 [39 to 140] [H = 40.74, $p < 0.0001$]; females: from a median of 4 [2 to 22] to 66 [12 to 119] [H = 39.45, $p < 0.0001$]).

Discussion

Grey seals are capital breeders and typically gather in remote islands to breed. During a 2-mo breeding season (Pomeroy et al., 1994), grey seals are strongly tied to land and are relatively easily observed. Females each give birth to a single pup and rarely leave during the 18-d suckling period (Pomeroy et al., 2000). In the meantime, males compete aggressively to maintain positions within the established aggregations of females (Twiss et al., 1994). Weaned pups do not leave the breeding area for even longer—they undergo a post-weaning fast for almost a month. By contrast, during the nonbreeding season, grey seals are highly mobile and spend at least 50 to 70% of their time at least 10 km off the coast (McConnell et al., 1999; Sjöberg & Ball, 2000; Karlsson et al., 2005; Breed, 2008). They chose unstable sand bars, remote onshore banks, and rocky islets as their haulout sites, all of which are usually found far from the coast.

Although grey seals are social and playful animals (Schusterman et al., 1970; Wilson, 1974; Hunter et al., 2002), it is not easy to observe their social play behavior in the wild during the nonbreeding season since, as mentioned before, they are typically found far from the coast—either in the water or on remote islets or sandbars. Thus, taken together, environmental conditions (i.e., rain, fog, changing water level, and waves), the instability of aggregations, the typically large haulout distance from the mainland, and the aquatic lifestyle of grey seals make observations in the wild during the nonbreeding season hard to plan and difficult to perform (Mellish et al., 2006). Therefore, most behavioral observations occur during the breeding season when groups of grey seals are more stable and easier to observe (Pomeroy et al., 2000; Lidgard et al., 2001; Ruddell et al., 2007; Twiss et al., 2007, 2012). This research provided important data of grey seal behavior outside the breeding season.

Group Size and Social Play

These results support the hypothesis that haulout group size has a positive effect on grey seal socialization. Play behavior is positively related to the number of individuals in a group and is most commonly performed when there are more individuals in a haulout than in a haulout with no interactions (median group sizes 220 vs 70 individuals).

According to the hypothesis, the number of PIs and the CR should increase with the number of individuals in the haulout group. However, this relationship was not consistently observed. The highest number of interactions and the highest CR were observed when there were between 100 and 200 individuals in the closest haulout group (Figures 9 & 10). This group size was reached during the second and third hours of HFP (Figure 6). As expected, there was a stronger relationship between group size and PI because there are more potential players in a bigger group. However, CR reflects the actual proportion of playing individuals and provides more information regarding how PIs increase with group size.

The inconsistent increase in CR with group size may be explained by tidal state and group structure and formation, particularly with respect to differences in the organization of adjacent haulout sites in the research area (Figure 4) and the use of the closest haulout space (Figure 7). Haulout group formation was closely related to the water level; thus, group size changed according to tidal state (Figure 7). Seals would start to haul out immediately after the sand bank appeared above the water. However, instead of constantly increasing towards the low tide, the number of individuals in haulout site A stopped increasing and started to decrease approximately 3 h before low tide (Figure 7) or after the third hour from the start of group formation as can be seen in Figure 5. This phenomenon occurred because animals tended to leave the closest site A and join other haulout sites (Figure 1b) towards low tide, most likely to avoid being left too far away from the water as the tide ebbed. Indeed, the number of haulout sites increased as the low tide approached because the receding water would disclose more sand dunes, and they would start to decrease just after low tide (Figure 4).

The first groups of grey seals to leave the closest site A would usually swim away. The remaining group of grey seals would join another close site B (Figure 1b), traveling all the way (approximately 100 m or more at a time) on land. They would usually return during the first or second hour after the low tide, and the formation of the haulout group A would start again.

The low CR after low tide might have been related to lower numbers of individuals in the group compared with the group size just after the high tide. It might also have been due to the activity of the grey seals because grey seals spent most of their time on the haulout site resting (Survilienė, pers. obs.). Thus, the second explanation for the variation between group size and CR might simply be that grey seals tended to enter a resting state after they hauled out. Even those animals that played on the edge of haulout sites usually did it temporarily and later hauled out completely. This corresponds with results observed in harbor seals by Wilson (1974) in which play behavior eventually resulted in two playing individuals hauling out on land next to the remaining group and entering a resting state. As a result, there still would be similar numbers of individuals playing since some individuals stop playing and enter the resting state while new ones come on land and begin to play; however, the CR stopped increasing at a certain period or remained stable, while the group size continued to grow.

Data from separate observations from the surrounding haulout sites around site A (Figure 1b) demonstrated that grey seals tended to distribute themselves into separate haulouts (up to five at a time) of 100 (50 to 250) individuals when space was available (Figure 4). This tendency to scatter instead of forming one large group requires further observations. However, the median number of individuals in a group is very close to the overall group size when the highest CR is visible (100 to 200 individuals; Figure 9). Groups of this size might ensure that all individuals can move within or leave the haulout site without a delay and allow animals to socialize and participate in play behavior.

Group Composition and Social Play

During haulout group formation, not only group size but also group structure was changing. Thus, group structure was another factor affecting grey seal social play behavior. The results suggest that CR and play behavior have a positive relationship with the proportion of young individuals in a group, although this relationship is weak. As was previously mentioned, this might be related to the fact that on most occasions, the active players—subadults and juveniles (Table 1)—would haul out at the end of a bout of play, similar to grey seal observations by Wilson (1974). Thus, there was an increase in the proportion of subadult males; however, the number of play behaviors remained the same or started to decrease (Figure 10).

Subadult males were the most active players. In common with many other polygynous species, play fighting turned out to be one of the main elements observed during social play for subadult male grey seals (Survilienė, unpub. material). Young submale grey seals, like other colonial pinniped species (i.e., fur seals [Arnold & Trillmich, 1985; Harcourt, 1991b], Steller sea lions [Gentry, 1974], and elephant seals [Reiter et al., 1978]), were more social and playful than females, most likely because many of the physical and psychological aspects of play help prepare them for future intraspecific combat, whereas females mature early (Pomeroy et al., 1999) and interact less physically (Boness & James, 1979; Burghardt, 2005). One interaction would usually serve as a trigger for other animals to engage in play, especially juveniles, and on some occasions five sequential interactions could be observed. Once two animals would start playing, smaller or equal size individuals began to play beside them. Sometimes, three or four pairs were seen playing beside each other (Survilienė, pers. obs.). This trigger effect was also seen with weaned southern elephant seal pups (Reiter et al., 1978).

Juveniles and subadult females, who are very conspicuous and come only during the second hour of group formation (Figure 11), might be attracted by already playing individuals on shore (e.g., subadult males) because the behavior indicates a safe environment for them to haul out and perhaps meet potential playmates. This may be particularly applicable to subadult females, who exhibited the strongest positive correlation with CR.

The number of adult individuals might have an indirect effect on the number of young individuals. Adults not only formed the core of the group and comprised 80% of the group size most of the time (Figure 8), they were also the first to haul out on land (Survilienė, pers. obs.). However, adult males were rarely seen playing, and no interactions were seen among adult females. Adult females usually spent time resting, occasionally displaying agonistic behavior towards each other over space or checking the environment. It is known that adults are not very playful in general (Fagen, 1981; Burghardt, 2005). Although adults had either a negative relationship (adult females) or no relationship (adult males) with CR and had no direct effect on the CR, given that they formed the majority of the group, they might have served as an attractive factor for the main social play interactants (i.e., young grey seals).

Adult and subadult males together comprised approximately 60% of the group most of the time (Figure 8). It is often stated that segregation of grey seals is due to intersexual competition and niche separation (Breed et al., 2006; Breed, 2008), which lead to different diet, diving, and spatial patterns (Beck et al., 2003a, 2003b, 2003c, 2007; Breed et al., 2009). These hypotheses often disregard social behavior as a potential factor in the formation of aggregations. However, social factors might indeed cause sexual segregation, at least for young grey seals, because subadult male grey seals dominate social play behavior. Social play might be one of the reasons for grey seals to form male-oriented haulout aggregations in which subadult males have a greater likelihood to meet potential playmates (and future rivals). Social play offers a chance to practice fighting skills and might serve as an "attraction" factor for young individuals to join the group. They begin to integrate into the core of the group, but their places will be taken by other individuals in the following year. As was demonstrated in cheetahs (*Acinonyx jubatus*), the amount of contact play is closely related to the number of contacts present in adult behaviors (Caro, 1995). Some subadult males were similar in size to adults and not all played at the beginning of the haulout group formations; thus, these individuals might have already been integrated into the group.

Sexual segregation of grey seals was observed in other areas throughout the UK. Leeney et al. (2010) reported that 80% of grey seals at haulout sites in the Celtic Sea were male; however, they noted that this ratio might be due to the different locations of females such as in caves or regions where prey is more abundant. Similar results were found by Sayer et al. (2012). A high male ratio was also observed on sand banks in Tentsmuir during the molting season (Pomeroy, pers. obs.). Conversely, Kiely et al. (2000) found a considerably higher proportion of females hauled out on the southeastern coast of Ireland. Ruckstuhl & Neuhaus (2000), in their social preference hypothesis, proposed that sexual segregation is caused by social affinities among males. They state that even though similarities in activity budgets and nutritional requirements should be the main forces that lead to segregation of individuals of a particular sex, social interactions should facilitate sexual segregation at least among young male individuals.

Grey seal yearlings and juveniles spend a large amount of time at haulout sites or near them instead of feeding (McConnell et al., 1999; Breed, 2008). Social activities are very important for practicing social skills. Young individuals do not need to prepare for the breeding season; thus, they can spend less time feeding at sea and more time near haulout sites. The high male sex ratio in the closest haulout site A and high subadult male activity during play behavior might suggest that young individuals are attracted to haulouts containing older individuals. The reasons that younger males are attracted to older ones, even though adults rarely participate in play, are unclear. However, research on seal interactions with fishing gear in the Baltic Sea demonstrated that adult male grey seals raiding fishing nets are followed by young grey seals (Königson et al., 2007, 2013). Thus, the development of social behavior may have an important learning benefit.

In summary, the haulout group's composition was related to haulout size. Young animals were attracted to haulout groups of a particular size and structure. They initiated play behavior directly or induced it by their presence. Young individuals could have been attracted by social play behavior because such behavior could indicate a safe environment. Thus, young grey seals played more in larger haulout groups with the possible additional benefits of acquiring social skill interactions with conspecifics and public information for other learning.

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Literature Cited

Almeida, S. S., & Araujo, M. D. (2001). Postnatal protein malnutrition affects play behavior and other social interactions in juvenile rats. *Physiology & Behavior*, *74*, 45-51. http://dx.doi.org/10.1016/S0031-9384(01)00554-6

Almeida, S. S., Tonkiss, J., & Galler, J. R. (1996). Prenatal protein malnutrition affects the social interactions of juvenile rats. *Physiology & Behavior*, *60*(1), 197-201. http://dx.doi.org/10.1016/0031-9384(95)02236-8

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3), 227-267. http://dx.doi.org/10.1163/156853974X00534

Arnold, W., & Trillmich, F. (1985). Time budget in Galapagos fur seal pups: The influence of the mother`s presence and absence on pup activity and play. *Behavior*, *92*, 302-321.

Balcombe, J. (2009). Animal pleasure and its moral significance. *Applied Animal Behaviour Science*, *118*, 208-216. http://dx.doi.org/10.1016/j.applanim.2009.02.012

Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and social play in squirrel monkeys (Saimiri). *American Zoologist*, *14*, 303-315. http://dx.doi.org/10.1093/icb/14.1.303

Beck, C. A., Bowen, W. D., & Iverson, S. J. (2003a). Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology*, *72*, 280-291. http://dx.doi.org/10.1046/j.1365-2656.2003.00704.x

Beck, C. A., Bowen, W. D. O. N., McMillan, J. I. M. I., & Iverson, S. J. (2003b). Sex differences in the diving behaviour of a size-dimorphic capital breeder: The grey seal. *Animal Behavior*, *64*, 1-13. http://dx.doi.org/10.1006/anbe.2002.2284

Beck, C. A., Bowen, W. D., McMillan, J. I. M. I. M., & Iverson, S. J. (2003c). Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. *Journal of Animal Ecology*, *72*, 979-993. http://dx.doi.org/10.1006/anbe.2003.2284

Beck, C. A., Iverson, S. J., Bowen, W. D., & Blanchard, W. (2007). Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: Evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology*, *76*, 490-502. http://dx.doi.org/10.1111/j.1365-2656.2007.01215.x

Bekoff, M. (1974). Social play in coyotes, wolves and dogs. *Bioscience*, *24*, 225-230. http://dx.doi.org/10.1093/icb/14.1.323

Bekoff, M. (2001). Social play behaviour: Cooperation, fairness, trust, and the evolution of morality. *Journal of Consciousness Studies*, *8*(2), 81-90.

Bell, H. C., Pellis, S. M., & Kolb, B. (2010). Juvenile peer play experience and the development of the orbitofrontal and medial prefrontal cortices. *Behavioural Brain Research, 207*(1), 7-13. http://dx.doi.org/10.1016/j.bbr.2009.09.029

Berger, J. (1979). Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): An ecological interpretation. *Zeitschrift für Tierpsychologie*, *50*, 188-200. http://dx.doi.org/10.1111/j.1439-0310.1979.tb01026.x

Boness, D. J., & James, H. (1979). Reproductive behaviour of grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology*, *188*(4), 477-500. http://dx.doi.org/10.1111/j.1469-7998.1979.tb03430.x

Brasseur, S., Creuwels, J., Vanderwerf, B., & Reijnders, P. (1996). Deprivation indicates necessity for haul-out in harbour seals. *Marine Mammal Science*, *12(4)*, 619-624. http://dx.doi.org/10.1111/j.1748-7692.1996.tb00077.x

Breed, G. A. (2008). *State-space analyses indicate experience, prey availability, competition, and reproductive status drive foraging behaviour in a top marine predator* (Unpublished doctoral dissertation). Dalhousie University, Halifax, Nova Scotia.

Breed, G. A., Bowen, W. D., McMillan, J. I., & Leonard, M. L. (2006). Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Zoological Society of London B*, *273*, 2319-2326. http://dx.doi.org/10.1098/rspb.2006.3581

Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D., & Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology*, *90*(11), 3209-3221. http://dx.doi.org/10.1890/07-1483.1

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge: MIT Press.

Caro, T. (1995). Short-term costs and correlates of play in cheetahs. *Animal Behaviour*, *49*, 333-345. http://dx.doi.org/10.1006/anbe.1995.9999

Da Silva, J., & Terhune, J. (1988). Harbour seal grouping as an anti-predator strategy. *Animal Behaviour*, *36*, 1309-1316. http://dx.doi.org/10.1016/S0003-3472(88)80199-4

Davies, J. L. M. A. (1949). Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire. *Proceedings of the Zoological Society of London*, *119*(3), 673-692. http://dx.doi.org/10.1111/j.1096-3642.1949.tb00896.x

Drea, C. M., Hawk, J. H., & Glickman, S. E. (1996). Aggression decreases as play emerges in infant spotted hyaenas: Preparation for joining the clan. *Animal Behavior*, *51*, 1323-1336. http://dx.doi.org/10.1006/anbe.1996.0136

Fagen, R. (1981). *Animal play behavior*. Oxford, UK: Oxford University Press.

Fagen, R., & Fagen, J. (2004). Juvenile survival and benefits of play behavior in brown bears, *Ursus arctos*. *Evolutionary Ecology Research*, *6*, 89-102.

Gentry, R. L. (1974). The development of social behavior through play in Steller sea lion. *American Zoologist*, *14*, 391-403. http://dx.doi.org/10.1093/icb/14.1.391

Graham, K. L., & Burghardt, G. M. (2010). Current perspectives on the biological study of play: Signs of progress. *The Quarterly Review of Biology*, *85*(4), 155-183. http://dx.doi.org/10.1086/656903

Harcourt, R. (1991a). Survivorship costs of play in the South American fur seal. *Animal Behaviour*, *42*, 509-511. http://dx.doi.org/10.1016/S0003-3472(05)80055-7

Harcourt, R. (1991b). The development of play in the South American fur seal. *Ethology*, *88*, 191-202. http://dx.doi.org/10.1111/ j.1439-0310.1991.tb00274.x

Harcourt, R. G., Kingston, J. J., Cameron, M. F., Waas, J. R., & Hindell, M. A. (2007). Paternity analysis shows experience, not age, enhances mating success in an aquatically mating pinniped, the Weddell seal (*Leptonychotes weddellii*). *Behavioral Ecology and Sociobiology*, *61*, 643-652. http://dx.doi.org/10.1007/s00265-006-0294-x

Hewer, H. R. (1964). The determination of age, sexual maturity, longevity and a life-table in the grey seal (*Halichoerus grypus*). *Proceedings of the Royal Society of London B*, *142*, 593-624. http://dx.doi.org/10.1111/j.1469-7998.1964.tb04631.x

Hol, T., Van den Berg, C. L., Van Ree, J. M., & Spruijt, B. M. (1999). Isolation during the play period in infancy decreases adult social interactions in rats. *Behavioural Brain Research*, *100*(1-2), 91-97. http://dx.doi.org/10.1016/S0166-4328(98)00116-8

Hunter, S. A., Bay, M. S., Martin, M. L., & Hatfield, J. S. (2002). Behavioral effects of environmental enrichment on harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*). *Zoo Biology*, *21*, 375-387. http://dx.doi.org/10.1002/zoo.10042

Karlsson, O., Hiby, L., Lundberg, T., Jüssi, M., Jüssi, I., & Helander, B. (2005). Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. *Ambio*, *34*(8), 628-634. http://doi.org/10.1579/0044-7447-34.8.628

Kiely, O., Lidgard, D., McKibben, M., Connolly, N., & Baines, M. (2000). *Grey seals: Status and monitoring in the Irish and Celtic Seas* (Maritimes Ireland/Ciales INTERREG Report, No. 3).

King, J. E. (1983). *Seals of the world*. Ithaca, NY: Cornell University Press.

Königson, S., Fjälling, A., & Lunneryd, S. (2007). Grey seal induced catch losses in the herring gillnet fisheries in the northern Baltic. *NAMMCO Scientific Publications*, *6*, 203-213. http://dx.doi.org/10.7557/3.2735

Königson, S., Fjälling, A., Berglind, M., & Lunneryd, S. (2013). Male gray seals specialize in raiding salmon traps. *Fisheries Research*, *148*, 117-123. http://dx.doi.org/10.1016/j.fishres.2013.07.014

Kovacs, K. M. (1987). Maternal behaviour and early behavioural ontogeny of grey seals (*Halichoerus grypus*) on the Isle of May, UK. *Journal of Zoology*, *213*, 697-715. http://dx.doi.org/10.1111/j.1469-7998.1987.tb03735.x

Leeney, R. H., Broderick, A. C., Mills, C., Sayer, S., Witt, M. J., & Godley, B. J. (2010). Abundance, distribution and haul-out behaviour of grey seals (*Halichoerus grypus*) in Cornwall and the Isles of Scilly, UK. *Journal of Marine Biological Association of the United Kingdom*, *90*, 1033-1040. http://dx.doi.org/10.1017/S0025315409991512

Lehner, P. N. (1996). *Handbook of ethological methods*. Cambridge, UK: Cambridge University Press.

Lidgard, D. C., Boness, D. J., & Bowen, W. D. (2001). A novel mobile approach to investigating mating tactics in male grey seals (*Halichoerus grypus*). *Journal of Zoology, London*, *255*, 313-320. http://dx.doi.org/10.1016/j.yhbeh.2007.10.003

Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge, UK: Cambridge University Press. http://dx.doi.org/10.1017/cbo9781139168342

McConnell, B. J., Fedak, M. A., Lovell, P., & Hammond, P. S. (1999). Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, *36*, 573-590. http://dx.doi.org/10.1578/AM.32.1.2006.58

Mellish, J. E., Iverson, S. J., & Bowen, W. D. (1999). Variation in milk production and lactation performance in grey seal and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, *72*(6), 677-690. http://dx.doi.org/10.1086/316708

Mellish, J. E., Calkins, A. G., Christen, D. R., Horning, M., Lorrie, D. R., & Atkinson, S. K. (2006). Temporary captivity as a research tool: Comprehensive study of wild pinnipeds under controlled conditions. *Aquatic Mammals*, *32*(1), 58-65. http://dx.doi.org/10.1578/AM.32.1.2006.58

Pellis, S. M., & Pellis, V. C. (1998). Play fighting of rats in comparative perspective: A schema for neurobehavioral analyses. *Neuroscience & Biobehavioral Reviews*, *23*, 87-101. http://dx.doi.org/10.1016/S0149-7634(97)00071-7

Pellis, S. M., Pellis, V. C., & Bell, H. C. (2010). The function of play in the development of the social brain. *The American Journal of Play*, *2*, 278-296.

Pomeroy, P. P., Twiss, S. D., & Redman, P. (2000). Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology*, *106*, 899-919. http://dx. doi.org/10.1046/j.1439-0310.2000.00610.x

Pomeroy, P. P., Anderson, S., Twiss, S. D., & McConnell, B. J. (1994). Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology*, *233*(3), 429-447. http://dx.doi.org/10.1111/j.1469-7998.1994.tb05275.x

Pomeroy, P. P., Fedak, M. A., Rothery, P., & Anderson, S. (1999). Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, *68*, 235-253. http://dx.doi.org/10.1046/j.1365-2656.1999.00281.x

Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, *3*, 337-367. http://dx.doi.org/10.1007/BF00303199

Riedman, M. (1990). *The pinnipeds: Seals, sea lions, and walruses*. Berkeley: University of California Press.

Ruckstuhl, K. E., & Neuhaus, P. (2000). Sexual segregation in ungulates: A new approach. *Behavior*, *137*, 361-377. http://dx.doi.org/10.1163/156853900502123

Ruddell, S. J. S., Twiss, S. D., & Pomeroy, P. P. (2007). Measuring opportunity for sociality: Quantifying social stability in a colonially breeding phocid. *Animal Behaviour*, *74*, 1357-1368. http://dx.doi.org/10.1016/j.anbehav.2007.01.024

Sayer, S., Hockley, C., & Witt, M. J. (2012). *Monitoring grey seals (*Halichoerus grypus*) in the Isles of Scilly during the 2010 pupping season* (Natural England Commissioned Reports #103).

Schusterman, R. J., Balliet, R. F., & John, S. S. (1970). Vocal displays under water by the gray seal, the harbor seal, and the Steller sea lion. *Psychonomic Science*, *18*(5), 303-305. http://dx.doi.org/10.3758/BF03331839

Sjöberg, M., & Ball, J. P. (2000). Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: Bathymetry or central-place foraging? *Canadian Journal of Zoology*, *78*, 1661-1667. http://dx.doi.org/ 10.1139/z00-108. http://dx.doi.org/10.1139/z00-1088

Special Committee on Seals (SCOS). (2010). *Scientific advice on matters related to the management of seal populations*. St Andrews, UK: SCOS, Sea Mammal Research Unit.

Terhune, J. M., & Brillant, S. W. (1996). Harbour seal vigilance decreases over time since haul out. *Animal Behavior*, *51*, 757-763. http://dx.doi.org/10.1006/anbe.1996.00800

Thompson, D., & Härkönen, T. (2008). *Halichoerus grypus*, In International Union for Conservation of Nature (IUCN), *IUCN red list of threatened species, Version 2013.2*. Retrieved from www.iucnredlist.org

Trezza, V., Baarendse, P. J. J., & Vanderschuren, L. J. M. J. (2010). The pleasures of play: Pharmacological insights into social reward mechanisms. *Trends in Pharmacological Sciences*, *31*(10), 463-469. http://doi.org/10.1016/j.tips.2010.06.008

Twiss, S. D., Culloch, R., & Pomeroy, P. P. (2012). An in-field experimental test of pinniped behavioral types. *Marine Mammal Science*, *28*(3), E280-E294. http://dx.doi.org/10.1111/j.1748-7692.2011.00523.x

Twiss, S. D., Pomeroy, P. P., & Anderson, S. S. (1994). Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology*, *233*(4), 683-693. http://dx.doi.org/10.1111/j.1469-7998.1994.tb05374.x

Twiss, S. D., Thomas, C., Poland, V., Graves, J. A., & Pomeroy, P. P. (2007). The impact of climatic variation on the opportunity for sexual selection. *Biology Letters*, *3*(1), 12-15. http://dx.doi.org/10.1098/rsbl.2006.0559

Vanderschuren, L. J. M. J. (2010). How the brain makes play fun. *American Journal of Play*, *2*, 315-337.

Vanderschuren, L. J. M. J., Stein, E. A., Wiegant, V. M., & Van Ree, J. M. (1995). Social play alters regional brain opioid receptor binding in juvenile rats. *Brain Research*, *680*, 148-156. http://dx.doi.org/10.1016/0006-8993(95)00256-P

Watts, P. (1996). The diel hauling-out cycle of harbour seals in an open marine environment: Correlates and constraints. *Journal of Zoology*, *240*, 175-200. http://dx.doi.org/10.1111/j.1469-7998.1996.tb05494.x

Wilson, S. (1974). Juvenile play of the Common seal (*Phoca vitulina vitulina*) with comparative notes of the grey seal (*Halichoerus grypus*). *Behavior*, *48*, 37-60. http://dx.doi.org/10.1163/156853974X00246