
**Personality and place: do fine-scale pupping site preferences relate to
behavioural types in lactating grey seals?**

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Abstract

Animal personalities can have differential context-dependent fitness consequences, leading to different personality types benefitting from different habitats. If individuals within the same population rely on different habitats, any environmental change could have important effects on population dynamics and resilience, due to reduction in behavioural variation. This is becoming increasingly pressing as climate change and habitat loss continue to be the biggest threats to species globally. This study investigated potential links between personality and pupping site choice in grey seals. Female grey seals have different stress-coping styles, with some being more proactive and some more reactive. Between 2013 to 2017, a subset of grey seal females, whose stress-coping style was known, were followed during the annual breeding season. The topography, substrate and social density of their selected site was regularly sampled throughout their lactation. It was expected seals would select different pupping site environments based on their stress-coping style potentially in an effort to optimise fitness. However, this was found not to be the case. Stress-coping style had no influence on an individual's topography and substrate, as well as the number of neighbouring females. There was a small negative relationship between stress-coping style and the wider density of conspecifics, although not very significant. This suggests there is another potentially more important influence on social density preference. Overall, these results could be positive regarding climate change, as grey seal populations may be able to cope with potential habitat changes, as well as have increased population diversity and therefore resilience.

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List of Abbreviations

AICc	Akaike Information Criterion (p.12)
CID	Consistent individual differences (p.4)
GLMM	General Linear Mixed Models (p.11)
HRV	Heart rate variability (p.9)
MCA	Multivariate Correspondence Analysis (p.12)
NA	Not available (p.11)
<i>Ne</i>	Effective population size (p.22)
SMRU	Sea Mammal Research Unit (p.8)

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1. Introduction

In recent decades there has been a growing interest in the significance of consistent individual differences (CIDs) in behaviour, with growing acknowledgement of the existence of ‘animal personality’ (also known as behavioural syndromes, coping styles and temperament) (Gosling, 2001; Koolhaas et al., 1999; Réale et al., 2007; Sih et al., 2004). There is now evidence of ‘personalities’ across a wide range of taxa, including cnidarians, arthropods, fish, lizards, birds and mammals (Batabyal and Thaker, 2019; Dingemanse et al., 2004; Hensley et al., 2012; Jolles et al., 2019; Riechert and Hedrick, 1993). The adaptive value and influence on individual fitness of different personality types has generated much speculation (Sih et al., 2004; Wolf and Weissing, 2010). Evolution based on natural selection would suggest over time animals’ behaviour will become optimised according to selective context. However, the consistency of personality traits often means some behaviours are beneficial in one context and detrimental in another (Sih et al., 2004; Wolf and Weissing, 2010). The widespread nature of CIDs along with the influence of an individual’s personality on its growth, fecundity, foraging success, and interactions with its environment, suggests individual personality has strong adaptive value or that limited plasticity restricts evolutionary processes (Biro and Stamps, 2008; Dingemanse and Réale, 2005; Dingemanse and Wolf, 2013; Réale et al., 2007; Réale and Dingemanse, 2011). Either way understanding the differential fitness consequences for an individual can have important implications on the evolution of personalities as well as population and species dynamics.

The term ‘animal personality’ refers to individual differences in animal behaviour which are consistent across time and situations/contexts, for example an individual may be highly aggressive towards both prey and conspecifics (Riechert and Hedrick, 1993; Wolf and Weissing, 2012). These consistent behaviours are called personality traits. It is possible for multiple personality traits to be correlated across contexts and situations, creating a behavioural syndrome, with specific combinations forming different personality types (Sih et al., 2004). One aspect of personality that has been widely studied, at least in laboratory studies, is individual stress-coping style (the proactive-reactive axis; Koolhaas et al., 1999). An individual’s ability to cope with stress has been correlated with a suite of other personality traits, including boldness, plasticity, dispersal, and aggression (Koolhaas et al., 2010, 1999). More proactive individuals tend to be bolder, more aggressive, disperse faster and readily form routines. On the other hand, more reactive individuals tend to be shyer, less aggressive, disperse slower and are more behaviourally flexible (Koolhaas et al., 1999). Such fundamental differences in coping style are likely to have profound influences on how individuals interact with their biotic and abiotic environment. However, there have been few studies which have examined coping styles in wild populations.

Grey seals (*Halichoerus grypus*) are capital breeders, whose annual breeding season is spent ashore in large colonies, usually returning to the same colony each year. This behaviour, combined with limited movement on land, has allowed extensive long-term behavioural observations of individuals. Previous work has identified CIDs in the behaviour of lactating female grey seals which fit the proactive-reactive axis (Shuert et al., 2020; Twiss et al., 2020, 2012). Proactive females consistently spent more time alert, both before and after exposure to a mildly alarming stimulus. Reactive females, however, spent more time resting and adjusted behaviour in response to stressors, becoming more alert after disturbance (Shuert et al., 2020; Twiss et al., 2012). Proactive females likely spent more time alert to mitigate overall stress response and reactive females are more behaviourally flexible, so can adjust to stressors accordingly (Shuert et al., 2020). As capital breeders, females need to spend most of their time resting to conserve their energy and optimise energy transfer to their pup (fig.1; Anderson and Harwood, 1985). It would be expected that

reactive females would have the fitness advantage over proactive females through higher energy transfer to their pup. Despite this both coping styles coexist in the same population and many wild populations contain multiple personality types. This poses the much-discussed question: how is the variation in personality types maintained?

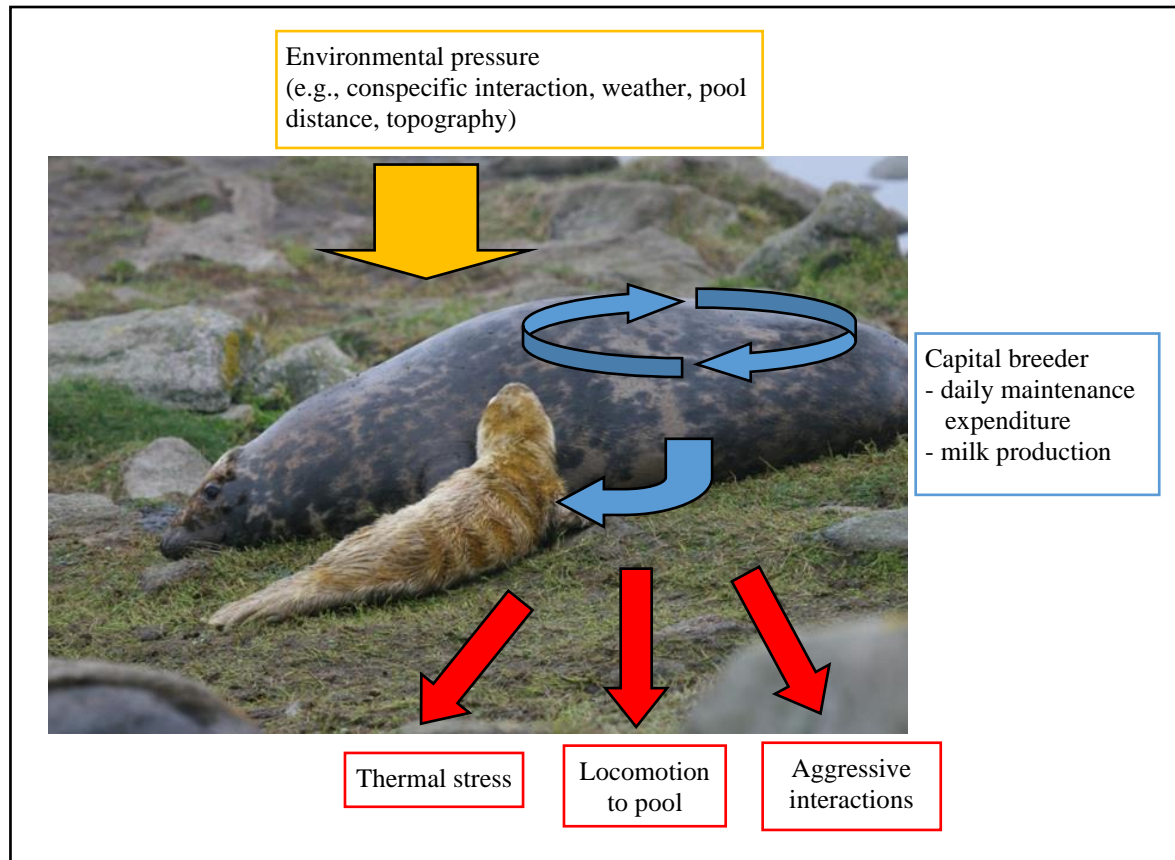


Figure 1: Influence of environmental pressure on the energy expenditure of lactating grey seals. The yellow arrow indicates the effect of environmental pressure on grey seal mothers. The blue arrows represent the optimised energy flow of the closed system of capital breeders, which allows provisioning of the mother and optimised energy transfer to the pup. The red arrows represent excess energy expenditure caused by the example environmental pressures, which reduces energy available for self and pup. Photo taken by Dr Sean Twiss.

One theory is that the adaptive value of personality is context- or situation-dependent (Dingemanse et al., 2004; Smith and Blumstein, 2008; Wolf and Weissing, 2010). Temporal changes in an individual's local environment can alter the fitness consequences of an individual's personality type. For example, in years with fewer resources, more aggressive female great tits (*Parus major*) performed better overall. However, when resources were abundant, less aggressive females outperformed the more aggressive individuals, as high aggression led to increased mortality (Dingemanse et al., 2004). Additionally, in a heterogenous environment, spatial variation of an environment can allow for multiple personality types to fit a niche (Pearish et al., 2013). It is widely accepted that an individual's behaviour can influence an animal's environment through processes including locating a suitable habitat (habitat-matching) or creating their own environment (niche construction) (Edelaar et al., 2008; Stamps and Groothuis, 2010). It is possible that specific environments may confer an advantage to specific personality types, with individuals either relocating to these environments or having reduced survival if restricted to sub-optimal habitats for their

personality type (Monestier et al., 2015; Santicchia et al., 2018). Multiple studies have already identified differential fitness consequences for different personalities according to their environment. The stress-coping style of female roe deer (*Capreolus capreolus*) combined with differential habitat selection was found to impact either positively or negatively fawn survival and individual fitness (Monestier et al., 2015). A similar phenomenon may account for the coexistence of proactive and reactive female grey seals. For grey seal mothers, both coping styles experience the same population level fitness outcomes in terms of mean pup mass gain (Twiss et al., 2020). However, there was more variation in this short-term fitness measure in reactive females, suggesting some females performed well and others performed poorly. By contrast proactive females were more uniform in their mass transfer to their pups. It was suggested that reactive females may employ phenotype-environment matching (Twiss et al., 2020). As female grey seals rely on their fat stores to provision their pups and themselves during the breeding season, this creates physiological constraints on fitness (fig.1; Fedak and Anderson, 1982). Pupping site selection plays an important role in reducing these constraints, due to limited pup mobility reducing later habitat adjustment. Higher than average heat output during lactation creates thermal stress in female seals, particular during hotter, drier weather (Twiss et al., 2002). Selection of sites near to fresh water relieves thermal stress and limits time spent travelling, in turn reducing energy expenditure and the chance of mother-pup separation (Twiss et al., 2000a; Twiss et al., 2003, 2002). Multiple environmental factors influence female proximity to a pool. Topography differences can alter the number of available pools and ease of access, affecting the time spent resting with their pup (Twiss et al., 2000a). Weather can not only affect pool availability, but shaded sites and rain can reduce female dependence on pools (Redman et al., 2001). This shared dependence on physical conditions creates a non-random distribution of seals (Twiss et al., 2003). Sites nearer to pools are usually correlated with higher numbers of aggressive interactions due to higher conspecific density, leading to higher energetic costs (Stephenson et al., 2007). When selecting a pupping site, females must trade off the energetic costs of traveling to a pool with energetic costs of conspecific interaction in order to balance energy conservation and reduced exposure to environmental stressors. As proactive individuals tend to be bolder and more aggressive, these individuals may choose sites closer to pools as they may be more able to cope with aggressive conspecifics. They may also have more uniform site selection due to lower behavioural flexibility. Reactive individuals on the other hand may be less uniform in their site choice due to their increased behavioural flexibility, matching their pupping site selection according to their context and situation as part of a high risk-high rewards strategy (Twiss et al., 2020). Some reactive females may fail to select an optimal site reducing their mass transfer efficiency, explaining the variation of daily mass transfer reported (Twiss et al., 2020). Understanding the extent of and mechanisms behind such fine-scale phenotype-environment matching may be critical in understanding population and species fitness outcomes, especially as anthropogenic activity continues to rapidly change environmental conditions globally.

Currently the biggest threats to species globally are anthropogenic changes, such as climate change and habitat destruction. Due to the rapid nature of these changes, animals are expected to respond by adapting to the changes or shift their range to track suitable environmental conditions. There have already been major shifts in global species distributions polewards, likely due to these species tracking climate suitability (Parmesan, 2006). Species-distribution models (SDMs) are widely used to predict species and population responses to environmental change, which can then be used to inform targeted protective and preventative measures (Guisan and Zimmermann, 2000). It is often assumed in SDMs that individuals in a population benefit equally from the same environmental

conditions and so will all respond in the same way to environmental change. Recent studies have challenged this assumption, proving that intraspecific-level SDMs outperform species-level SDMs. When mapping individual spatial use, individuals appear to have different selection strategies and varying degrees of preference for particular conditions (Chardon et al., 2020; Leclerc et al., 2016). If different personalities within a population are better adapted to different spatial and temporal environmental conditions, failure to account for these differences and manage populations accordingly could alter the personality-dynamics within a population. Altering of particular environmental conditions could create a novel selection pressure favouring specific behavioural types. A high level of population biodiversity is vital for population persistence and resilience against stochastic changes (Frankham, 1999, 1995). Behavioural variation, including different personality types, is a form of biodiversity (Anthony and Blumstein, 2000). Loss of particular personality types from populations could make a population more vulnerable to extinction from stochastic events. To better conserve populations, personality may need to be included when predicting population responses (Owen et al., 2017).

This study aims to identify if a grey seal's stress-coping style influences the environment of their chosen pupping site. During 2013-2017, the stress-coping style was identified for a subset of known females pupping on the well-established Isle of May colony (56.1856° N, 2.5575° W; Twiss et al., 2020). The physical and social characteristics of their chosen location throughout their season was recorded. It was expected that as flatter locations are more favourable to reduce energy expenditure via locomotion effort, these sites would be sought after and have a higher density of conspecifics present. As proactive individuals are bolder, they may be better able to cope with more aggressive interactions that accompanies selecting a favoured site with more conspecifics present. Reactive individuals, being shyer, may select a site with fewer conspecifics but in a more strenuous physical environment. They may be unable to cope with the stress of aggressive interactions or may be outcompeted by proactive individuals for sites near pools. Another potential outcome is that reactive individuals may show more variation in their site choice due to increased behavioural flexibility, whereas proactive individuals may be more rigid in their preference. Interactions with weather may influence differential trade-offs between stress-coping styles based on prevailing conditions. Any evidence of environmental preference based on personality in grey seals could have implications for personality dynamics at other grey seal colonies. Different breeding colonies have different substrate and topographical compositions (Stirling, 1975), so may also have different compositions of personality within a population. If environmental change caused by anthropogenic activity favours certain environmental conditions, one personality type may have increased fitness over another, altering population dynamics and resilience. Therefore, understanding personality-driven habitat choice may allow for more accurate prediction of how different populations may be affected by environmental change.

The main objectives were to identify whether stress-coping style had any influence on the topography, substrate and conspecific density of pupping sites chosen by lactating grey seals. Additionally, if weather conditions had any influence on this relationship.

2. Methods

2.1 Study site and data collection

Between late October to early December on the Isle of May, female grey seals will come ashore to give birth to, raise and wean a single pup, often within 18 days. Females will come ashore throughout this time, creating a turn-over of females throughout the season. During this time, females are mostly sedentary with occasional commutes to and from pools of water (Twiss et al., 2000a). The Isle of May is highly heterogenous, with

areas ranging from grass to mud to completely made of rock with a range of different topographies (fig.2). High inter-annual site fidelity means that individual females can be identified returning to the colony for multiple years, although not necessarily every year (Pomeroy et al., 1994). These individuals can be identified using flipper tags and/or pelage patterns. Between the years 2013 and 2017, a range of data was obtained on a subset of known females as part of a long-term study conducted by the Sea Mammal Research Unit (SMRU) (Smout et al., 2020). When present during a breeding season, these females were captured and weighed twice: once at the beginning of lactation and once towards the end of lactation, allowing estimation of daily mass loss (kg/day). As female grey seals fast during breeding season, rate of maternal mass loss can be used to estimate rate of energy expenditure (Twiss et al., 2012). During handling events, heart rate monitors were applied during the first capture and recovered during the second capture as part of another study investigating stress-coping styles in grey seals (Twiss et al., 2020). Birth date and pup sex was recorded during first capture. Pup mass was recorded during the first and second captures so pup mass gain could be calculated. Regular video focals were recorded following individual females throughout lactation. Focal video observations were recorded using two high-definition video recorders (Panasonic HC-V700 1920x1080 resolution with 46x zoom; Panasonic Corp and a Canon LEGRIA HF R36 HD camcorder with a 32x optical zoom). The video recorders were placed 50m away from the focal seal, with observers hidden from seals. The general protocol for video focals began with the camera zoomed out, allowing observation of the wider context, then zoomed in until the focal seal was approximately 1/4 to 1/5 width of the frame. Each female was recorded multiple times throughout their lactation period to capture any possible diurnal variation in behaviour, as well as changes in behaviour across the lactation period. Females could alter site choice as their pup ages, for example.



Figure 2: A and B are examples of areas used by grey seals on the Isle of May during the breeding season, showcasing the variety of substrates and topographies used by females. Photos taken by Dr Sean Twiss.

2.2 Stress-coping style assignment

Resting heart rate variability (HRV) can be reliably used to identify an individual's stress-coping style (Koolhaas et al., 2010, 1999). Using the heart rate data recovered from the females, the average across-season variation in successive inter-beat intervals while resting was calculated for each individual as part of another study (Twiss et al., 2020). Reactive individuals have a higher HRV, due to relatively higher parasympathetic activity, whereas proactive individuals have a lower HRV due to higher sympathetic activity (Koolhaas et al., 2010, 1999). The study by Twiss et al (2020) identified that an

individual's resting HRV was consistent throughout the breeding season. Some individuals' resting HRV could be recorded across multiple breeding seasons (table 1) and these were found to be consistent across years. Behavioural observations have already revealed CIDs in grey seal behaviour which fit the proactive-reactive axis (Twiss et al., 2020, 2012). These behavioural-based assignments match the findings of resting HRV, making resting HRV a reliable method for indicating a female grey seal's stress-coping style. More detail on how resting HRV was derived for each individual can be found at Twiss et al.'s (2020) paper.

Table 1: The number of years (between 2013 to 2017) individual seals were recorded for.

Number of years data recorded	Number of seals
1	32
2	15
3	6
4	2
5	1

2.2 Environmental data extraction

Videos were decoded by the same observer (SM) employing a scan sampling protocol and a bespoke Visual Basic for Applications Macro in Microsoft Excel to record behaviours. Sampling interval was initially 5 minutes; however, this was increased to sampling every 10 minutes due to little seal movement in over such short time periods. Observations were conducted randomly in regard to individual and the individual's stress-coping style was unknown *a priori*. Some videos contained more than one individual, so were decoded as a separate sample for each individual present. Environmental information was split into physical environment and social environment. Physical environment was further divided into substrate and topography. Due to the highly heterogenous nature of the Isle of May, physical environment was determined based on the surface within a radius two body lengths of the focal individual. Topography was recorded as the ordinal categorical variables flat, moderate or rough. Substrate was divided into the categories grass, mud and rock. If more than one of these categories was present within the individual's radius, the more predominant category was chosen (i.e. accounted for more than 60% of the radius). Topography and substrate have already been found to affect female movement and likely energy expenditure (Twiss et al., 2000a). When comparing sites, females on predominantly rough, rocky terrain were less able to gain sites closer to water so made fewer, longer trips to water. However, females on predominantly flatter terrain were likely to access a site closer to water, allowing shorter, more frequent trips (Twiss et al., 2000a). Physical environment therefore clearly plays an important role in balancing energy expenditure via thermal stress and locomotion, resulting in different behavioural strategies. Social density of conspecifics can also create increased stress for lactating females. As lactating females tend to maintain 1.5 body lengths between themselves and conspecifics due to high levels of aggression (Twiss et al., 2000a), social density was split into two measurements to account for neighbour density and wider density. The number of neighbouring seals was measured by the number of females, pups and males less than 2m of the focal individual (using seal body lengths as an estimate for metres; adult female body length is approximately 1.8 metres). Wider conspecific density was measured as the number of females, pups and males between 2m to 5m from the focal individual. The zoom level of the camera was also recorded as widths in seal body lengths to account for samples where individuals further from the individual could not be seen and accounted for. High conspecific density has been correlated with increased aggressive

interactions (Stephenson et al., 2007). As higher conspecific densities are also located around pools, travelling to and from water can be a source of stress (Redman et al., 2001; Stephenson et al., 2007; Twiss et al., 2002). Additionally, harassment from males has been found to affect maternal attendance (Boness et al., 1995). Females which travel further to pools are also more likely to encounter male harassment (Twiss et al., 2000a). Therefore, the level and dynamics of social density in a selected pupping site may be different according to stress-coping style.

Weather conditions can alter thermal stress and frequency of trips to pools. During hotter, drier weather females spent more time in locomotion to and from pools due to increased thermal stress (Twiss et al., 2002). Females may select their environment based on prevailing weather conditions. These conditions were recorded per focal sample based on visual indications of raining or dry (rain/dry) and sunny or shaded (sun/shade) prevailing conditions. During observations, it was noted that some females engaged in a ‘corralling’ behaviour. Pups of these females would be located in a corner/crevice or against a high-raised surface (such as a wall or sheer rock face), with the mothers in front of them as if corralling them. As females could potentially perform this based on their environment or as a method of reducing stress levels by physically protecting their pup, the behaviour was included in the study. Females tended to corral or not for the duration of a focal video, therefore, it was recorded as whether a female performed this behaviour during a video or not. Pool access is important for females to regulate thermal stress, is related to topography and substrate, and affects social density (Redman et al., 2001; Stephenson et al., 2007; Twiss et al., 2000a; Twiss et al., 2002). Female proximity to pool during each sample was recorded in body lengths and whether the female was in a pool or not. If a pool was not visible within the sample, pool proximity was recorded as ‘Not available’ (NA). Proximity of the focal female to her pup (mother-pup proximity) was recorded in body lengths, with samples where the pup was out of sight recorded as ‘POOS’ and mother out of sight as ‘MOOS’. Orientation of mother and pup was simplified into whether the pup was in the mother’s line of sight or not, determined by if the mother could see her pup without moving her head.

2.4 Statistical Analysis

All statistical analysis was conducted using R 4.0.4 (R Core Team, 2021). Only samples for where individual resting HRV data, pup sex and birth date were available were used in analysis. Samples where the mother was out of sight or the zoom level was above six body lengths were removed. The environmental conditions of a subset of 56 individual females were investigated, with 723 focals and 6406 samples in total, with some females recorded across multiple years (table 1). Average resting HRV was z-transformed. General Linear Mixed Models (GLMM) were used to investigate potential effects of stress-coping style (indicated by resting HRV) on an individual’s pupping environment selection using the ‘lme4’ package (Bates et al., 2015). Variables were checked for collinearity using the package ‘GGally’ (Schloerke et al., 2021). The number of males in both social density measures were left out of analysis due to a high number of zero values. The number of females within 2m and number of pups within 2m were strongly correlated, as were the number of females between 2m and 5m and the number of pups between 2m and 5m. Therefore, only the number of females at both distances were used as these were not correlated and the main form of social stress likely comes from female-female conflict. Six common potential predictors were used in all environmental (physical and social) models. Pup age in days, which was calculated using sample date and birthdate, as female behaviour may change depending on the pup’s age (Kovacs, 1987). Pup sex as some studies have suggested females may invest in pups differentially according to sex (Anderson and Fedak, 1987). Year to account for annual variation. Z-

transformed resting HRV was included as an indicator of stress-coping style. Finally, any potential differential effects of weather on pupping site environment according to stress-coping style were detected by investigating any potential interactions with rain/dry and sun/shade as response variables. Two random effect variables were used. Individual ID alone to account for variation in individuals within the population and the effects of the Focal nested within individual ID (ID:Focal) to account for similarity of measures within focals due to typically limited movement of seals over time scales of a few hours. For each response variable, full models were fitted using all potential predictor variables and alternate models with all possible combinations of predictor variables were computed using the function 'dredge' from the R package 'MuMIn' (Barton, 2020). The model with the lowest corrected Akaike Information Criterion (AICc) was retained as the 'best model'. Other models were also retained and examined as part of a confidence set which were within $\Delta AICc \leq 6$ and were the simplest models within the initial subset (Richards, 2008). Null models were also provided for comparison if not within the confidence set.

Topography and substrate categories were initially converted into binomial variables. The response variable was whether the individual was found on a specific substrate or topography category or not in a sample. For example, one response variable was whether the individual was on rock or not. This was repeated for the substrate categories grass and mud and the topography categories rough, moderate and flat. Full models included the six common predictor variables plus the number of females within 2m and between 2 to 5m, as social density may have potential interactions affecting physical environment choice. The full model used the binomial family and logit link response. Additionally, to summarise the spread of substrate and topography combinations for each focal into linear variables, a Multivariate Correspondence Analysis (MCA) was applied using the package 'PCAmixdata' (Chavent et al., 2017). A varimax orthogonal rotation was applied so the substrate and topography variables aligned with the axes (x-line = 0, y-line = 0) (fig.3). Axes were labelled 'grassiness' and 'roughness'. The coordinates for each individual focal were then used to fit the model, with either grassiness or roughness acting as the response variable. The same process was followed as described above for fitting the GLMMs and selecting the best model(s). The same predictors as the binomial topography and substrate models were used. As some individuals were recorded over multiple years (table 1), repeatability of the grassiness and roughness scores within a population and an individual was tested using the package 'rptR' (Schielzeth et al., 2016). A Mann-Whitney U test was conducted for any variable with significant repeatability to test for significant difference in repeatability for pro- and reactive females.

To test for any effects of stress-coping style on social environment, GLMMs were fitted using the response variables of the number of females less than 2m and the number of females between 2m to 5m. The six common potential predictor variables were included, with the addition of substrate, topography, sun/shade and rain/dry, as these have been shown to affect female density in other studies (Stephenson et al., 2007; Twiss et al., 2000a; Twiss et al., 2002). In addition, the number of females between 2m to 5m was used as a predictor variable for the response variable of the number of females within 2m, and vice versa, due to the lack of correlation between the two. Although proximity to pool has been shown to affect social density (Stephenson et al., 2007), most video angles did not allow detection of nearby pools leaving only 1159 samples with data for pool proximity. Therefore, pool proximity was not used in analysis.

Corralling behaviour was recorded for 594 focals. Due to corralling behaviour already being a binomial variable, the full model was fitted using the binomial family and logit link response. In addition to the six common predictor variables, topography,

substrate, the number of females within 2m and the number of females between 2m and 5m were used. It is possible that different physical and social environments may expose pups to more threats. For example, higher conspecific density may expose pups to attacks from other females (Stephenson et al., 2007). Therefore, mothers may respond by guarding their pup in an enclosed area.

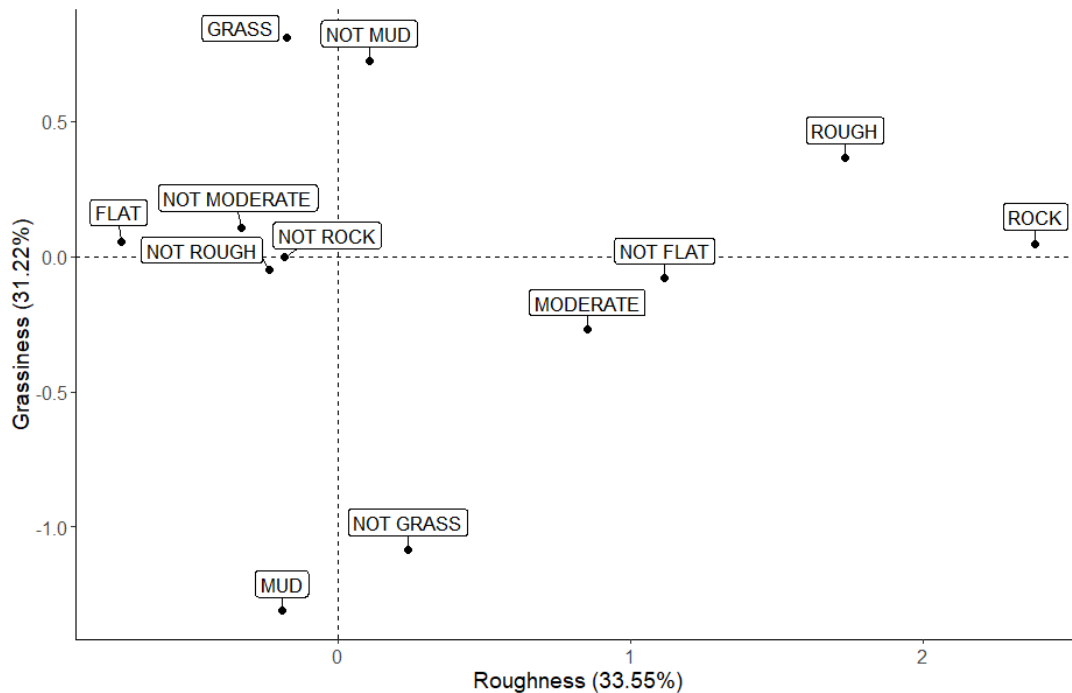


Figure 3: MCA plot with varimax orthogonal rotation applied. Variables included are substrate (rock, grass and mud) and topography (rough, moderate and flat) as binomial factors.

2.5 Ethical statement

All animal handling procedures when deploying the heart rate monitors conformed to the UK Animals (Scientific Procedures) Act, 1986 and were performed in collaboration with the Sea Mammal Research Unit (University of St Andrews) operating under UK Home Office project license #60/4009. This study is reusing existing footage so does not need to be approved by the Durham University Animal Welfare Ethical Review Board. Reusing footage ensures the maximum amount of information is gained and none of the resources available are wasted, whilst also reducing the amount of stress caused to wild seals.

3. Results

3.1 Physical Environment

Stress-coping was not found to have an effect on any of the substrate or topography response variables, with resting HRV not retained in all but one of the models in the confidence set (table 2). The analysis of variables which influenced focal seals occupancy of rocky substrate generated nine plausible alternative models using the criteria for retention within the confidence set. This confidence set includes the null model and therefore little inference can be drawn about factors that influence the use of rocky versus non-rocky

locations. In addition, the alternate models tended to contain a single parameter and all of the parameters in the full model are featured within the confidence set. The best model is presented in table 2 and retained Sun/Shade as the only predictor. However overall, the analysis was unable to produce a convincing model of the factors which influence use of rocky locations. Seven models were retained in the confidence set for grass as a binary response variable. Local female density within 2m and Pup Age featured in all of these models as well as the best model (table 2) where they show a negative relationship with occupancy on grass sites (table 3). Lower close proximity female density and younger pups tend to relate to grassy sites. The analysis of factors influencing individual occupancy of mud also showed female density within 2m having a positive effect on mud as a response variable, featuring within the two models retained in the confidence set and the best model (table 2). A higher density of females within 2m has a positive relationship with occupancy on muddy sites. Pup Age also has a significant positive relationship with muddy site selection in the best model. Muddy sites tend to have older pups and a higher density of females in close proximity (table 3).

In terms of substrate, the female density parameters for less than 2m and between 2m to 5m are the only predictor variables featured in the confidence set for rough and moderate as response variables. In the analysis for rough substrate as the predictor variable, four models were retained in the confidence set including the null model (table 2). The number of females less than 2m had a small positive effect on rough site selection or not (table 3). Factors which influence selection of rough sites or not cannot be determined. Two models have been retained in the confidence set in the analysis of moderate site selection (table 2). The density of females in close proximity is present in both retained models and has a significant positive relationship with whether an individual uses moderate topography or not, such that more females within 2m of the individual are related to moderate site use (table 3). The analysis for flat topography retained seven alternative models with the number of neighbouring females (within 2m) as a contributory parameter in all of them (table 2). A lower density of female neighbours was associated with flat individual locations. Pup age and year also show influence on flat site preference, with older pups more associated with flat sites and a decline in occupation of flat sites from 2013 to 2017 (table 3).

Table 2: Summary of all models retained in the confidence set, including the ‘best’ model (AICc = 0) and the null model, for all substrate (rock, grass and mud) and topography (rough, moderate and flat) variables investigated. Model details: n(observations) = 6406, n(ID:Focal) = 723, n(ID) = 56. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Type	Response variable	Covariates	AICc	Δ AICc	Weight
Substrate	Rock	Sun/Shade	789.8	0.00	0.051
		NFEM.2M	791.3	1.49	0.024
		Year	791.4	1.62	0.023
		Rain/Dry	791.7	1.91	0.019
		Pup Sex	791.7	1.98	0.019
		Pup Age	791.9	2.11	0.018
		HRV	791.9	2.18	0.017
		NFEM.5M	792.0	2.24	0.016
		Null Model	794.2	4.41	0.006
	Grass	NFEM.2M + NFEM.5M + Pup Sex + Pup Age + Rain/Dry	1661.1	0.00	0.085
		NFEM.2M + Pup Sex + Pup Age + Rain/Dry	1661.6	0.49	0.067
		NFEM.2M + Pup Age + Rain/Dry	1662.4	1.34	0.044
		NFEM.2M + NFEM.5M + Pup Sex + Pup Age	1663.5	2.42	0.025
		NFEM.2M + NFEM.5M + Pup Age	1663.7	2.66	0.022
		NFEM.2M + Pup Sex + Pup Age	1663.8	2.75	0.022
		NFEM.2M + Pup Age	1664.2	3.12	0.018
		Null Model	1856.4	195.40	3.197e-44
	Mud	NFEM.2M + NFEM.5M + Pup Age	1729.5	0.00	0.057
		NFEM.2M + NFEM.5M	1729.5	0.06	0.055
		Null Model	1833.9	104.45	1.188e-24
Topography	Rough	NFEM.2M + NFEM.5M	793.2	0.00	0.064
		NFEM.2M	795.1	1.85	0.025
		NFEM.5M	797.4	4.23	0.008
		Null	799.2	5.95	0.003
	Moderate	NFEM.2M + NFEM.5M	1970.2	0.00	0.134
		NFEM.2M	1974.7	4.48	0.014
		Null	1985.2	14.98	7.504e-05
	Flat	NFEM.2M + Pup Age + Rain/Dry + Sun/Shade + Year	1898.9	0.00	0.116
		NFEM.2M + Pup Age + Rain/Dry + Year	1899.0	0.17	0.106
		NFEM.2M + Pup Age + Rain/Dry	1899.4	0.54	0.088
		NFEM.2M + Pup Age + Rain/Dry + Sun/Shade	1900.2	1.30	0.060
		NFEM.2M + Pup Age + Year	1902.8	3.89	0.017
		NFEM.2M + Pup Age + Sun/Shade + Year	1903.8	4.97	0.010
		NFEM.2M + Pup Age	1904.0	5.09	0.009
		Null	1948.7	49.82	1.754e-12

Table 3: Estimate, standard error, Z value and P value for the retained fixed effects in the best models (AICc = 0; table 2) for individual substrate (rock, grass and mud) and topography (rough, moderate and flat) measurements. Highly significant terms ($p < 0.001$) are bold. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Type	Response variable	Fixed effect	Estimate	Standard Error	Z	p value
Substrate	Rock	Intercept	-13.449	0.942	-14.282	<0.0001
		Sun/Shade (Sun)	1.012	0.660	1.533	0.1250
	Grass	Intercept	38.593	5.931	6.508	<0.0001
		NFEM.2M	-1.333	0.159	-8.391	<0.0001
		NFEM.5M	-0.200	0.126	-1.587	0.1125
		Pup Sex (Male)	-3.663	2.404	-1.524	0.1276
		Pup Age	-1.738	0.260	-6.680	<0.0001
		Rain/Dry (Rain)	1.024	0.494	2.073	0.0381
	Mud	Intercept	-31.189	3.460	-9.015	<0.0001
		NFEM.2M	1.176	0.141	8.358	<0.0001
		NFEM.5M	0.180	0.124	1.448	0.1480
		Pup Age	1.376	0.186	7.385	<0.0001
Topography	Rough	Intercept	-14.157	0.945	-14.984	<0.0001
		NFEM.2M	0.460	0.181	2.549	0.0108
		NFEM.5M	-0.401	0.215	-1.864	0.0623
	Moderate	Intercept	-12.012	0.558	-21.529	<0.0001
		NFEM.2M	0.319	0.094	3.377	<0.0001
		NFEM.5M	0.229	0.090	2.539	0.0111
	Flat	Intercept	2860.578	30.753	93.017	<0.0001
		NFEM.2M	-0.505	0.106	-4.764	<0.0001
		Pup Age	-0.613	0.150	-4.089	<0.0001
		Rain/Dry (Rain)	-1.151	0.436	-2.638	0.0083
		Sun/Shade (Sun)	-0.395	0.352	-1.120	0.2628
		Year	-1.413	0.015	-91.706	<0.0001

Resting HRV did not have any influence on either the roughness or grassiness of an individual's pupping site (table 4). The analysis using grassiness as a response variable retained two models in the confidence set. Both of these models contained the number of females within 2m and between 2m and 5m, and pup age. All three of these parameters had a negative influence on the grassiness of a seal's location (table 5). Higher conspecific density and younger pups were associated with less grassy sites. The repeatability of the mean grassiness value associated with the pupping site of the 24 females that had been present across multiple seasons was significant but still low ($R = 0.349 \pm 0.146$, $CI = 0.036-0.600$, $LRT p = 0.0111$). Repeatability within individuals appeared to be low in some individuals and high in others (R_i range = 0.1264-1.000, median = 0.6221, $LQ = 0.2981$, $UQ = 0.9250$). There was no significant difference in repeatability of site grassiness between pro- and reactive mothers (classified as being below or above the mean resting HRV) ($W = 66$, $p = 0.8376$).

Eight models were retained in the confidence set for the roughness of the site occupied by females (table 4). The number of females within 2m shows a significant positive influence on roughness as a response variable and was present in all retained models (table 4 & 5). Sites attributed to higher roughness scores were associated with higher densities of females in close proximity. Repeatability for the mean roughness value associated with the subset of 24 females was low and not significant ($R = 0.216 \pm 0.139$, $CI = 0 -0.481$, $LRT p = 0.108$). Repeatability within individuals was also low (R_i range = 0.0371-1.000, median = 0.4912, $LQ = 0.1498$, $UQ = 0.9970$).

Table 4: Summary of all models retained in the confidence set, including the ‘best’ model (AICc = 0) and the null model, for roughness and grassiness. Model details: n(observations) = 6406, n(ID:Focal) = 723, n(ID) = 56. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Response Variable	Covariates	AICc	Δ AICc	Weight
Grassiness	NFEM.2M + NFEM.5M + Pup Age + Rain/Dry	8428.2	0.00	0.087
	NFEM.2M + NFEM.5M + Pup Age	8428.3	0.07	0.084
	Null	8671.5	243.26	1.309e-54
Roughness	NFEM.2M + NFEM.5M + Pup Age + Sun/Shade	10433.6	0.00	0.037
	NFEM.2M + NFEM.5M + Sun/Shade	10434.2	0.61	0.027
	NFEM.2M + NFEM.5M + Pup Age	10434.2	0.63	0.027
	NFEM.2M + NFEM.5M	10434.9	1.28	0.019
	NFEM.2M + Pup Age + Sun/Shade	10436.0	2.43	0.011
	NFEM.2M + Sun/Shade	10436.6	3.02	0.008
	NFEM.2M + Pup Age	10437.0	3.36	0.007
	NFEM.2M	10437.6	3.98	0.005
	Null	10471.1	37.50	2.662e-10

Table 5: Estimate, standard error and t value for the retained fixed effects in the best models (AICc = 0; table 4) for individual site grassiness and roughness measurements. ANOVA p values are provided with highly significant terms ($p < 0.001$) are bold. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Response variable	Fixed effect	Estimate	Standard error	t value	p value (ANOVA)
Grassiness	Intercept	0.712	0.167	4.271	
	NFEM.2M	-0.118	0.008	-14.987	>0.0001
	NFEM.5M	-0.031	0.008	-4.043	>0.0001
	Pup Age	-0.049	0.011	-4.621	>0.0001
	Rain/Dry (Rain)	0.038	0.026	1.442	0.1493
Roughness	Intercept	-0.019	0.191	-0.100	
	NFEM.2M	0.056	0.009	6.029	>0.0001
	NFEM.5M	0.019	0.009	2.107	0.0351
	Pup Age	0.017	0.010	1.620	0.1052
	Sun/Shade (Sun)	0.039	0.024	1.623	0.1045

3.2 Social Environment

Stress-coping style did not influence preferences for locations with respect to immediate neighbour density (number of females within 2m of the focal female). Resting HRV did not feature in any of the retained models for female density within 2m (table 6). A range of parameters with relatively small effect sizes were retained (table 7), with the most important being number of females between 2m to 5m, substrate and year. Higher female densities within 2m were associated with lower female densities between 2m and 5m. Greater female densities were associated with muddy substrate relative to grassy substrates, with intermediate densities on rocky substrates. Densities within 2m of focal females were generally higher in 2017 compared to previous years.

Resting HRV featured in the ‘best model’ in the retained confidence set for the response variable indicating the density of females between 2m to 5m, as well as in three other alternative models (table 6). There may be a possible contributory negative influence of stress-coping style on the wider female density (number of females between 2m to 5m), although not strong (table 7). Proactive individuals were associated with higher numbers

of females between 2m to 5m and reactive individuals with lower densities (fig.4). The parameters with the strongest influence on wider female density were the number of females within 2m having an inverse influence and the weather parameters, sun and rain having a positive influence (table 7). Higher female numbers between 2m to 5m were associated with sunny and rainy weather.

Table 6: Summary of all models retained in the confidence set, including the ‘best’ model (AICc = 0) and the null model, for the number of females with 2m and the number of females between 2m to 5m. Model details: n(observations) = 6406, n(ID:Focal) = 723, n(ID) = 56. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Response Variable	Covariates	AICc	Δ AICc	Weight
NFEM.2M	NFEM.5M + Pup Age + Substrate + Sun/Shade + Topography + Year	13657.4	0.00	0.181
	NFEM.5M + Substrate + Sun/Shade + Topography + Year	13657.5	0.12	0.171
	NFEM.5M + Pup Age + Substrate + Topography + Year	13662.8	5.42	0.012
	NFEM.5M + Substrate + Topography + Year	13662.8	5.45	0.012
	Null	13964.0	306.65	4.670e-68
NFEM.5M	NFEM.2M + Pup Sex + Rain/Dry + Substrate + Sun/Shade + Topography + HRV	14253.8	0.00	0.165
	NFEM.2M + Pup Sex + Rain/Dry + Substrate + Sun/Shade + Topography	14255.2	1.43	0.081
	NFEM.2M + Pup Sex + Rain/Dry + Sun/Shade + Topography + HRV	14256.1	2.35	0.051
	NFEM.2M + Rain/Dry + Substrate + Sun/Shade + Topography + HRV	14256.5	2.72	0.042
	NFEM.2M + Rain/Dry + Substrate + Sun/Shade + Topography	14257.2	3.36	0.031
	NFEM.2M + Pup Sex + Rain/Dry + Sun/Shade + Topography	14257.8	4.01	0.022
	NFEM.2M + Rain/Dry + Sun/Shade + Topography + HRV	14259.2	5.37	0.011
	Null	14311.8	58.05	4.097e-14

Table 7: Estimate, standard error and t value for the retained fixed effects in the best models (AICc = 0; table 6) for the number of females within 2m and the number of females between 2m to 5m of focal individual. ANOVA p values are provided with highly significant terms ($p < 0.001$) are bold. NFEM.2M = number of females less than 2m, NFEM.5M = number of females between 2m to 5m.

Response Variable	Fixed effect	Estimate	Standard error	t value	p value (ANOVA)
NFEM.2M	Intercept	-2.840e+02	6.519e+01	-4.357	
	NFEM.5M	-5.379e-02	1.188e-02	-4.527	>0.0001
	Pup Age	-1.263e-02	8.653e-03	-1.459	0.1446
	Substrate (Mud)	7.700e-01	5.073e-02	15.178	
	Substrate (Rock)	3.229e-01	8.001e-02	4.036	
	Sun/Shade (Sun)	8.794e-02	3.226e-02	2.726	0.0064
	Topography (L)	1.979e-01	5.834e-02	3.392	
	Topography (Q)	-9.136e-02	4.023e-02	-2.271	
	Year	1.413e-01	3.235e-02	4.367	>0.0001
NFEM.5M	Intercept	0.450	0.113	4.001	
	NFEM.2M	-0.063	0.013	-4.813	>0.0001
	Pup Sex (Male)	0.213	0.097	2.186	0.0288
	Rain/Dry (Rain)	0.152	0.041	3.724	0.0002
	Substrate (Mud)	0.138	0.053	2.516	
	Substrate (Rock)	0.091	0.084	1.076	
	Sun/Shade (Sun)	0.118	0.034	3.502	0.0005
	Topography (L)	-0.034	0.062	-0.554	
	Topography (Q)	-0.173	0.043	-4.066	
	HRV	-0.182	0.096	-1.898	0.0577

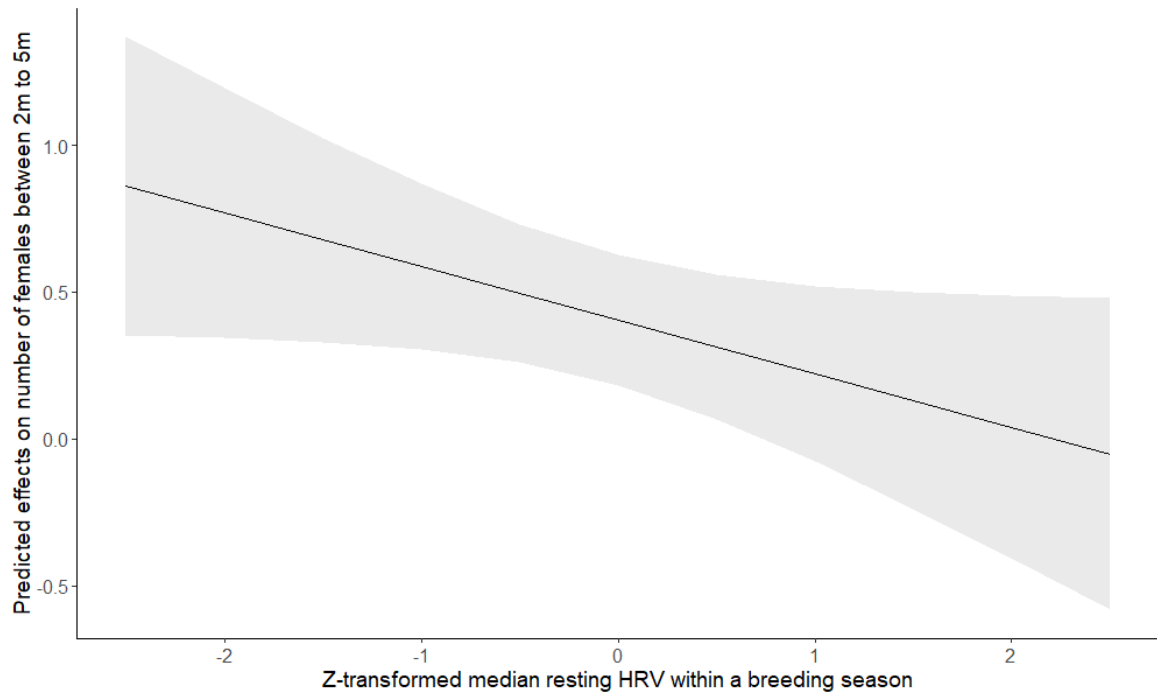


Figure 4: Predicted effects of an individual's median resting HRV within a breeding season on the number of females between 2m and 5m of the occupied site.

3.3 Corralling

Stress-coping style was not associated with corralling behaviour and the best model produced was the null model (AICc = 286.5, Δ AICc = 0, Weight = 0.125).

4. Discussion

Despite expectations, this study found that individuals with different stress-coping styles did not prefer a particular substrate or topography for their pupping site. Other variables did have some relationship with an individual's topography and substrates. The analyses did not determine any clear predictor of whether seals preferred rocky or rough sites. When combined with the other topography variables (moderate and flat) into the scale of roughness, there appeared to be a slight positive influence on the number of neighbouring females within 2m of the focal individual. The number of neighbouring females was also significant for grass and mud substrates along with pup age, with a higher density and older pups associated with muddy sites and a lower density and younger pups associated with grassy sites. This relationship was repeated when considering these variables combined in the grassiness scale. Stress-coping style was also unrelated to individual preference for the number neighbouring females. However, there was a weak negative association between stress-coping style and the wider density of female seals (2m to 5m) at individual's chosen site. Twiss et al's (2012) study on stress-coping style in female grey seals found similar results to this. It was identified that proactive mothers tended to be found in higher conspecific density locations compared to reactive mothers, however this relationship was found to be non-significant after Bonferroni adjustment application (Twiss et al., 2012). Other predictor variables had significant effects, with an inverse relationship found between the number of neighbouring females and the wider density of females at an individual's location. The effects of weather (sun and rain) were mostly non-significant regarding an individual's chosen site topography, substrate and number of neighbours. Surprisingly, both sunny and rainy weather were associated with a higher density of females between 2m and 5m of a focal mother. Overall, in terms of the study's aims, the results suggest that different stress-coping styles do not have different pupping site preferences based on topography and substrate, in order to optimise their own and their pup's fitness. Different stress-coping styles may prefer different wider conspecific densities, however, there appears to be stronger influences on this relationship.

Multiple studies have identified personality types experiencing different fitness outcomes according to overall abiotic conditions (Dingemanse et al., 2004; Kontiainen et al., 2009; Monestier et al., 2015; Santicchia et al., 2018). For example, in times where food is abundant, aggressive female Ural owls (*Strix uralensis*) successfully raised more chicks compared to less aggressive females (Kontiainen et al., 2009). However, pro- and reactive grey seal mothers have been found on average to produce pups with the same post-weaning mass and therefore the same fitness outcomes (Twiss et al., 2020). Monestier et al's (2015) study on roe deer found that pro- and reactive mothers select different habitats which are related to maximising fawn survival. Proactive mothers experienced increased fawn survival in more open areas of the forest, likely because these individuals were better able to cope with increased exposure to predation and able to protect their fawns against threats. In turn these females can take advantage of resource abundance in these areas. Reactive mothers trade off lower resource availability in closed areas with the ability to hide their fawn from predators. Therefore, it was expected that as topography, substrate and conspecific density are potential indicators of site favourability in grey seals, female grey seals with different stress-coping styles may benefit differentially from different sites and so select these sites to optimise their fitness. In

addition, reactive grey seal females tended to experience more variation in daily mass loss compared to proactives (Twiss et al., 2020). In spite of this, grey seal mothers did not exhibit significant repeatability in site roughness or high levels of repeatability of site grassiness. The level of repeatability in site grassiness for an individual was not determined by stress-coping style. It does not appear that reactive females employ a phenotype-environment matching strategy, hence being more varied in their site selection compared to proactive individuals being more uniform in site choice.

In both this study and Twiss et al.'s (2012) study, proactive individuals appeared to select sites with a higher density of conspecifics compared to reactive individuals. The lack of significance in this relationship may suggest other more powerful influences have an effect on conspecific density preference in female grey seals. One such influence may be reliance on conspecific density to identify favourable sites. The increasing population size of the Isle of May colony has led to more area being occupied by grey seals (Pomeroy et al., 2000). When considering topographical 'costs', more recently colonised sites are more likely to be less favourable compared to previously occupied sites. Surprisingly there are seemingly more favourable areas elsewhere on the isle which remained uncolonized. Therefore, arriving females may rely on the presence of other seals to indicate site favourability. Females who arrive early in the season are able to select more favourable sites, with those arriving later in the season restricted to unoccupied areas that become more unfavourable as the season progresses (Anderson et al., 1975; Pomeroy et al., 2000). Seal density in these favoured areas has not increased despite overall colony size increasing (Pomeroy et al., 2000). This is likely because female seals are generally intolerant of neighbouring seals. The results from this study likely indicate that intolerance of conspecifics in close proximity is a universal trait, regardless of stress-coping style. Higher density areas have been correlated with higher levels of female-female aggression (Stephenson et al., 2007). Mothers often maintain 1.5 body lengths between each other (Twiss et al., 2000a). As aggregation and site selection tends to follow a similar pattern each breeding season (Pomeroy et al., 2000), it is possible timing of arrival has a stronger influence on site selection than stress-coping style. Mothers with pups will threaten passing females that come closer than two body lengths (Caudron, 1998). Early arriving females in favourable, higher-density areas will likely have pups. It is probably not worth those yet to give birth travelling past these aggregated females to find a site and risk many aggressive encounters, even if these individuals are bold proactives.

Twiss et al (2000b) identified that early arriving mothers tended to be larger compared to those who arrived later in the breeding season and Pomeroy et al. (2000) suggested that smaller, later arriving females may be younger and therefore less experienced, so are restricted to sites on the periphery. Over time, as these females gain experience, they may shift pupping sites further into the colony to more favourable. Primiparous females are unlikely to know where favourable sites on the isle are located. Females have limited time ashore before birth (they often spend two days selecting a site; Pomeroy et al., 1994), and this, combined with the heterogeneity of the Isle of May and the selection pressure to conserve energy expenditure to optimise energy transfer to their pup (Shuert et al., 2020), restrict an individual's ability to locate an ideal site. Animals can use the presence of conspecifics to identify suitable habitats when other cues are not available, known as conspecific attraction (Stamps, 1988). This would explain why the colony seems to expand from originally colonised sites, with other seemingly suitable sites yet to be colonised. Therefore, the importance of site selection on fitness and the dependence on the presence of conspecifics to indicate suitable pupping sites, may overcome any potential aversion more shy reactive individuals have towards high conspecific density.

The implication of this study that higher neighbour density is associated with more muddy sites, whereas grassy sites tend to have lower female density, seems to support these hypotheses. As cause and effect is unable to be established with any relationships found in this study, there are multiple possible explanations. Muddy sites are likely wetter and closer to pools so could attract a higher density of females seeking to regulate their thermal stress levels. As wetter sites are more favoured (Stephenson et al., 2007; Twiss et al., 2000a; Twiss et al., 2002), it is possible that higher densities of conspecifics indicate suitable sites so attract more females to muddy areas. Due to the restricted viewing frame of the video footage, pool proximity was often unable to be determined. Comparing pool proximity of females on muddy or grassy sites may have provide more insight, by revealing whether individuals on muddy sites have more access to pools making these sites more favourable. Another likely explanation is that early season arrivals congregate in these areas, leading to more erosion of vegetation cover over time and so becoming muddier. On the other hand, later arrivals are left with peripheral sites where there are fewer conspecifics, so sites remain grassy. This explains why older pups are found on muddier sites and vice versa for grassy sites. Moderate and flat sites showed a similar association with the number of neighbouring females with lower female density in flat sites and vice versa for moderate topography. A plausible explanation for this is that flat sites allow seals to maintain their distance more easily, whereas any rougher land features found on moderate topography may force seals to be in more close proximity to each other. Flat site occupation was associated with pup age; older pups were found on flat sites. This may further relate to early individuals obtaining more favourable flatter sites, with later arrivals left with less favourable sites.

The fact that this study showed no evident preference for different topographies/substrate by seals with different coping styles has important implications for grey seal population ecology. Grey seals breed on a variety of substrates, from ice to sand (Stirling, 1975). Therefore, we could expect other colonies to also exhibit a mixture of stress-coping styles regardless of substrate. High levels of diversity within populations increases population resilience and persistence, with these populations being more likely to contain individuals able to survive sudden stochastic changes, reducing likelihood of extinction (Frankham, 1999, 1995). Effective population size (N_e) is used to estimate the likelihood of a population persisting over time and can inform conservation efforts through identification of populations at risk of extinction due to lack of diversity (Gilpin and Soule, 1986; Powell and Gartner, 2011). Intraspecific variation in behaviour, including dispersal ability, conspecific attraction and habitat choice, can influence N_e (Powell and Gartner, 2011). As personality can drive these behaviours (Belgrad and Griffen, 2017; Monestier et al., 2015; Santicchia et al., 2018; Spiegel et al., 2017), intraspecific variation in personality types will also likely affect N_e . Therefore, understanding the personality-driven dependencies on different pupping sites could be important for predicting the viability of different grey seal colonies in the future. Climate change and habitat loss are huge threats to species globally. 86% of threatened birds and mammals are affected by habitat loss and climate change is expected to cause movement of ecosystem boundaries (Baillie et al., 2004). The main response populations are expected to show to these changes is to track suitable environmental conditions and shift their habitat ranges, with many populations already showing a shift polewards to track suitable climates (Parmesan, 2006). If there is a mixture of stress-coping styles in different colonies, we would not expect a scenario where an entire population made up of single stress-coping style dependent on a specific environment becomes extinct due to loss of suitable habitat. It would be expected that diversity in stress-coping styles would increase population persistence.

Weather did not appear to influence the topography and substrate choice for pupping sites for females on the Isle of May. If individuals were dependent on a specific substrate according to overall weather conditions, climate change combined with habitat loss could have serious consequences for populations. Thermal stress creates a reliance on pool and this reliance is influenced by overall weather conditions (Twiss et al., 2002). In drier, hotter years females were found aggregate around pools compared to colder, wetter years where females were more dispersed (Twiss et al., 2002). Additionally, hotter, drier conditions can reduce the number of pools available. Mothers further from pools then spend significantly more time travelling to and from pools compared to wetter seasons. Pups of these females spent 40% of their time in close proximity to their mother, whereas in wetter seasons these mothers would be able to spend 100% of their time near their pups (Redman et al., 2001). This increase in time the pup spends alone increases the chances of mother-pup separation and makes pups more vulnerable to predation by gulls (Twiss et al., 2003). Climate change is likely to increase hotter, drier conditions. Pool proximity would therefore have been interesting to include in this study, as any relationship with stress-coping style and pool proximity could be influenced by weather. In the future, if a stress-coping style is unable to gain proximity to pools, they may suffer reduced fitness in the increase in drier, hotter seasons. Additionally, weather conditions are likely to become more unpredictable and extreme. Individuals may not be able to adapt their physiology to the fluctuating conditions, placing a selective advantage on behavioural flexibility (and therefore reactive individuals) as a method of responding to climate change.

Findings from this study can also direct future research into personality in grey seals. Rather than physical traits of an individual's site, the utilisation of different environmental features may be more important to consider. Proactive and reactive roe deer mothers both use forests, however forest openness was more important due to differences in ability to cope with predator exposure (Monestier et al., 2015). Additionally, grey seal pup fitness is affected by site selection on Sable Island based on a site's exposure to tidal or storm-surge influence rather than topography (Weitzman et al., 2017). It was already suggested in this study that grey seals reactive individuals may have to overcome any aversion to high-density areas in order to locate suitable sites. However, high-density areas are still linked to exposure to more aggressive interactions (Stephenson et al., 2007). Differences in ability to cope may lead to reactive individual's seeking cover at the edge of an area, for example nearer a wall. This could reduce stress in reactive mothers as the area needed to observe for threats is reduced. Proactives may select more exposed areas due to ability to cope with aggression. Although similar to corralling behaviour recorded in this study, the corralling definition may have been too narrow. This study only recorded this behaviour when females herded their pup into a corner. It may be more useful to measure female distance from high-rise surfaces. Additionally, animals are unlikely to have to just cope with novel physical habitat conditions in the future, but also potential novel ecosystem interactions, novel predators and human disturbance (Descombes et al., 2021; Smith et al., 2017). Recent studies have identified that urban environments have likely created novel selection pressures on personality types in rural populations. For example, urban dark-eyed juncos (*Junco hyemalis*) are bolder and more exploratory than rural populations (Atwell et al., 2012). On the other hand, behavioural flexibility is more important in urban populations of the tropical lizard species, *Psammophilus dorsalis* (Batabyal and Thaker, 2019). Depending on the threats faced by grey seals in the future, one personality type may not be selected for and so lead to a loss of diversity in populations in certain areas. An even bleaker scenario could be that neither personality types are able to adapt to novel changes. Therefore, studies into how different stress-coping styles respond to predicted changes should be considered.

The overall findings are that stress-coping style does not influence the physical characteristics of grey seal pupping sites. This may benefit different colonies by increasing population persistence in the face of anthropogenic-driven environmental change if different colonies contain a mixture of stress-coping styles. Future research should consider behavioural flexibility and adaptation of different stress-coping styles to predicted ecosystem changes, as climate change is unlikely to just affect physical environment.

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