

Variability in individual rates of aggression in wild gray seals: fine-scale analysis reveals importance of social and spatial stability

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Abstract Aggressive interactions are costly for individuals in time, energy, or physical damage, and in polygynous mating systems, there is high variability in the rates and intensity of aggression across individuals and within breeding seasons. However, examinations into the drivers of this variability are often conducted in isolation, in non-wild systems, or the predictor variables in question, for example, dominance, are averaged across large spatial, social, or temporal scales. The aim of this study was to adopt a fine spatial and temporal scale approach to investigate the factors associated with inter-individual variation in aggression in wild, breeding male gray seals within three consecutive breeding seasons. To do this, we fit models examining if the daily frequency of aggression and probability of escalated aggression for males was best explained by factors such as dominance score, proximity to competitors or females, local social stability, and the occurrence of stochastic environmental events. Stability of neighbor identities was the strongest correlate of reduced male aggression. Dominance status did not correlate with aggression at the daily scale, with the exception of one period after a natural disturbance to the breeding colony where dominant males had relatively reduced rates of aggression. These findings

emphasize the importance of local social stability in explaining inter-individual variation in aggression in a wild population and suggest that factors associated with aggression are context dependent in relation to the natural environment. Furthermore, we highlight the utility of a fine temporal scale and incorporating spatial parameters when investigating variability in aggression in wild systems.

Keywords *Halichoerus grypus* · Conflict reduction · Male aggression · Dominance · Social stability

Introduction

Animals face conflict within social groups as members compete for access to contested resources such as food, habitat, or mates, but conflict can be costly in time, energy, or physical injury (Maynard Smith and Price 1973; Maynard Smith 1974; Briffa and Elwood 2004). Individual variation in rates of aggression can be driven by characteristics of individuals such as size, age, or experience (Briffa and Elwood 2004), or by the presence of dominance hierarchies, winner/loser effects, honest signals of resource holding potential (RHP), and social relationships (Arnott and Elwood 2009; Kokko 2013). The importance of these factors can be context dependent in relation to broader ecological processes such as resource availability (Leiser 2003), physiological constraints (Bohórquez-Herrera et al. 2014), and the underlying social system within a population or species (Ang and Manica 2010).

For social animals, the formation of a linear, transitive dominance hierarchy based on RHP asymmetries between individuals can minimize costs associated with aggression. In stable hierarchies, dominant individuals typically gain increased mating success (Anderson and Fedak 1985; Drews 1993; Haley et al. 1994; Herberholz et al. 2007; Gerber et al.

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2010), but an individual's position in the hierarchy can also influence the rate or the probability of escalation (Rosenthal et al. 1992; Drews 1993; Goessmann et al. 2000; Ang and Manica 2010). In some breeding systems, high rank is associated with a greater intensity or increased frequency of aggression associated with defending a territory or mates (Francis 1988; Rosenthal et al. 1992; Goessmann et al. 2000; Ang and Manica 2010). However, other studies have demonstrated that dominant individuals have relatively reduced costs and experience lower rates or intensity of directed aggression in comparison to subordinates (Twiss 1991; Heitor et al. 2006; Ostner et al. 2008).

These differing relationships between dominance and aggression might be driven by the spatial distribution and social systems wherein the aggression occurs (Hemelrijk 2000). Alternatively, until recently, the available methodologies for calculating an individual's dominance score or rank were best applied to data spanning relatively long temporal scales (Boyd and Silk 1983; David 1987; Gammell et al. 2003; de Vries et al. 2006). Recent additions to the dominance score calculation toolbox such as Elo ranking (Neumann et al. 2011) now allow for calculations of dominance in sequence and at a finer temporal scale. If dominance or social structures vary within breeding seasons, adopting these methods of dominance calculation might provide insights into what drives the observed fine-scale variation in individuals' rates or intensities of aggression. In order to tease apart these mechanisms and relationships, this study aimed to investigate the natural variation in aggression by using a spatially and temporally relevant scale, and by considering the structure of the physical and social environment.

The polygynous breeding pinnipeds provide an ideal model for such investigations, and previous work has addressed the drivers of aggression and dominance in these systems (Anderson and Fedak 1985; Haley et al. 1994; Twiss et al. 1998; Lidgard et al. 2005; Carlini et al. 2006; Bohórquez-Herrera et al. 2014). The gray seal (*Halichoerus grypus*) is a colonial, capital breeder where there is high skew in male mating and reproductive success (Twiss et al. 2006, 2007). Male energy is limited during the approximately 8-week annual breeding season (Twiss 1991), and there is considerable variability between years, colonies, and individuals in the frequency of male-male agonistic interactions (Boness 1984; Twiss 1991; Lawson 1993; Twiss et al. 1998). Inter-male aggression during the gray seal breeding season occurs as males strive to maintain access to shifting groups of females (Anderson et al. 1975; Twiss 1991; Twiss et al. 1994, 2007). Males form a non-linear dominance hierarchy where, apart from a few clearly dominant and subordinate individuals, most males have very similar dominance scores (Twiss 1991; Twiss et al. 1998). In general, dominant males experience the greatest levels of mating success

through increased tenure duration and also experience relatively reduced aggression intensity and rates across a breeding season (Boness and James 1979; Anderson and Fedak 1985; Twiss 1991; Twiss et al. 1998, 2006, 2007; Worthington-Wilmer et al. 2000; Lidgard et al. 2004). However, previous studies investigating individual rates of aggression (Twiss 1991) compared individuals at the scale of a whole season and did not consider spatial and temporal fluctuations in aggression, sex ratios, distributions of competitors, and distributions of females, all of which shift throughout a season (Pomeroy et al. 1994; Twiss et al. 1994). Furthermore, gray seal males and females exhibit site fidelity between seasons (Pomeroy et al. 1994; Twiss et al. 1994). Inter-annual male associations and within-year spatial social stability have been suggested as potential drivers of conflict reduction in gray seals (Anderson et al. 1975; Twiss 1991), but the relative importance of such factors in explaining the fine-scale variation in individuals' rates of aggression has not been previously examined.

Hemelrijk (2000) advocated studying animal behavior not in isolation but with attention to spatially explicit individual, environmental, and social variables. Therefore, the aim of our study was to use the wild gray seal breeding system to investigate, at a fine temporal and spatial scale, which factors best explain the variability in individual males' rates of aggression and probability of engaging in an escalated interaction. We hypothesize that at the daily scale, based on the previous findings of Twiss (1991), the more dominant males will have lower rates of aggression. In addition to dominance, we included two density-related spatial factors that vary at a fine temporal scale within a breeding season (Twiss et al. 1994) but have not been included in previous models of aggression for this system: proximity to competitors as a measure of intensity of competition and proximity to females as a measure of ease of access to the contested "resource". These variables were chosen because although male gray seals do not form distinct territories, male and female attendance shifts within a breeding season, changing the social structure at a fine temporal and spatial scale (Pomeroy et al. 1994; Twiss et al. 1994). Finally, male gray seals demonstrate inter-annual site fidelity (Twiss et al. 1994) and social stability within breeding seasons influences female gray seal breeding behaviors (Pomeroy et al. 2005). Recent evidence also suggests that when weaned gray seals of both sexes were penned together, subsequent interactions between familiar individuals had less aggression than when the pups were "strangers" (Robinson et al. 2015). Therefore, we included a daily measure of the stability of a male's local "neighborhood" in our models and predict that males with high local social stability will have lower rates and intensities of aggression (Anderson and Fedak 1985; Twiss 1991; Booksmythe et al. 2010; Cross et al. 2013). These factors were modeled within three successive breeding seasons to

examine how within-season stochastic environmental events and broad environmental variability across seasons might change which factors drive individual rates and intensity of aggression.

Methods

Field site

Data were collected at the Donna Nook breeding colony on the North Lincolnshire coast, eastern England (53.47°N, 0.15°E). Field observations were conducted during all daylight hours (mean=8 h 48 min daily) across three autumn breeding seasons from 3 November to 12 December in 2011, and from 27 October to 12 December in 2012 and 2013. Weather patterns varied across study years. The 2011 breeding season was considerably warmer and drier relative to the other 2 years of study (mean air temperature 2011, 8.17 °C; 2012, 6.42 °C; 2013, 6.79 °C; and mean rainfall 2011, 0.58 mm per day; 2012, 2.87 mm per day; 2013, 2.14 mm per day).

Two approximately 200×200 m sites within the Donna Nook colony were selected to cover the range of topography: the public (PUB) site had grassy dunes and mud wallows (53.476°N, 0.155°E) and the Royal Air Force (RAF) site primarily comprised sand flats (53.474°N, 0.155°E). In 2011, one observer alternated between study sites within Donna Nook (Bishop et al. 2014); in 2012–2013, a second observer, trained by the primary, was added. Both alternated daily between sites in order to provide full observational coverage and minimize observer bias. At Donna Nook, two main breeding aggregations form, one along the waterfront and another approximately a mile inshore along the dune line. This study was conducted on the inshore breeding aggregation. Males in the study area were identified daily via unique, natural pelage markings in the field or post hoc from high-resolution pictures taken with a Canon EOS 30D, 100–400 mm lens (Twiss et al. 1994; Bishop et al. 2014). The photo-ID catalogue contained a total of 170 individual males identified in 2011, increasing to 287 in 2012, and 398 males in 2013.

Male-male aggressive interactions

Male-male aggressive interactions (AIs) were defined as any agonistic interaction between two or more males (Twiss 1991; Bishop et al. 2014). Inter-male aggression is typically characterized by low-cost, noncontact displays, but some interactions escalate to fights (Boness 1984; Twiss 1991). In the preflight noncontact stage, males use a suite of nonvocal behaviors such as the Open-Mouth Threat (Miller and Boness 1979; Twiss 1991; Lawson 1993; Twiss et al. 1998) and, at some colonies, the Body Slap (Bishop et al. 2014, 2015a).

Contact AIs, or fights, are characterized by a series of lunges, bites, and bouts of “wrestling” behavior (Twiss 1991). AIs involving at least one identified male were recorded with notation of participants’ IDs, start and end times, and coarse details of behaviors performed. Agonistic interactions are sufficiently conspicuous (particularly in open terrain with no visual obstructions) and rare, which allowed for all occurrence records to be kept while performing other observations (Altmann 1974). For aggressive interactions, the record was labeled as noncontact (threat phase) or contact (fight) and the outcome was noted as either draw or win-loss (Bishop et al. 2014). A male was determined to have won an encounter if his opponent moved or was chased away and lost his position among a group of females; otherwise, the outcome was defined as a draw (Anderson and Fedak 1985; Twiss 1991; Twiss et al. 1998; Bishop et al. 2014). From this, the daily number of aggressive interactions (DAI) was calculated for each male. To standardize for unequal observation times within and between days, the number of aggressive interactions observed in a day for each male was divided by the number of hours he was present to get a rate of aggression per hour. This metric was then converted to a rate per 8 h to allow for comparison to published data from other colonies which also reported rates per 8 h (day) of observation (Twiss 1991). To account for potential bias due to extrapolation (e.g., if a male partook in a large number of AIs observed over a short time period), for each male, only the days in which he was observed for a minimum of 4 h were used.

Spatial distribution of males

Locations of all males were mapped hourly on printed aerial photos of the colony using a Nikon laser 550 rangefinder (6×21), with accuracy of 0.5 m up to 100 m and ±1 m at >100 m distance, and horizon reference points to determine distance and location of males. Female gray seals typically move <10 m per day, and none of the rare “long-distance” traveling behaviors observed at other colonies (Redman et al. 2001) were noted at Donna Nook (James 2013). As such, females were mapped once daily (Pomeroy et al. 2000, 2005; Twiss et al. 2007), with differentiation noted for the age class of pups (Kovacs and Lavigne 1986). Post hoc, the images of the hourly maps of male locations were georectified to OSGB coordinate system and male locations digitized using ArcInfo and ArcMap 10.1 (ESRI). For each male, the distance to the nearest male and nearest female in meters during each hour of mapping was calculated using the NEAR function in ArcMap 10.1 (ESRI). In order to provide accurate estimates of female to male distance, if a male was not present at the hour for which females were mapped, then distance to female was not calculated for him that day. Distance to female and distance to male were then averaged for each individual by day.

Measures of dominance

Due to sample-size requirements, dominance score calculations such as the David's Score (David 1987; Gammell et al. 2003; de Vries et al. 2006) generate one score per male for an arbitrary time period (e.g., a month, a year, a breeding season) using the results of all of the male's interactions in relation to other males in the specified sample. This limitation obscures temporal variation within individual males' scores and ignores the variability in timing or presence on the colony between males (Neumann et al. 2011). If David's Score is used, a male gray seal who was only present for the final week of the breeding season, but won every interaction, could have a higher score than a male who was present all season and lost a handful of interactions. Additionally, males may be expressing or asserting dominance at different points of the season, but this trajectory of dominance would be lost or masked in a dominance metric that relies on seasonal averages. This temporal disconnect has rarely been considered in dominance literature due to lack of appropriate methodology or adequate samples sizes to allow analysis at fine temporal scales; however, a recent addition to the dominance-score calculation toolbox, Elo ranking, has been advocated for ecological systems by Neumann et al. (2011).

Elo score calculations generate real-time updates of ranks that are temporally fixed, in sequence, and can account for draws and incomplete interaction matrices (Neumann et al. 2011). Mean Elo is comparable to David's Score (Neumann et al. 2011), so broad assessments and comparisons can still be made. For this study, we calculated Elo scores for males who were present for a minimum of 2 days and ten AIs for consistency with previous work (Twiss 1991; Bishop et al. 2014). The parameters of the Elo calculations included a starting value of 1000 for every male (P rschmann et al. 2010) and a k value of 200, where k is the amount a male's score will shift depending on if the outcome was a win or loss, or $0.5*k$ for draws, weighted by the score of his opponent (Neumann et al. 2011). A study on Galapagos sea lions (*Zalophus wollebaeki*) set k at 50 (P rschmann et al. 2010), but we selected to use the higher default value of 200 to account for the heavy costs associated with losing in this system (Anderson and Fedak 1985; Twiss 1991). Males exhibit site fidelity and are long-lived, and evidence suggests that males do not shift dominance ranks substantially between years (Twiss 1991; Twiss et al. 1994). Therefore, while initial starting values were set at 1000, if a male was present for more than 1 year, his final Elo score from the previous year was used as the starting value in the subsequent year. Using these calculations, a male's daily Elo score (DayElo) was the average of all his scores for a given day, within each year. As the range of possible Elo scores can vary depending on the individuals and aggressive events within a given day, year, or site (Neumann et al. 2011), DayElo values for individuals were normalized to allow for

comparisons: $\text{DayEloN} = (\text{DayElo}_{\text{ID}} - \min(\text{DayElo}_{\text{day}})) / (\text{range of DayElo}_{\text{day}})$, which resulted in a range of individuals' average scores per day of 0–1, from low to high dominance.

Stability of neighbor identity

Hierarchy stability is one way to track changes in inter-individual relationships for large social groups (Neumann et al. 2011). It is suitable for tracking broad changes in the hierarchy composition, but it does not take into account how localized spatial differences in individual identities change over time. Therefore, we selected to calculate a measure of the local social stability, which could be extracted for individuals at a daily scale. Localized social stability has been previously estimated for female gray seals using the definition that neighbor affiliations were any females within 10 m of each other (Ruddell et al. 2007); however, since male gray seals do not form discrete territories and are typically more dispersed than females (Twiss et al. 1994), this method was not deemed suitable. Instead, we calculated localized associations by deriving Theissen polygons around each individual male using ArcMap 10.1 (ESRI; Fig. 1). Theissen polygons are generated by creating lines at the midpoint between two adjacent points for each hourly map (Fig. 1). From this, any male whose polygon was adjoined to the focal male's polygon was classified as a neighbor for that hour. Jaccard's similarity index (JSI) was the best metric for quantifying local social stability in colonial pinnipeds (Ruddell et al. 2007), so we calculated a measure of neighbor similarity for each focal male as a measure of how many of his neighbors were similar between two consecutive hours (1).

$$(1) \text{ Neighbor Similarity} = \# \text{Same} / (\# \text{Same} + \# \text{New} + \# \text{Lost})$$

Due to a number of transient, non-identified males on the colony at any given time, we selected to amend the neighbor similarity calculation to account for un-identified neighbors as part of the total neighbor pool (2):

$$(2) \text{ Neighbor similarity} = \# \text{Same} / (\# \text{Same} + \# \text{New} + \# \text{Lost} + \text{Unknown}_{\text{Hour } n} + \text{Unknown}_{\text{Hour } n-1})$$

This assumed that any unknown males from the previous hour were not the same individuals as the unknowns from the present hour. This likely overestimates changes in neighbors, but all males present for more than 1 h in the study area were photographed and cross-checked against the photo-ID catalogue for matches, thus reducing the probability of double-counting. Also, under this assumption, we provide a more conservative estimate of stability as any transient males that were not identified were unlikely to be present long enough to contribute to the social stability of the system (Twiss 1991). Neighbor similarity values were then averaged per day for

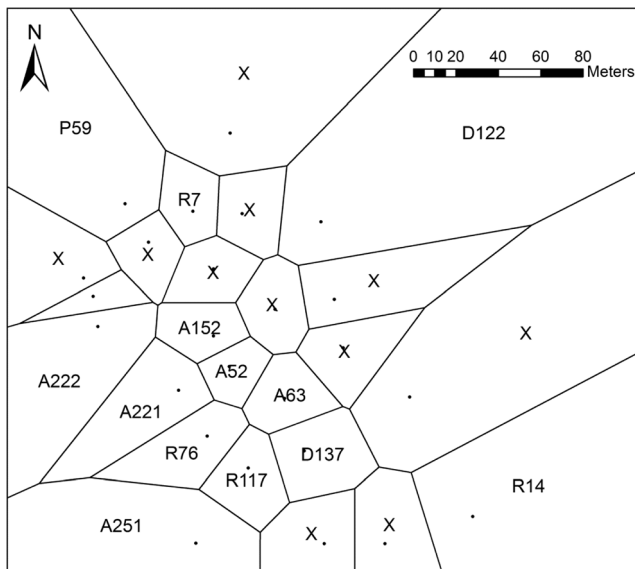


Fig. 1 An example of Thiessen polygons generated around male positions on day of year 325 at the RAF site in 2012. *Black points* represent mapped locations of males for the given hour (known=alphanumeric code; unknown=x). The lines are drawn at the midpoints between adjacent points, creating polygons. Males were considered “neighbors” if their polygons shared an edge for the given hour

each male and ranged from 0 (unstable—all new neighbors) to 1 (stable—no new neighbors).

Statistical analyses

We first examined how neighbor similarity and other spatial metrics for males on the colony changed within and between seasons. Individual daily averages for neighbor similarity, distance to nearest male, and distance to nearest female were assessed for differences between sites at Donna Nook (RAF $n=590$; PUB $n=827$) and years (2011 $n=277$; 2012 $n=634$; 2013 $n=504$) using linear mixed effects models (LMMs) with male ID ($n=147$) and observer ID (in 2012 and 2013, $n=2$) as random effects to account for pseudoreplication and observer variance. For measures across years, only days that were present in all 3 years (day of year (DOY) 309–343) were used for calculating means/medians. In 2011, a storm-surge, tidal event occurred on 26 November (DOY 330) which resulted in spring tide waters >8 m, female-pup separations, and a general disorganization of the breeding colony. To test if this event changed the local social or spatial structure, LMMs similar to those above were fit with neighbor similarity, distance to nearest male, and distance to nearest female as the response variables, but with SITE (RAF $n=590$; PUB $n=827$), Tidal Event (Before $n=220$; After $n=57$), and SITE*Tidal Event as the categorical predictor variables.

We then examined the factors driving individual daily rates of aggression by fitting generalized LMMs (GLMM, Poisson distribution; link=log) with male ID and observer ID (in 2012 and 2013) as random effects to account for repeat measures of

the same male within each year and potential observer variance. The response variable was the rounded daily rate of aggression (DAI) per male per day, and the predictor variables included were the male’s mean normalized dominance score that day, his average distance to nearest male that day, average distance to nearest female that day, and his average neighbor similarity that day. These predictor variables accounted for individual quality, density effects, and social determinants of rates of aggression. The model also included SITE as an interactive, fixed explanatory variable to test for site-specific differences. Models were fit for 2011, 2012, and 2013 separately to allow for inclusion of year-specific variables. Specifically, an additional predictor variable of Tidal Event (TDEV) was included in the 2011 model as an interactive term to test if the continuous predictor variables differed in their effect prior to or after the tidal event. Finally, the same modeling procedure was followed to predict the probability of a male engaging in at least one aggressive interaction which involved contact per day using binomial GLMMs (logit-link). Models for all analyses were run in R 2.13.2 (R Development Core Team 2011) with the lme4 package (Bates et al. 2011). Final models were selected following AIC minimization criteria (Richards 2008); all models within $\Delta 6$ AIC were retained, and any models within this set that were more complex versions of their nested counterparts, but with higher Δ AIC values, were excluded. Δ AIC values presented for “null models” represent the models with no fixed effects, and only random effects.

Results

Patterns in local social stability and spatial distributions of males across years and sites

Generally, there was little evidence of inter-annual or site differences in average neighbor similarity (neighbor similarity, Δ AIC_{Null}=0; second best model, Δ AIC_{Site}=6.5) or distance to male (distance to nearest male, Δ AIC_{Null}=0; second best model, Δ AIC_{Site}=7.0). Distance to the nearest female was significantly greater at the RAF site (12.75 ± 0.6 m SE) than the PUB site (9.98 ± 0.4 m SE) in all 3 years (distance to nearest female, Δ AIC_{Site}=0, Δ AIC_{Null}=6.9), and there was also some evidence of inter-annual differences in distance to nearest female, with greatest distances observed in 2011 (13.29 ± 0.9 m SE, 2012= 11.25 ± 0.5 m SE, 2013= 9.79 ± 0.6 m SE; second best model—distance to nearest female, Δ AIC_{Site+Year}=2.7, Δ AIC_{Null}=6.9).

Effect of stochastic tidal event on measures of spatial distribution and local social stability

Distances to the nearest male did not differ pre- and post-tidal event at either site (distance to male, Δ AIC_{Null}=0; second best

model, $\Delta AIC_{\text{Site}}=4.05$; Fig. 2a). The tidal event increased the distance to the nearest female from an average of 10.88 ± 0.74 m SE pre-tidal event, to 22.42 ± 1.49 m SE following the tidal event, but there was no difference across sites (distance to female, $\Delta AIC_{\text{Tidal}}=0$, $\Delta AIC_{\text{Tidal+Site+Tidal*Site}}=6.9$, $\Delta AIC_{\text{Null}}=18.51$; Fig. 2b). Individuals' neighbor similarity decreased after the tidal event from an average of 0.51 ± 0.015 to 0.33 ± 0.01 SE, and there was some evidence that the tidal event resulted in a relatively greater reduction in neighbor similarity at the RAF site (neighbor similarity, $\Delta AIC_{\text{Tidal+Site+Tidal*Site}}=0$, $\Delta AIC_{\text{Null}}=22.07$; Fig. 2c). However, the second-best model for neighbor similarity did not include the interaction between the tidal event and SITE (neighbor similarity, $\Delta AIC_{\text{Tidal}}=0.08$), suggesting the evidence for different effects across sites might be limited.

Prediction of individual rates of aggression

Models provided evidence that neighbor similarity and proximity to competitors were important factors explaining individual rates of aggression in all 3 years (Table 1). Increasing neighbor similarity was associated with reduced rates of aggression (Table 2 and Fig. 3a). This pattern was conserved at

the RAF site in all years, but in 2012 and 2013 at the PUB site, neighbor similarity shared no significant relationship with aggression (Table 2 and Fig. 3a). Males farther away from competitor males also exhibited reduced aggression (Table 1). This pattern was apparent at the RAF site in all years (Table 2 and Fig. 3b), though again, in 2012 and 2013 at the PUB site, the effect was slightly reduced (Table 2 and Fig. 3b). There was less evidence supporting distance to the nearest female or dominance score as important factors in explaining variation in aggression. While both were retained in the best models in all years, dominance was often excluded as a factor in subsequent models retained under the AIC criteria (Table 1). Additionally, the effect sizes of both parameters were small relative to other factors, and the direction, significance, and sizes of effects varied across years and sites (Table 2 and Fig. 3c, d). Finally, the tidal event in 2011 was retained as a fixed and interactive effect (Table 1). The relationship between the distance to the nearest male and aggression was lost after the tidal event (Table 2 and Fig. 3b). Dominance had no relationship with aggression prior to the tidal event, but after the tidal event in 2011, dominant males had less aggression per day than subordinate males (Table 2 and Fig. 3d).

Prediction of individual daily contact aggression

Neighbor similarity and distance to male competitor were again the strongest predictors for the probability of engaging in a Contact AI in a given day (Table 3). As neighbor similarity and distance to nearest male increased, the probability of engaging in a Contact AI was reduced across all 3 years, with the effect of neighbor similarity again showing a tendency to have a stronger effect at the RAF site (Tables 3 and 4 and Fig. 4a, b). Dominance was retained in the 2011 model with an interaction with the tidal event (Table 3), but its effect on the probability of escalation was not significant (Table 4). Distance to nearest female was not a strong predictor of the probability of escalated aggression (Tables 3 and 4).

Discussion

Our results demonstrate that the variation in aggression between individual male gray seals is highly associated with the local stability of neighbor identity and competitor proximity, and less influenced by resource (female) proximity and dominance rank. Males with full neighbor similarity had an approximately 50 % reduction in the frequency of aggression and the probability of escalated aggression compared to males with no neighbor similarity. There was some temporal and spatial variability for this relationship, which suggests that the effectiveness of specific factors might be dependent on local conditions. For example, there was very little evidence suggesting dominance score shared a relationship with

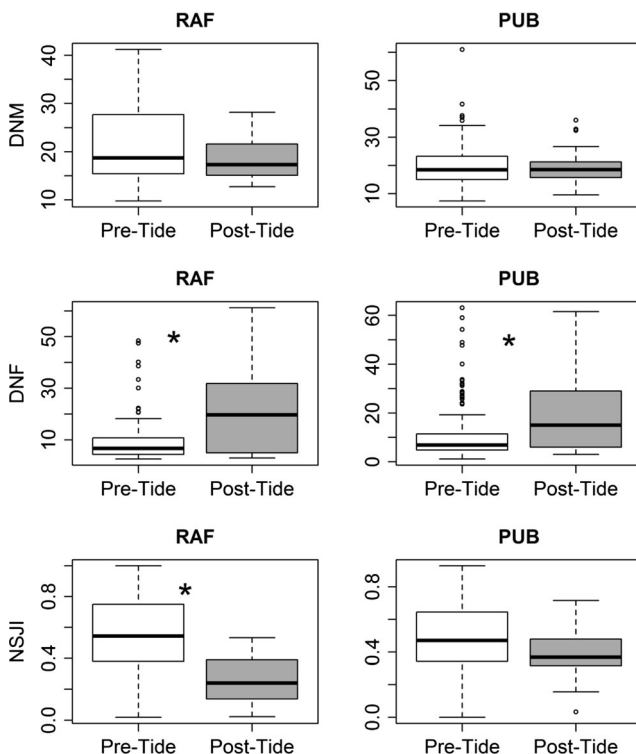


Fig. 2 The differences in **a** mean daily distance (m) to nearest male (DNM), **b** distance (m) to nearest female (DNF), and **c** neighbor similarity (NSJI, 0=unstable, 1=stable) at the RAF and PUB site pre- and post-tidal event in 2011 (day of year 330). Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentiles. Circles outside of whiskers represent possible outliers. Significant differences are denoted by an asterisk

Table 1 Retained GLMMs for predicting individual male DAI (daily rate of aggression) in 2011–2013

Year	AICc	Δ AIC	Weight
2011 ($N_{\text{samples}}=277$, $N_{\text{MID}}=48$)			
DAI ~ TDEV + NJSI + DNF + DNM + ELO + ELO:TDEV + DNM:TDEV	701.78	0	0.09
DAI ~ TDEV + NJSI + DNF + DNM + ELO + ELO:TDEV	703.58	1.8	0.04
DAI ~ TDEV + NJSI + DNF + DNM + DNM:TDEV	706.66	4.88	0.01
2012 ($N_{\text{samples}}=635$, $N_{\text{MID}}=75$, $N_{\text{OBSR}}=2$)			
DAI ~ (ELO + NJSI + DNF + DNM + SITE) * SITE	2635.12	0	0.36
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNF:SITE + NJSI:SITE	2636.16	1.05	0.21
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + DNM:SITE + NJSI:SITE	2636.31	1.2	0.20
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + NJSI:SITE	2637.88	2.77	0.09
2013 ($N_{\text{samples}}=504$, $N_{\text{MID}}=82$, $N_{\text{OBSR}}=2$)			
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNM:SITE + NJSI:SITE	1551.58	0	0.26
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNF:SITE + NJSI:SITE	1553.42	1.03	0.15
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + DNM:SITE + NJSI:SITE	1554.05	1.19	0.14
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + NJSI:SITE	1554.08	1.59	0.12
DAI ~ NJSI + DNF + DNM + SITE + DNM:SITE + NJSI:SITE	1554.21	2.6	0.07
DAI ~ ELO + NJSI + DNF + DNM + SITE + DNF:SITE + NJSI:SITE	1556.59	3.17	0.05
DAI ~ NJSI + DNF + DNM + SITE + NJSI:SITE	1556.67	4.55	0.03

Random effects included in the models were MID (male ID) in 2011, and MID and OBSR (primary or secondary observer) in 2012. All continuous predictor variables are averages per day

ELO DayEloN, *NJSI* neighbor similarity, *DNF* distance to nearest female (m), *DNM* distance to nearest male (m), *TDEV* tidal event 2011

individual frequency of aggression, or probability of escalated aggression, during typical breeding seasons. However, after a stochastic tidal surge caused redistribution of seals and disruption of local social stability, the dominant males had approximately 50 % less aggression compared to the most subordinate males.

Social stability and aggression

Instead of dominance score showing a strong correlation to rates of aggression (Twiss 1991), we found a strong association between increasing local social stability and lower rates and intensity of aggression at the daily temporal scale. This relationship likely reflects the potential for greater mating success through conservation of energy and prolonged tenure found in this and other closely related systems (Twiss 1991; Twiss et al. 1994, 2006; Lidgard et al. 2005; P rschmann et al. 2010; Bishop et al. 2015b). For other territorial species, the importance of local social stability is supported in that losing to a stranger often results in expulsion from a territory, but a loss to a neighbor might only result in a small loss of territory or a few resources (Husak and Fox 2003a, b; Bee 2003; Lachish and Goldizen 2004; Booksmythe et al. 2010; Cross et al. 2013). For male gray seals, “not losing” a position near females is considered more important than “winning” in terms of securing mating success (Anderson et al. 1975;

Anderson and Fedak 1985; Twiss 1991), and length of stay, not dominance, is an important driver of mating success in pinniped breeding systems (Twiss 1991; P rschmann et al. 2010). As such, individuals’ relative dominance scores, as measures of ability to “win” (Drews 1993; Neumann et al. 2011), might not determine rates of aggression if selection favors “not losing”. Instead, regardless of dominance rank or score, males might benefit when the local social neighborhood is stable by not having to defend their positions to intruders, but only maintain the boundaries with their neighbors. Dominant males on North Rona, Scotland, often maintained positions in the core of the colony where they were buffered from exposure to “roaming” transient males (Anderson et al. 1975; Twiss 1991; Twiss et al. 1994); therefore, the previous link between high dominance and lower aggression for gray seals could be an artifact of not including appropriate spatial or social variables (Twiss 1991).

While it was not explicitly tested in this study, neighbor consistency is a key requirement for the dear enemy phenomenon (DEP—Jaeger 1981; Getty 1987). Thus, the potential for DEP to be in effect in this system merits some consideration. There is currently some evidence of individual recognition for gray seals. Female gray seals exhibit some level of sociality not explained by spatial metrics alone (Pomeroy et al. 2000, 2005; Insley et al. 2003; Ruddell et al. 2007; Robinson et al. 2015), and they also have the capacity for discerning the identity of their pups (McCulloch et al. 1999; McCulloch and

Table 2 Coefficient estimates for the retained fixed effects in the best models for predicting individuals' daily rates of aggression ($\Delta AIC=0$; Table 1)

Year		Coefficient estimate	Standard error	<i>P</i> value
2011	Intercept: PRE TIDE	2.02	0.16	<0.0001
	Intercept: POST TIDE	1.54	0.35	0.17
	NJSI	-0.65	0.18	0.0003
	DNF	0.008	0.003	0.003
	ELO: PRE TIDE	0.17	0.13	0.194
	ELO: POST TIDE	-0.67	0.26	0.01
	DNM: PRE TIDE	-0.03	0.005	<0.0001
	DNM: POST TIDE	0.006	0.02	0.67
2012	Intercept: RAF	3.69	0.20	<0.0001
	Intercept: PUB	2.45	0.20	<0.0001
	ELO: RAF	0.06	0.07	0.41
	ELO: PUB	-0.17	0.08	0.03
	NJSI: RAF	-0.92	0.12	<0.0001
	NJSI: PUB	0.24	0.14	0.09
	DNF: RAF	-0.007	0.002	<0.0001
	DNF: PUB	0.006	0.003	0.03
	DNM: RAF	-0.05	0.005	<0.0001
	DNM: PUB	-0.04	0.005	<0.0001
2013	Intercept: RAF	3.69	0.15	<0.0001
	Intercept: PUB	2.39	0.19	<0.0001
	DNF	-0.004	0.002	0.004
	ELO: RAF	0.17	0.08	0.04
	ELO: PUB	-0.16	0.10	0.11
	NJSI: RAF	-1.01	0.12	<0.0001
	NJSI: PUB	0.11	0.14	0.46
	DNM: RAF	-0.04	0.006	<0.0001
	DNM: PUB	-0.02	0.004	<0.0001

All predictor variables are averages per day

ELO DayEloN, *NJSI* neighbor similarity, *DNF* distance to nearest female (m), *DNM* distance to nearest male (m), *PRE TIDE* DOY <330, *POST TIDE* DOY \geq 330

Boness 2000; Insley et al. 2003). Aggression was reduced among weaned gray seal pups of both sexes when individuals had previous exposure to each other (Robinson et al. 2015). In other pinnipeds, male northern elephant seals, *Mirounga angustirostris*, rely on characteristics of vocalizations to identify individuals (Casey et al. 2013). Male gray seals exhibit spatial site fidelity and roughly 30–40 % return across years (Twiss et al. 1994), suggesting males are exposed to similar individuals over time. However, to our knowledge, there have not been any rigorous attempts to investigate individual recognition capability in adult male gray seals. Therefore, at this time, we cannot ascertain if the DEP, via local social stability, is driving the observed reduction in rates and intensity of conflict male gray seals, but the evidence from female gray seals and pups suggests that there could be a component of individual recognition in play. Very little is known about DEP driving conflict reduction in wild systems which do not assort into clearly defined territories. As controlled, paired trials are not

feasible for adult gray seals, a more comprehensive examination of the role of local social stability and DEP would benefit by coupling neighbor similarity metrics with auditory playbacks (Casey et al. 2013), visual or scent manipulations which test for individual recognition (Cross et al. 2013), or hormonal analysis which can test for physiological indicators of recognition (Robinson et al. 2015).

Context dependence of social and spatial variables

The fine spatial and temporal scale of the present study allows us to make some observations about how natural environmental variation shapes conflict and conflict reduction. In the present study, the correlates of male aggression appeared to be conserved across years; however, some factors such as male proximity and neighbor similarity varied in the size or in the direction of their effect between years and sites. There is

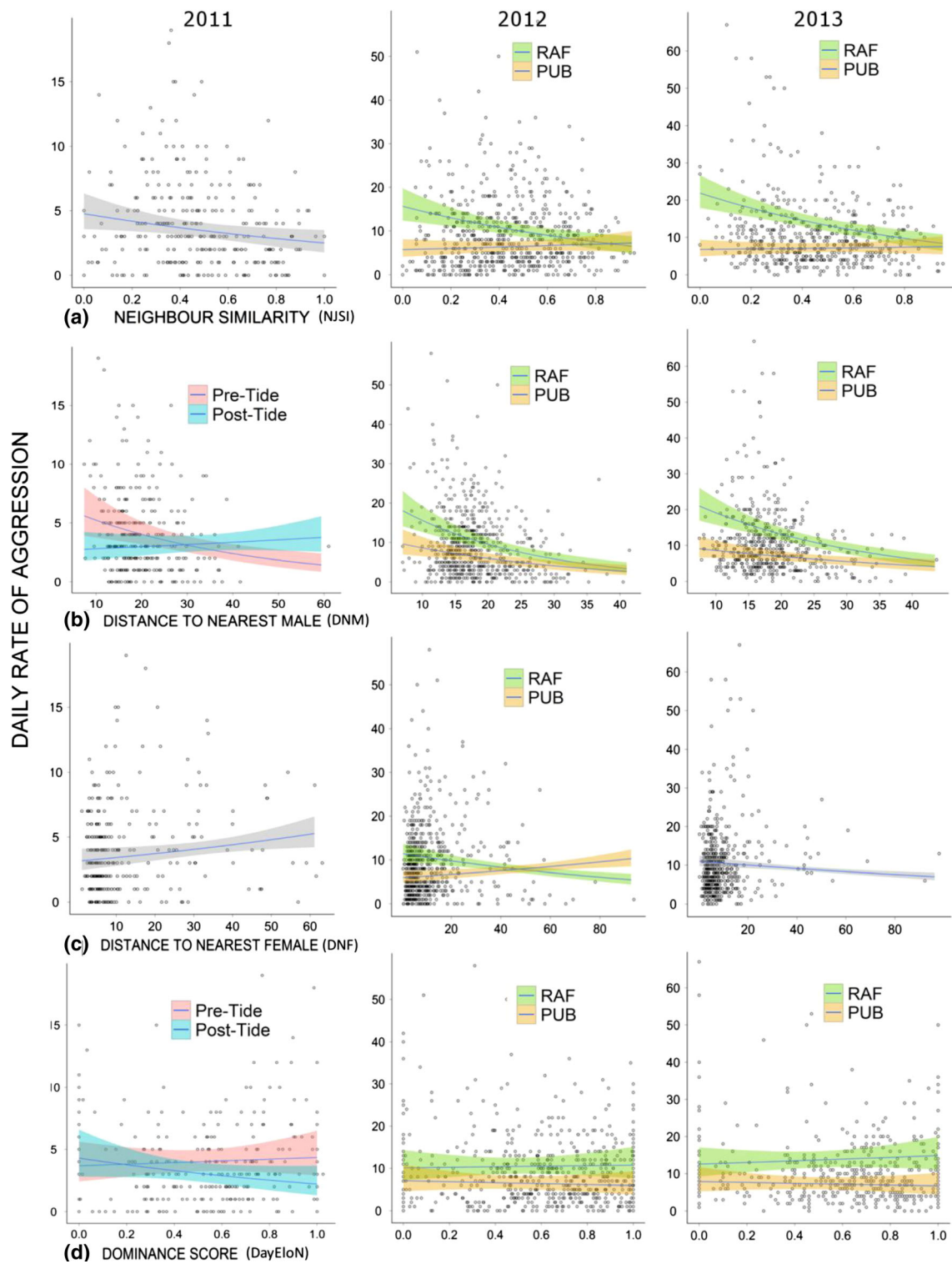


Fig. 3 The effects of **a** neighbor similarity (NJSI, 0=unstable, 1=stable), **b** distance (m) to nearest male (DNM), **c** distance (m) to nearest female (DNF), and **d** Elo dominance score (DayEloN) in 2011, 2012, and 2013 on an individual male’s frequency of ALS daily. If there was an interaction

effect of the tidal event, separate responses are differentiated as pre-tidal event (*pink*) and post-tidal (*blue*). Similarly, if SITE interacted, the responses are differentiated as RAF (*green*) and PUB (*orange*) (shaded area is 95 % CI)

evidence that the relationship between the local environment and conflict reduction is context dependent in other systems (Graham and Herberholz 2009; Tierney et al. 2013; Monclús

et al. 2014). The presence of a female in the test arena reduced the effect of DEP for male pupfish *Cyprinodon variegatus* (Leiser 2003), male Galápagos sea lions congregate in shaded

Table 3 Retained GLMMs for predicting the probability of a contact AI (PF) per day in 2011–2013

Year	AICc	ΔAIC	Weight
2011 ($N_{\text{samples}}=277, N_{\text{MID}}=48$)			
PF ~ ELO + NJSI + DNM + ELO:TDEV	343.14	0	0.03
PF~ELO + NJSI + ELO:TDEV	345.65	2.51	0.01
PF ~ NJSI + DNM	345.69	2.55	0.01
PF ~ DNM	345.99	2.85	0.01
PF ~ NJSI + DNF	347.30	4.15	0.004
PF ~ NJSI	348.28	5.14	0.002
PF ~ 1	348.81	5.60	0.002
2012 ($N_{\text{samples}}=635, N_{\text{MID}}=75, N_{\text{OBSR}}=2$)			
PF ~ NJSI + DNF + DNM + SITE + NJSI:SITE + DNF:SITE	799.69	0	0.20
PF ~ NJSI + DNF + DNM + SITE + DNF:SITE	803.22	3.53	0.03
PF ~ NJSI + DNF + DNM + SITE + NJSI:SITE	803.58	3.89	0.03
PF ~ DNM	803.61	3.92	0.03
PF ~ NJSI + DNF + SITE + NJSI:SITE + DNF:SITE	803.98	4.87	0.02
2013 ($N_{\text{samples}}=504, N_{\text{MID}}=82, N_{\text{OBSR}}=2$)			
PF ~ NJSI + DNM	606.56	0	0.12
PF ~ NJSI + DNF + SITE + NJSI:SITE	610.79	4.24	0.02
PF ~ NJSI	611.36	4.81	0.01

Random effects included in the models were MID in 2011, and MID (male ID) and Observer (primary or secondary) in 2012

PF daily probability of escalating to a fight/contact AI, ELO DayEloN, NJSI neighbor similarity, DNF distance to nearest female (m), DNM distance to nearest male (m), TDEV tidal event 2011 only

Table 4 Coefficient estimates for the retained fixed effects in the best models across years for predicting the probability of an individual engaging in an escalated interaction on a given day (ΔAIC=0; Table 3)

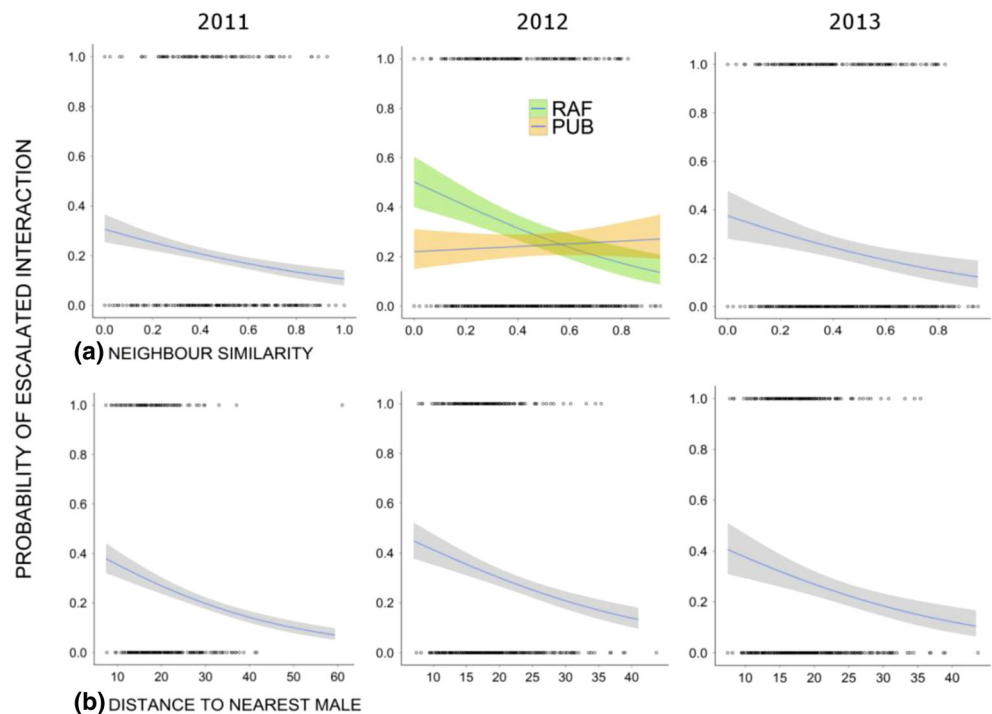
Year		Coefficient estimate	Standard error	P value
2011	Intercept	0.50	0.57	0.38
	NJSI	-1.42	0.63	0.02
	DNM	-0.04	0.02	0.04
	ELO: PRE TIDE	0.64	0.45	0.16
	ELO: POST TIDE	-0.70	0.64	0.28
2012	Intercept: RAF	1.63	0.63	0.01
	Intercept: PUB	-0.25	0.58	0.001
	DNM	-0.05	0.02	0.01
	NJSI: RAF	-2.06	0.72	0.004
	NJSI: PUB	0.30	0.70	0.67
	DNF: RAF	-0.04	0.01	0.005
	DNF: PUB	0.01	0.02	0.39
2013	Intercept	0.75	0.55	0.16
	NJSI	-1.62	0.52	0.002
	DNM	-0.05	0.02	0.01

All continuous predictor variables are averages per day
 ELO DayEloN, NJSI neighbor similarity, DNF distance to nearest female (m), DNM distance to nearest male (m), PRE TIDE DOY <330, POST TIDE DOY ≥330 in 2011 only

areas during periods of thermal stress (Wolf et al. 2005), and the location of aggressive behaviors for California sea lions, *Zalophus californianus*, were related to temperature (Bohórquez-Herrera et al. 2014).

Thermal stress, and the associated physiological responses, selects against high levels of aggression in warm environments for animals such the mole rat *Spalax ehrenbergi* (Ganem and Nevo 1996). Although gray seals breed in the autumn in temperate climates, they exhibit variation in behaviors in relation to thermal stress and weather (Twiss et al. 2000, 2002, 2007; Redman et al. 2001). Female gray seals prefer breeding sites in close proximity to pools of water for the presumed function of thermoregulation and as a source of drinking water (Stewart et al. 2014). In years with increased rainfall, the variation in mating success between male gray seals was greater due to females not traveling to gain access to pools and thus allowing for greater monopolization of mating opportunities (Twiss et al. 2007). Increased topographic variation has also been associated with an overall reduction in conflict (Anderson and Harwood 1985; Twiss et al. 1998). At Donna Nook, dunes and muddy wallows create fine-spatial-scale topographic variation at the PUB site. Aggression at this site was lower for dominant males and positively correlated with increased competitor proximity. However, at the flat RAF site, particularly in wetter and colder years, neighbor stability appears to be most important for facilitating a reduction of aggression. Due to only three seasons of data being

Fig. 4 The effects of **a** neighbor similarity (NJSI, 0=unstable, 1=stable) and **b** distance (m) to nearest male (DNM) in 2011, 2012, and 2013 on the probability of a male engaging in a Contact AI on a given day. When SITE was retained as an interaction term, response of RAF (green) and PUB (yellow) are separate (shaded area is 95 % CI)



available, additional data would be needed for any firm conclusions to be drawn regarding the effects of broad weather patterns or differences in resource availability on gray seal aggression. However, by investigating individual variation in aggression in the wild at a fine temporal and spatial scale, we have begun to unravel how individuals' aggression responds to local environmental patterns, natural fluctuations, and subsequent changes in resource availability. Similar methods can be applied to systems in which only large-scale data has previously been available.

Finally, reductions in conflict driven by dominance hierarchies and DEP can be context dependent in regards to rapid changes in natural conditions (Graham and Herberholz 2009; Monclús et al. 2014). When features of the environment are highly variable, inter-individual differences in behaviors can be masked or their effects diminished (Killen et al. 2013). At Donna Nook, in comparison to colonies such as North Rona, Scotland, individuals are exposed to relatively greater environmental variability in the form of daily tidal fluctuations due to the open access to the sea. Individuals are also exposed to relatively greater anthropogenic presence due to the colony's position on the mainland coast. The generally variable environment at Donna Nook could be increasing the costs associated with relying on factors such as dominance under normal conditions, and instead be selecting for maintaining local social stability as a means of reducing conflict. By using a fine-temporal-scale measure of dominance, we found that following the tidal event in 2011, when individuals' average local social stability were greatly reduced, dominance was a stronger predictor of conflict reduction, even though under

“normal” conditions, relying on this alone would presumably have a greater cost. This could again be evidence of the strong selection for “not losing” in this system (Anderson and Fedak 1985). Our work has begun to discern the importance of including fine-scale variability measures, such as natural disturbance events within a breeding season, when investigating the drivers of individual rates of aggression. Further work which links measures of social stability, dominance, and spatial distribution of resources to direct measures of costs will be vital for predicting how individuals, colonies, or populations will respond to stressors such as anthropogenic presence or climate change.

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Ethical Approval This study was observational in nature, and all work complies with the current UK laws of animal welfare. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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