1 **Variability in individual rates of aggression in wild gray seals: Fine-scale**
2 **analysis reveals importance of social and spatial stability**

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

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.

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 (Lieser 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. 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 individuals' dominance score or rank were best applied to data spanning relatively long temporal scales (Boyd and Silk 1983; David 1987; Gammell et

80   al. 2003; de Vries et al. 2006). Recent additions to the dominance score calculation toolbox such as Elo

81   ranking (Neumann et al. 2011) now allow for calculations of dominance in sequence, and at a finer

82   temporal scale. If dominance or social structures vary within breeding seasons, adopting these methods of

83   dominance calculation might provide insights into what drives the observed fine-scale variation in

84   individuals' rates or intensities of aggression. In order to tease apart these mechanisms and relationships,

85   this study aimed to investigate the natural variation in aggression by using a spatially and temporally

86   relevant scale, and by considering the structure of the physical and social environment.

87   The polygynous breeding pinnipeds provide an ideal model for such investigations, and previous

88   work has addressed the drivers of aggression and dominance in these systems (Anderson and Fedak 1985;

89   Haley et al. 1994; Twiss et al. 1998; Lidgard et al. 2005; Carlini et al. 2006; Bohórquez-Herrera et al.

90   2014). The gray seal (*Halichoerus grypus*) is a colonial, capital breeder where there is high skew in male

91   mating and reproductive success (Twiss et al. 2006, 2007). Male energy is limited during the

92   approximately 8 week annual breeding season (Twiss 1991), and there is considerable variability between

93   years, colonies and individuals in the frequency of male-male agonistic interactions (Boness 1984; Twiss

94   1991; Lawson 1993; Twiss et al. 1998). Inter-male aggression during the gray seal breeding season

95   occurs as males strive to maintain access to shifting groups of females (Anderson et al. 1975; Twiss

96   1991; Twiss et al. 1994, 2007). Males form a non-linear dominance hierarchy, where apart from a few

97   clearly dominant and subordinate individuals, most males have very similar dominance scores (Twiss

98   1991; Twiss et al. 1998). In general, dominant males experience the greatest levels of mating success

99   through increased tenure duration and also experience relatively reduced aggression intensity and rates

100   across a breeding season (Boness and James 1979; Anderson and Fedak 1985; Twiss 1991; Twiss et al.

101   1998, 2006, 2007; Worthington Wilmer et al. 2000; Lidgard et al. 2004). However, previous studies

102   investigating individual rates of aggression (Twiss 1991) compared individuals at the scale of a whole-

103   season, and did not consider spatial and temporal fluctuations in aggression, sex-ratios, distributions of

104   competitors, and distributions of females, all of which shift throughout a season (Pomeroy et al. 1994;

105   Twiss et al. 1994). Furthermore, gray seal males and females exhibit site-fidelity between seasons

106   (Pomeroy et al. 1994; Twiss et al. 1994). Inter-annual male associations and within-year spatial social

107   stability have been suggested as potential drivers of conflict reduction in gray seals (Anderson et al. 1975;

108   Twiss 1991), but the relative importance of such factors in explaining the fine-scale variation in

109   individuals' rates of aggression has not been previously examined.

110   Hemelrijk (2000) advocated studying animal behavior not in isolation, but with attention to

111   spatially explicit individual, environmental and social variables. Therefore, the aim of our study was to

112   use the wild gray seal breeding system to investigate, at a fine temporal and spatial scale, which factors

113   best explain the variability in individual males' rates of aggression and probability of engaging in an

114   escalated interaction. We hypothesize that at the daily scale, based on the previous findings of Twiss

115   (1991), the more dominant males will have lower rates of aggression. In addition to dominance, we

116   included two density related spatial factors that vary at a fine temporal scale within a breeding season

117   (Twiss et al. 1994) but have not been included in previous models of aggression for this system:

118   proximity to competitors as a measure of intensity of competition and, proximity to females as a measure

119   of ease of access to the contested 'resource'. These variables were chosen because although male gray

120   seals do not form distinct territories, male and female attendance shifts within a breeding season,

121   changing the social structure at a fine temporal and spatial scale (Pomeroy et al. 1994, Twiss et al. 1994).

122   Finally, male gray seals demonstrate inter-annual site-fidelity (Twiss et al. 1994) and social stability

123   within breeding seasons influences female gray seal breeding behaviors (Pomeroy et al. 2005). Recent

124   evidence also suggests that when weaned gray seals of both sexes were penned together, subsequent

125   interactions between familiar individuals had less aggression than when the pups were 'strangers'

126   (Robinson et al. 2015). Therefore, we included a daily measure of the stability of a male's local

127   'neighborhood' in our models, and predict that males with high local social stability will have lower rates

128   and intensities of aggression (Anderson and Fedak 1985; Twiss 1991; Booksmythe et al. 2010; Cross et

129   al. 2013). These factors were modelled within 3 successive breeding seasons to examine how within-

130   season stochastic environmental events and broad environmental variability across seasons might change

131   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 = 8h 48min daily) across three autumn breeding seasons from 3 November to 12 December in 2011, and from 27 October – 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 two years of study (mean air temp 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 200m x 200m 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 was primarily comprised of 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, 100-400mm lens (Twiss et al. 1994; Bishop et al. 2014). The photo-ID catalogue contained a total of 170 individual males identified 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 prefight noncontact stage, males use a suite of nonvocal behaviors such as the Open-Mouth Threat

157   (Miller and Boness 1979; Twiss 1991; Lawson 1993; Twiss et al. 1998) and, at some colonies, the Body

158   Slap (Bishop et al. 2014, 2015a). Contact AIs, or fights, are characterized by series of lunges, bites and

159   bouts of 'wrestling' behavior (Twiss 1991). AIs involving at least one identified male were recorded with

160   notation of participants' IDs, start and end times, and coarse details of behaviors performed. Agonistic

161   interactions are sufficiently conspicuous (particularly in open terrain with no visual obstructions) and

162   rare, which allowed for all occurrence records to be kept while performing other observations (Altmann,

163   1974). For aggressive interactions, the record was labelled as noncontact (threat phase) or contact (fight)

164   and the outcome was noted as either draw or win-loss (Bishop et al. 2014). A male was determined to

165   have won an encounter if his opponent moved or was chased away and lost his position amongst a group

166   of females; otherwise the outcome was defined as a draw (Anderson and Fedak 1985; Twiss 1991; Twiss

167   et al. 1998; Bishop et al. 2014). From this, the daily number of aggressive interactions (DAI) was

168   calculated for each male. To standardize for unequal observation times within and between days, the

169   number of aggressive interactions observed in a day for each male was divided by the number of hours he

170   was present to get a rate of aggression per hour. This metric was then converted to a rate per 8 hours to

171   allow for comparison to published data from other colonies which also reported rates per 8 hrs (day) of

172   observation (Twiss 1991). To account for potential bias due to extrapolation (*e.g.* if a male partook in a

173   large number of AIs observed over a short time period), for each male, only the days in which he was

174   observed for a minimum of 4 hours were used.

175   ***Spatial distribution of males***

176   Locations of all males were mapped hourly on printed aerial photos of the colony using a Nikon

177   laser 550 rangefinder (6x21), with accuracy of 0.5m up to 100m and ±1m at >100m distance, and horizon

178   reference points to determine distance and location of males. Female gray seals typically move <10m per

179   day, and none of the rare 'long-distance' travelling behaviors observed at other colonies (Redman et al.

180   2001) were noted at Donna Nook (James 2013). As such, females were mapped once daily (Pomeroy et

181   al. 2000, 2005; Twiss et al. 2007), with differentiation noted for the age class of pups (Kovacs and

182   Lavigne 1986). *Post-hoc*, the images of the hourly maps of male locations were georectified to OSGB

183   coordinate system, and male locations digitized using ArcInfo and ArcMap 10.1 (ESRI). For each male,

184   the distance to the nearest male and nearest female in meters during each hour of mapping were

185   calculated using the NEAR function in ArcMap 10.1 (ESRI). In order to provide accurate estimates of

186   female to male distance, if a male was not present at the hour for which females were mapped, then

187   distance to female was not calculated for him that day. Distance to female and distance to male were then

188   averaged for each individual by day.

189   ***Measures of Dominance***

190   Due to sample-size requirements, dominance score calculations such as the David's Score (David

191   1987; Gammell et al. 2003; de Vries et al. 2006) generate one score per male for an arbitrary time period

192   (e.g., a month, a year, a breeding season) using the results of all of the male's interactions in relation to

193   other males in the specified sample. This limitation obscures temporal variation within individual males'

194   scores and ignores the variability in timing or presence on the colony between males (Neumann et al.

195   2011). If David's Score is used, a male gray seal who was only present for the final week of the breeding

196   season, but won every interaction, could have a higher score than a male who was present all season and

197   lost a handful of interactions. Additionally, males may be expressing or asserting dominance at different

198   points of the season but this trajectory of dominance would be lost or masked in a dominance metric that

199   relies on seasonal averages. This temporal disconnect has rarely been considered in dominance literature

200   due to lack of appropriate methodology or adequate samples sizes to allow analysis at fine temporal

201   scales; however, a recent addition to the dominance-score calculation toolbox, Elo ranking, has been

202   advocated for ecological systems by Neumann et al. (2011).

203   Elo score calculations generate real-time updates of ranks that are temporally fixed, in sequence

204   and can account for draws and incomplete interaction matrices (Neumann et al. 2011). Mean Elo is

205   comparable to David's Score (Neumann et al. 2011), so broad assessments and comparisons can still be

206   made. For this study, we calculated Elo scores for males who were present for a minimum of 2 days and

207 10 AIs for consistency with previous work (Twiss 1991; Bishop et al. 2014). The parameters of the Elo

208 calculations included a starting value of 1000 for every male (Pörschmann et al. 2010) and a k value of

209 200, where k is the amount a males' score will shift depending on if the outcome was a win or loss, or

210 0.5*k for draws, weighted by the score of his opponent (Neumann et al. 2011). A study on Galàpagos sea

211 lions (*Zalophus wollebaeki*) set k at 50 (Pörschmann et al. 2010), but we selected to use the higher default

212 value of 200 to account for the heavy costs associated with losing in this system (Anderson and Fedak

213 1985; Twiss 1991). Males exhibit site-fidelity, are long-lived and evidence suggests that males do not

214 shift dominance ranks substantially between years (Twiss 1991; Twiss et al. 1994). Therefore, while

215 initial starting values were set at 1000, if a male was present for more than one year, his final Elo score

216 from the previous year was used as the starting value in the subsequent year. Using these calculations, a

217 male's daily Elo score (DayElo) was the average of all his scores for a given day, within each year. As

218 the range of possible Elo scores can vary depending on the individuals and aggressive events within a

219 given day, year, or site (Neumann et al. 2011), DayElo values for individuals were normalized to allow

220 for comparisons: $DayEloN = (DayElo_{ID} - min(DayElo_{day})) / (Range\ of\ DayElo_{day})$, which resulted in a

221 range of individuals' average scores per day of 0-1, from low to high dominance.

222 *Stability of neighbor identity*

223 Hierarchy stability is one way to track changes in inter-individual relationships for large social

224 groups (Neumann et al. 2011). It is suitable for tracking broad changes in the hierarchy composition but it

225 does not take into account how localized spatial differences in individual identities change over time.

226 Therefore, we selected to calculate a measure of the local social stability, which could be extracted for

227 individuals at a daily scale. Localized social stability has been previously estimated for female gray seals

228 using the definition that neighbor affiliations were any females within 10m of each other (Ruddell et al.

229 2007); however, since male gray seals do not form discrete territories and are typically more dispersed

230 than females (Twiss et al. 1994) this method was not deemed suitable. Instead, we calculated localized

231 associations by deriving Theissen polygons around each individual male using ArcMap 10.1 (ESRI; Fig.

232 1). Theissen Polygons are generated by creating lines at the midpoint between two adjacent points for

233 each hourly map (Fig. 1). From this, any male whose polygon was adjoined to the focal male's polygon

234 was classified as a neighbor for that hour. Jaccard's Similarity index (JSI) was the best metric for

235 quantifying local social stability in colonial pinnipeds (Ruddell et al. 2007); so we calculated a measure

236 of neighbor similarity for each focal male as a measure of how many of his neighbors were similar

237 between two consecutive hours (1).

238 **(1) Neighbor Similarity = #Same / (#Same + #New + #Lost)**

239 Due to a number of transient, non-identified males on the colony at any given time, we selected to amend

240 the neighbor similarity calculation to account for un-identified neighbors as part of the total neighbor

241 pool (2):

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

243 This assumed that any unknown males from the previous hour were not the same individuals as the

244 unknowns from the present hour. This likely over-estimates changes in neighbors, but all males present

245 for more than 1 hour in the study area were photographed and cross-checked against the photo-ID

246 catalogue for matches, thus reducing the probability of double-counting. Also, under this assumption, we

247 provide a more conservative estimate of stability as any transient males that were not identified were

248 unlikely to be present long enough to contribute to the social stability of the system (Twiss 1991).

249 Neighbor similarity values were then averaged per day for each male and ranged from 0 (unstable: all

250 new neighbors) to 1 (stable: no new neighbors).

251 *Statistical Analyses*

252   We first examined how neighbor similarity and other spatial metrics for males on the colony

253 changed within and between seasons. Individual daily averages for neighbor similarity, distance to

254 nearest male, and distance to nearest female were assessed for differences between sites at Donna Nook

255 (RAF $n = 590$; PUB $n = 827$) and years (2011 $n = 277$; 2012 $n = 634$; 2013 $n = 504$) using linear mixed

256 effects models (LMMs) with male ID ($n = 147$) and observer ID (in 2012 and 2013, $n = 2$) as random

257 effects to account for pseudoreplication and observer variance. For measures across years, only days that

258   were present in all three years (Day of Year (DOY) 309-343) were used for calculating means/medians.

259   In 2011, a storm-surge, tidal-event occurred on November 26th (DOY 330) which resulted in spring tide

260   waters >8m, female-pup separations and a general disorganization of the breeding colony. To test if this

261   event changed the local social or spatial structure, LMMs similar to those above were fit with neighbor

262   similarity, distance to nearest male, and distance to nearest female as the response variables, but with

263   SITE (RAF $n = 590$; PUB $n = 827$), Tidal Event (Before $n = 220$; After $n = 57$), and SITE*Tidal Event as

264   the categorical predictor variables.

265   We then examined the factors driving individual daily rates of aggression by fitting generalized

266   LMMs (GLMM, Poisson distribution; link= log) with male ID and observer ID (in 2012 and 2013) as

267   random effects to account for repeat measures of the same male within each year and potential observer

268   variance. The response variable was the rounded daily rate of aggression (DAI) per male per day, and the

269   predictor variables included were the male's mean normalized dominance score that day; his average

270   distance to nearest male that day; average distance to nearest female that day; and his average neighbor

271   similarity that day. These predictor variables accounted for individual quality, density effects and social

272   determinants of rates of aggression. The model also included SITE as an interactive, fixed explanatory

273   variable to test for site specific differences. Models were fit for 2011, 2012 and 2013 separately to allow

274   for inclusion of year-specific variables. Specifically, an additional predictor variable of Tidal Event

275   (TDEV) was included in the 2011 model as an interactive term to test if the continuous predictor

276   variables differed in their effect prior to or after the tidal event. Finally, the same modeling procedure was

277   followed to predict the probability of a male engaging in at least one aggressive interaction which

278   involved contact per day using binomial GLMMs (logit-link). Models for all analyses were run in R

279   2.13.2 (R Development Core Team 2011) with the lme4 package (Bates et al. 2011). Final models were

280   selected following AIC minimization criteria (Richards 2008); all models within Δ6 AIC were retained,

281   and any models within this set that were more complex versions of their nested counterparts, but with

282   higher ΔAIC values, were excluded. ΔAIC values presented for "null models" represent the models with

283   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: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 6.5$) or distance to male (Distance to Nearest Male: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 7.0$). Distance to the nearest female was significantly greater at the RAF site (12.75 ± 0.6m SE) than the PUB site (9.98 ± 0.4m SE) in all three years (Distance to Nearest Female: $\Delta AIC_{Site} = 0$, $\Delta AIC_{Null} = 6.9$), and there was also some evidence of interannual differences in distance to nearest female, with greatest distances observed in 2011 (13.29 ± 0.9m SE, 2012: 11.25 ± 0.5m SE, 2013: 9.79 ± 0.6m SE; second best model: Distance to Nearest Female: $\Delta AIC_{Site + Year} = 2.7$, $\Delta AIC_{Null} = 6.9$).

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: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 4.05$; Fig. 2a). The tidal event increased the distance to the nearest female from an average of 10.88m ± 0.74 SE pre-tidal event, and to 22.42 ± 1.49 SE following the tidal event, but there was no difference across sites (Distance to Female: $\Delta AIC_{Tidal} = 0$, $\Delta AIC_{Tidal+Site+Tidal*Site} = 6.9$, $\Delta AIC_{Null} = 18.51$, Fig. 2b). Individuals' neighbor similarity decreased after the tidal event from an average of 0.51 ± 0.015 SE, 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: $\Delta AIC_{Tidal+Site+Tidal*Site} = 0$; $\Delta AIC_{Null} = 22.07$; Fig. 2c). However, the second-best model for neighbor similarity did not include the interaction between the tidal event and SITE (Neighbor similarity: $\Delta AIC_{Tidal} = 0.08$); 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 three years (Table 1). Increasing neighbor similarity was associated with reduced rates of aggression (Table 2; Fig. 3a). This pattern was conserved

309   at the RAF site in all years, but in 2012 and 2013 at the PUB site, neighbor similarity shared no

310   significant relationship with aggression (Table 2; Fig. 3a). Males farther away from competitor males

311   also exhibited reduced aggression (Table 1). This pattern was apparent at the RAF site in all years (Table

312   2; Fig. 3b), though again, in 2012 and 2013 at the PUB site the effect was slightly reduced (Table 2; Fig.

313   3b). There was less evidence supporting distance to the nearest female or dominance score as important

314   factors in explaining variation in aggression. While both were retained in the best models in all years,

315   dominance was often excluded as a factor in subsequent models retained under the AIC criteria (Table 1).

316   Additionally, the effect sizes of both parameters were small relative to other factors, and the direction,

317   significance and sizes of effects varied across years and sites (Table 2; Fig. 3c-d). Finally, the tidal event

318   in 2011 was retained as a fixed and interactive effect (Table 1). The relationship between the distance to

319   the nearest male and aggression was lost after the tidal event (Table 2; Fig. 3b). Dominance had no

320   relationship with aggression prior to the tidal event, but after the tidal event in 2011, dominant males had

321   less aggression per day than subordinate males (Table 2; Fig. 3d).

322   *Prediction of individual daily contact aggression*

323   Neighbor similarity and distance to male competitor were again the strongest predictors for the

324   probability of engaging in a Contact AI in a given day (Table 3). As neighbor similarity and distance to

325   nearest male increased, the probability of engaging in a Contact AI was reduced across all three years,

326   with the effect of neighbor similarity again showing a tendency to have a stronger effect at the RAF site

327   (Table 3, 4; Fig. 4a-b). Dominance was retained in the 2011 model with an interaction with the tidal event

328   (Table 3), but its effect on the probability of escalation was not significant (Table 4). Distance to nearest

329   female was not a strong predictor of the probability of escalated aggression (Table 3, 4).

DISCUSSION

331   Our results demonstrate that the variation in aggression between individual male gray seals is

332   highly associated with the local stability of neighbor identity and competitor proximity, and less

333   influenced by resource (female) proximity and dominance rank. Males with full neighbor similarity had

334   an approximately 50% reduction in the frequency of aggression, and the probability of escalated

335   aggression compared to males with no neighbor similarity. There was some temporal and spatial

336   variability for this relationship, which suggests that the effectiveness of specific factors might be

337   dependent on local conditions. For example, there was very little evidence suggesting dominance score

338   shared a relationship with individual frequency of aggression, or probability of escalated aggression,

339   during typical breeding seasons. However, after a stochastic tidal surge caused redistribution of seals and

340   disruption of local social stability, the dominant males had approximately 50% less aggression compared

341   to the most subordinate males.

342   **Social stability and aggression**

343   Instead of dominance score showing a strong correlation to rates of aggression (Twiss 1991), we

344   found a strong association between increasing local social stability and lower rates and intensity of

345   aggression at the daily temporal scale. This relationship likely reflects the potential for greater mating

346   success through conservation of energy and prolonged tenure found in this and other closely related

347   systems (Twiss 1991; Twiss et al. 1994, 2006; Lidgard et al. 2005; Pörschmann et al. 2010; Bishop et al.

348   2015b). For other territorial species, the importance of local social stability is supported in that losing to a

349   stranger often results in expulsion from a territory, but a loss to a neighbor might only result in a small

350   loss of territory or a few resources (Husak and Fox 2003a, b; Bee 2003; Lachish and Goldizen 2004;

351   Booksmythe et al. 2010; Cross et al. 2013). For male gray seals, 'not losing' a position near females is

352   considered more important than 'winning' in terms of securing mating success (Anderson et al. 1975;

353   Anderson and Fedak 1985; Twiss 1991), and length of stay, not dominance, is an important driver of

354   mating success in pinniped breeding systems (Twiss 1991; Pörschmann et al. 2010). As such, individuals'

355   relative dominance scores, as measures of ability to 'win' (Drews 1993; Neumann et al. 2011), might not

356   determine rates of aggression if selection favours 'not losing'. Instead, regardless of dominance rank or

357   score, males might benefit when the local social neighborhood is stable by not having to defend their

358   positions to intruders, but only maintain the boundaries with their neighbors. Dominant males on North

359   Rona, Scotland, often maintained positions in the core of the colony where they were buffered from

360   exposure to 'roaming' transient males (Anderson et al. 1975; Twiss 1991; Twiss et al. 1994), therefore

361   the previous link between high dominance and lower aggression for gray seals could be an artefact of not

362   including appropriate spatial or social variables (Twiss 1991).

363   While it was not explicitly tested in this study, neighbor consistency is a key requirement for the

364   dear enemy phenomenon (DEP: Jaeger 1981; Getty 1987). Thus, the potential for DEP to be in effect in

365   this system merits some consideration. There is currently some evidence of individual recognition for

366   gray seals. Female gray seals exhibit some level of sociality not explained by spatial metrics alone

367   (Pomeroy et al. 2000, 2005; Insley et al. 2003; Ruddell et al. 2007; Robinson et al. 2015) and they also

368   have the capacity for discerning the identity of their pups (McCulloch et al. 1999; McCulloch and Boness

369   2000; Insley et al. 2003). Aggression was reduced amongst weaned gray seal pups of both sexes when

370   individuals had previous exposure to each other (Robinson et al. 2015). In other pinnipeds, male northern

371   elephant seals, *Mirounga angustirosis,* rely on characteristics of vocalizations to identify individuals

372   (Casey et al. 2013). Male gray seals exhibit spatial site-fidelity and roughly 30-40% return across years

373   (Twiss et al. 1994), suggesting males are exposed to similar individuals over time. However, to our

374   knowledge, there have not been any rigorous attempts to investigate individual recognition capability in

375   adult male gray seals. Therefore, at this time we cannot ascertain if the DEP, via local social stability, is

376   driving the observed reduction in rates and intensity of conflict male gray seals, but the evidence from

377   female gray seals and pups suggests that there could be a component of individual recognition in play.

378   Very little is known about DEP driving conflict reduction in wild systems which do not assort into clearly

379   defined territories. As controlled, paired-trials are not feasible for adult gray seals, a more comprehensive

380   examination of the role of local social stability and DEP would benefit by coupling neighbor similarity

381   metrics with auditory playbacks (Casey et al. 2013), visual or scent manipulations which test for

382   individual recognition (Cross et al. 2013), or hormonal analysis which can test for physiological

383   indicators of recognition (Robinson et al. 2015).

384   **Context-dependence of social and spatial variables**

385   The fine spatial and temporal-scale of the present study allows us to make some observations

386   about how natural environmental variation shapes conflict and conflict reduction. In the present study, the

387   correlates of male aggression appeared to be conserved across years; however, some factors such as male

388   proximity and neighbor similarity varied in the size or in the direction of their effect between years and

389   sites. There is evidence that the relationship between the local environment and conflict reduction is

390   context-dependent in other systems (Graham and Herberholz 2009; Tierney et al. 2013; Monclús et al.

391   2014). The presence of a female in the test arena reduced the effect of DEP for male pupfish *Cyprinodon*

392   *variegatus* (Leiser 2003), male Galápagos sea lions congregate in shaded areas during periods of thermal

393   stress (Wolf et al. 2005), and the location of aggressive behaviors for California sea lions, *Zalophus*

394   *californianus* were related to temperature (Bohórquez-Herrera et al. 2014).

395   Thermal stress, and the associated physiological responses, selects against high levels of

396   aggression in warm environments for animals such the mole-rat *Spalax ehrenbergi* (Ganem and Nevo

397   1996). Although gray seals breed in the autumn in temperate climates, they exhibit variation in behaviors

398   in relation to thermal stress and weather (Twiss et al. 2000, 2002, 20007; Redman et al 2001). Female

399   gray seals prefer breeding sites in close proximity to pools of water for the presumed function of

400   thermoregulation and as a source of drinking water (Stewart et al. 2014). In years with increased rainfall,

401   the variation in mating success between male gray seals was greater due to females not traveling to gain

402   access to pools and thus allowing for greater monopolization of mating opportunities (Twiss et al. 2007).

403   Increased topographic variation has also been associated with an overall reduction in conflict (Anderson

404   and Harwood 1985; Twiss et al. 1998). At Donna Nook, dunes and muddy wallows create fine-spatial

405   scale topographic variation at the PUB site. Aggression at this site was lower for dominant males, and

406   positively correlated with increased competitor proximity. However, at the flat RAF site, particularly in

407   wetter and colder years, neighbor stability appears to be most important for facilitating a reduction of

408   aggression. Due to only three seasons of data being available, additional data would be needed for any

409   firm conclusions to be drawn regarding the effects of broad weather patterns or differences in resource

410   availability on gray seal aggression. However, by investigating individual variation in aggression in the

411   wild at a fine temporal and spatial scale we have begun to unravel how individuals' aggression responds

412   to local environmental patterns, natural fluctuations, and subsequent changes in resource availability.

413   Similar methods can be applied to systems in which only large scale data has previously been available.

414   Finally, reductions in conflict driven by dominance hierarchies and DEP can be context-

415   dependent in regards to rapid changes in natural conditions (Graham and Herberholz 2009; Monclús et al.

416   2014). When features of the environment are highly variable, inter-individual differences in behaviors

417   can be masked or their effects diminished (Killen et al. 2013). At Donna Nook, in comparison to colonies

418   such as North Rona, Scotland, individuals are exposed to relatively greater environmental variability in

419   the form of daily tidal fluctuations due to the open access to the sea. Individuals are also exposed to

420   relatively greater anthropogenic presence due to the colony's position on the mainland coast. The

421   generally variable environment at Donna Nook could be increasing the costs associated with relying on

422   factors such as dominance under normal conditions, and instead be selecting for maintaining local social

423   stability as a means of reducing conflict. By using a fine-temporal scale measure of dominance, we found

424   that following the tidal event in 2011, when individuals' average local social stability were greatly

425   reduced, dominance was a stronger predictor of conflict reduction, even though under 'normal'

426   conditions, relying on this alone would presumably have a greater cost. This could again be evidence of

427   the strong selection for 'not losing' in this system (Anderson and Fedak 1985). Our work has begun to

428   discern the importance of including fine-scale variability measures, such as natural disturbance events

429   within a breeding season, when investigating the drivers of individual rates of aggression. Further work

430   which links measures of social stability, dominance and spatial distribution of resources to direct

431   measures of costs will be vital for predicting how individuals, colonies or populations will respond to

432   stressors such as anthropogenic presence or climate change.

433   **ETHICAL APPROVAL**
434   This study was observational in nature, and all work complies with the current UK laws of animal
435   welfare. All applicable international, national, and/or institutional guidelines for the care and use of
436   animals were followed.
437

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607

Figure Captions

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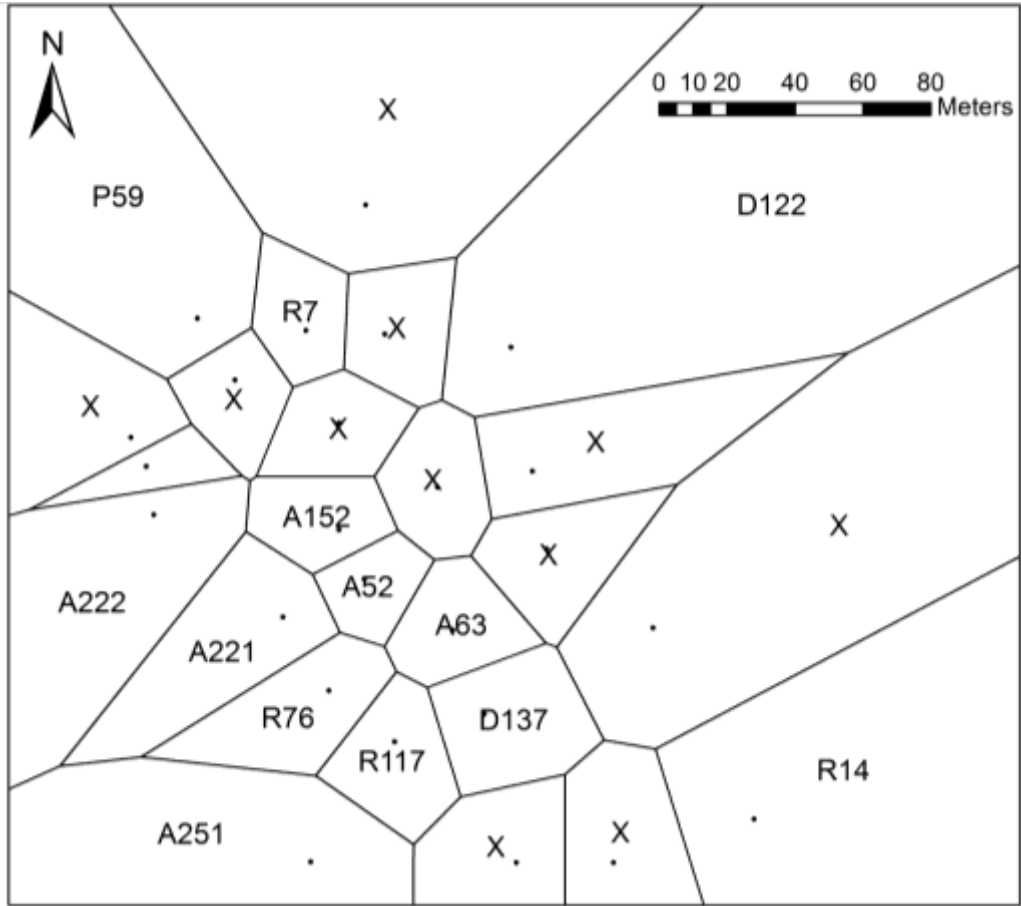
Fig. 2 The differences in (a) mean daily distance (m) to nearest male (DNM); (b) distance (m) to nearest female (DNF); and (c) neighbor similarity (NJSI, 0 = unstable, 1 = stable) at the RAF and PUB site pre and post tidal event in 2011 (Day of year 330). Boxes represent the interquartile range around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

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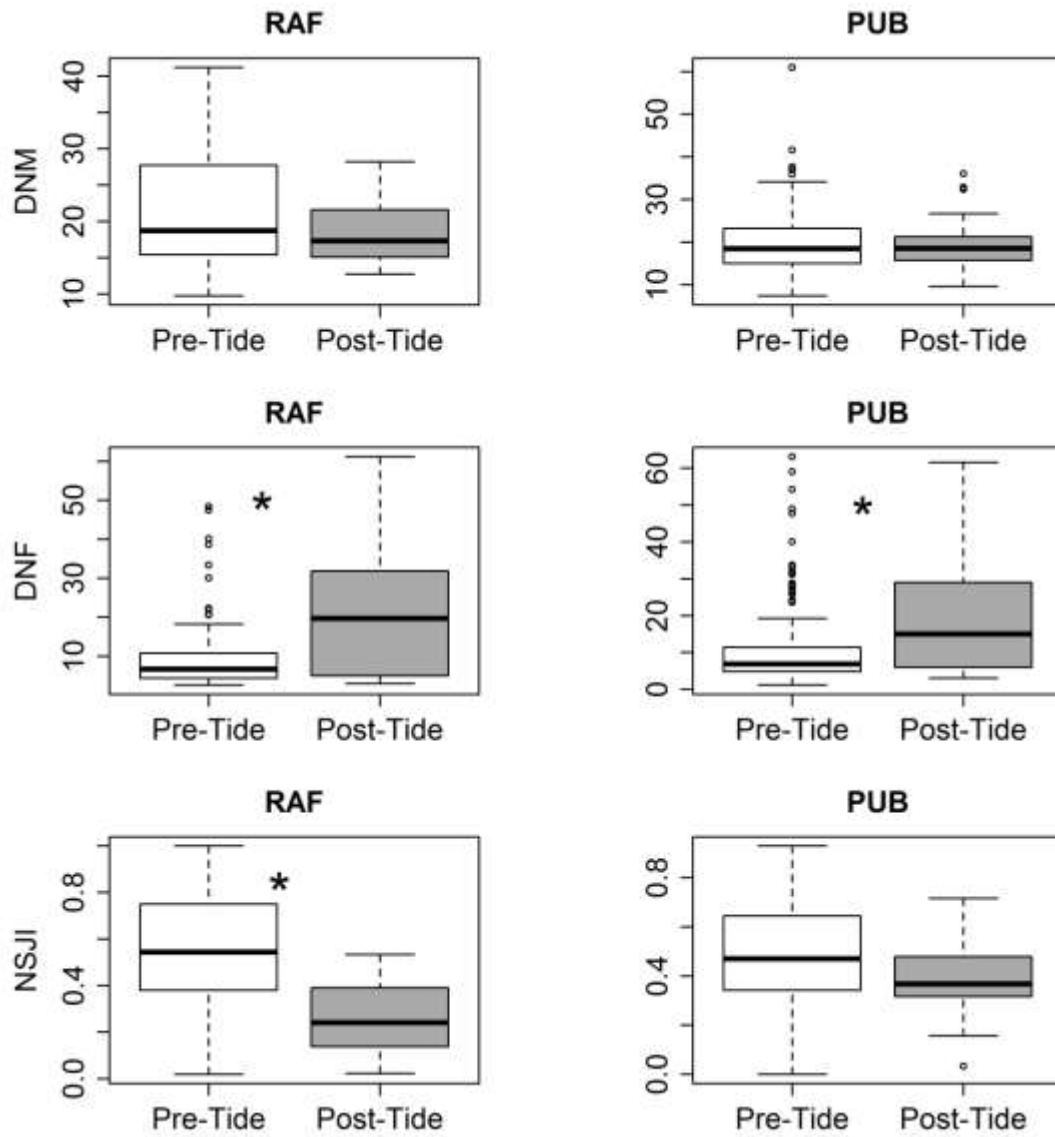
Fig. 4 The effects of (a) neighbor similarity (NJSI: 0 = unstable, 1 = stable) and (b) distance (m) to nearest male (DNM) in 2011, 2012 and 2013 on the probability of a male engaging in a contact AI on a given day. When SITE was retained as an interaction term; response of RAF (green) and PUB (yellow)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

631

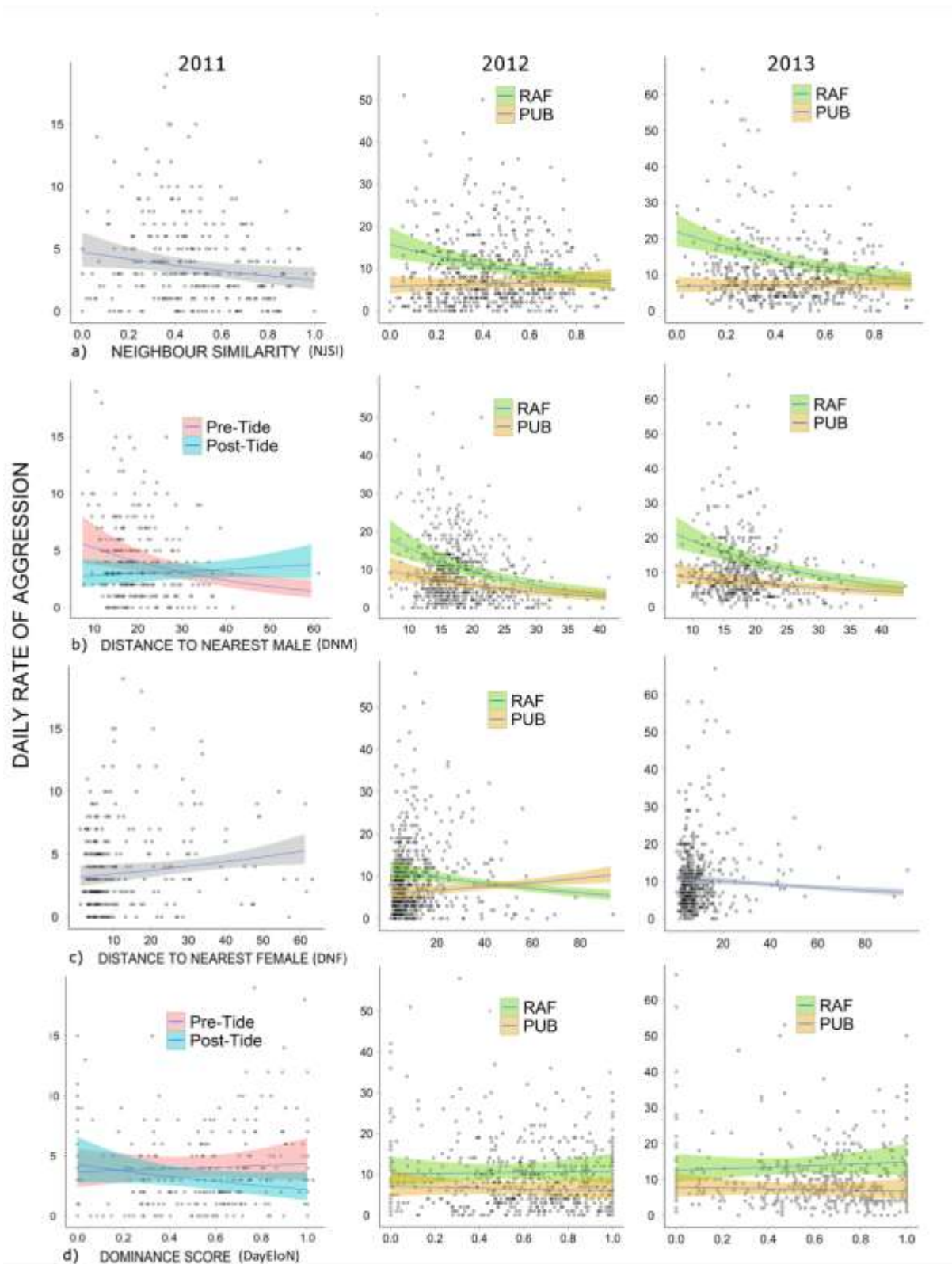632 **Fig. 1**

633

634   **Fig. 2**
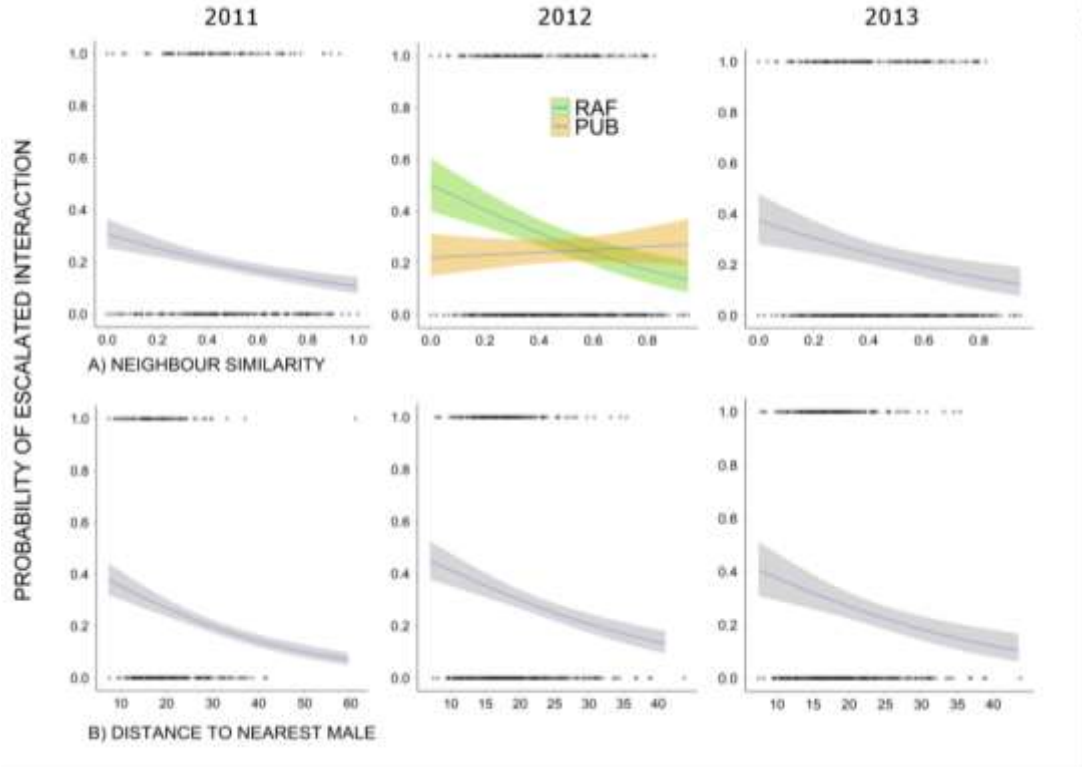
a) NEIGHBOUR SIMILARITY (NJSI)

b) DISTANCE TO NEAREST MALE (DNM)

c) DISTANCE TO NEAREST FEMALE (DNF)

d) DOMINANCE SCORE (DayEloN)

DAILY RATE OF AGGRESSION

635   **Fig. 3**

DAILY RATE OF AGGRESSION

a) NEIGHBOUR SIMILARITY (NJSI)

b) DISTANCE TO NEAREST MALE (DNM)

c) DISTANCE TO NEAREST FEMALE (DNF)

d) DOMINANCE SCORE (DayEloN)

636
637 **Fig. 3 (grayscale)**

638
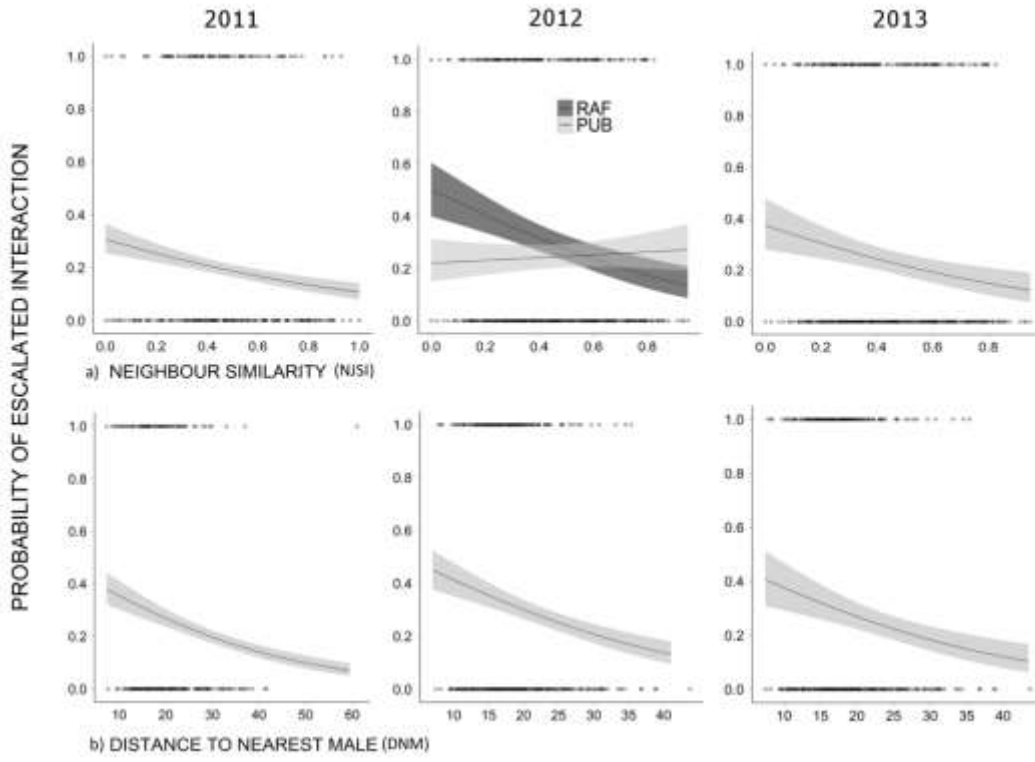
Fig. 4

Fig. 4 (grayscale)

Table 1 Retained GLMMs for predicting individual male DAI (daily rate of aggression) in 2011-2013. Random effects included in the models were MID (male ID) in 2011, and MID and OBSR (primary or secondary observer) in 2012

YEAR	AICc	ΔAIC	Weight
2011($N_{samples}$ =277, N_{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 ($N_{samples}$ =635, N_{MID} = 75, N_{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($N_{samples}$ =504, N_{MID} = 82, N_{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

†ELO = DayEloN; NJSI = neighbor similarity; DNF = distance to nearest female (m); DNM = distance to nearest male (m); TDEV = Tidal event 2011. All continuous predictor variables are averages per day

683 **Table 2** Coefficient estimates for the retained fixed effects in the best
684 models for predicting individuals' daily rates of aggression (ΔAIC $= 0$;
685 Table 1). All predictor variables are averages per day

YEAR		Coefficient Estimate	Standard Error	*P*-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

686 † ELO = DayEloN; NJSI = neighbor similarity; DNF = distance to nearest
687 female (m); DNM = distance to nearest male (m); Pre Tide = DOY < 330;
688 Post Tide = DOY ≥ 330

689   **Table 3** Retained GLMMs for predicting the probability of a contact AI (PF) per day
690   in 2011-2013. Random effects included in the models were MID in 2011, and MID
691   (male ID) and Observer (primary or secondary) in 2012

YEAR	AICc	ΔAIC	Weight
2011 ($N_{samples}$ =277, N_{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 ($N_{samples}$ =635, N_{MID} = 75, N_{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 ($N_{samples}$ =504, N_{MID} = 82, N_{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

692   † PF = Daily probability of escalating to a fight/contact AI. ELO = DayEloN; NJSI =
693   neighbor similarity; DNF = distance to nearest female (m); DNM = distance to nearest
694   male (m); TDEV = Tidal event 2011 only

695 **Table 4** Coefficient estimates for the retained fixed effects in the best
696 models across years for predicting the probability of an individual
697 engaging in an escalated interaction on a given day (ΔAIC = 0;
698 Table 3). All continuous predictor variables are averages per day

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

699 † ELO = DayEloN, NJSI = neighbor similarity; DNF = distance to
700 nearest female (m); DNM = distance to nearest male (m); Pre Tide =
701 DOY < 330; Post Tide = DOY ≥ 330 in 2011 only

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