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2 **analysis reveals importance of social and spatial stability**

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

32

33 **Abstract**

34 Aggressive interactions are costly for individuals in time, energy or physical damage, and in polygynous
35 mating systems, there is high variability in the rates and intensity of aggression across individuals and
36 within breeding seasons. However, examinations into the drivers of this variability are often conducted in
37 isolation, in non-wild systems, or the predictor variables in question, for example, dominance, are
38 averaged across large spatial, social, or temporal scales. The aim of this study was to adopt a fine spatial
39 and temporal scale approach to investigate the factors associated with inter-individual variation in
40 aggression in wild, breeding male gray seals within three consecutive breeding seasons. To do this, we fit
41 models examining if the daily frequency of aggression and probability of escalated aggression for males
42 was best explained by factors such as dominance score, proximity to competitors or females, local social
43 stability, and the occurrence of stochastic environmental events. Stability of neighbor identities was the
44 strongest correlate of reduced male aggression. Dominance status did not correlate with aggression at the
45 daily scale, with the exception of one period after a natural disturbance to the breeding colony where
46 dominant males had relatively reduced rates of aggression. These findings emphasize the importance of
47 local social stability in explaining inter-individual variation in aggression in a wild population, and
48 suggest that factors associated with aggression are context-dependent in relation to the natural
49 environment. Furthermore, we highlight the utility of a fine temporal scale and incorporating spatial
50 parameters when investigating variability in aggression in wild systems.

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54 INTRODUCTION

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

65 For social animals, the formation of a linear, transitive dominance hierarchy based on RHP
66 asymmetries between individuals can minimize costs associated with aggression. In stable hierarchies,
67 dominant individuals typically gain increased mating success (Anderson and Fedak 1985; Drews 1993;
68 Haley et al. 1994; Herberholz et al. 2007; Gerber et al. 2010), but an individual's position in the hierarchy
69 can also influence the rate or the probability of escalation (Rosenthal et al. 1992; Drews 1993;
70 Goessmann et al. 2000; Ang and Manica 2010). In some breeding systems, high rank is associated with a
71 greater intensity or increased frequency of aggression associated with defending a territory or mates
72 (Francis 1988; Rosenthal et al. 1992; Goessmann et al. 2000; Ang and Manica 2010). However, other
73 studies have demonstrated that dominant individuals have relatively reduced costs, and experience lower
74 rates or intensity of directed aggression in comparison to subordinates (Twiss 1991; Heitor et al. 2006;
75 Ostner et al. 2008).

76 These differing relationships between dominance and aggression might be driven by the spatial
77 distribution and social systems wherein the aggression occurs (Hemelrijk 2000). Alternatively, until
78 recently, the available methodologies for calculating an individuals' dominance score or rank were best
79 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; Bookmythe 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.

132 **Methods**

133 *Field Site*

134 Data were collected at the Donna Nook breeding colony on the North Lincolnshire coast, eastern
135 England (53.47°N, 0.15°E). Field observations were conducted during all daylight hours (mean = 8h
136 48min daily) across three autumn breeding seasons from 3 November to 12 December in 2011, and from
137 27 October – 12 December in 2012 and 2013. Weather patterns varied across study years. The 2011
138 breeding season was considerably warmer and drier relative to the other two years of study (mean air
139 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
140 mm per day; 2013: 2.14 mm per day).

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

152 *Male-male aggressive interactions*

153 Male-male aggressive interactions (AIs) were defined as any agonistic interaction between two or
154 more males (Twiss 1991; Bishop et al. 2014). Inter-male aggression is typically characterized by low-
155 cost, noncontact displays, but some interactions escalate to fights (Boness 1984; Twiss 1991). In the
156 preflight 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 ± 1 m at >100 m distance, and horizon
178 reference points to determine distance and location of males. Female gray seals typically move <10 m 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: $\text{DayElo}_N = (\text{DayElo}_{ID} - \min(\text{DayElo}_{\text{day}})) / (\text{Range of DayElo}_{\text{day}})$, 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 Thiessen polygons around each individual male using ArcMap 10.1 (ESRI; Fig.
232 1). Thiessen 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).

$$238 \quad (1) \text{ Neighbor Similarity} = \#Same / (\#Same + \#New + \#Lost)$$

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):

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

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 $\Delta 6$ AIC were retained,
281 and any models within this set that were more complex versions of their nested counterparts, but with
282 higher Δ AIC values, were excluded. Δ AIC values presented for "null models" represent the models with
283 no fixed effects, and only random effects.

284 RESULTS

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

286 Generally there was little evidence of inter-annual or site differences in average neighbor
 287 similarity (Neighbor Similarity: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 6.5$) or distance to male
 288 (Distance to Nearest Male: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 7.0$). Distance to the nearest
 289 female was significantly greater at the RAF site ($12.75 \pm 0.6m$ SE) than the PUB site ($9.98 \pm 0.4m$ SE) in
 290 all three years (Distance to Nearest Female: $\Delta AIC_{Site} = 0$, $\Delta AIC_{Null} = 6.9$), and there was also some
 291 evidence of interannual differences in distance to nearest female, with greatest distances observed in 2011
 292 ($13.29 \pm 0.9m$ SE, 2012: $11.25 \pm 0.5m$ SE, 2013: $9.79 \pm 0.6m$ SE; second best model: Distance to Nearest
 293 Female: $\Delta AIC_{Site + Year} = 2.7$, $\Delta AIC_{Null} = 6.9$).

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

295 Distances to the nearest male did not differ pre- and post-tidal event at either site (Distance to
 296 Male: $\Delta AIC_{Null} = 0$, second best model: $\Delta AIC_{Site} = 4.05$; Fig. 2a). The tidal event increased the distance to
 297 the nearest female from an average of $10.88m \pm 0.74$ SE pre-tidal event, and to 22.42 ± 1.49 SE following
 298 the tidal event, but there was no difference across sites (Distance to Female: $\Delta AIC_{Tidal} = 0$,
 299 $\Delta AIC_{Tidal+Site+Tidal*Site} = 6.9$, $\Delta AIC_{Null} = 18.51$, Fig. 2b). Individuals' neighbor similarity decreased after the
 300 tidal event from an average of 0.51 ± 0.015 SE, to 0.33 ± 0.01 SE, and there was some evidence that the
 301 tidal event resulted in a relatively greater reduction in neighbor similarity at the RAF site (Neighbor
 302 similarity: $\Delta AIC_{Tidal+Site+Tidal*Site} = 0$; $\Delta AIC_{Null} = 22.07$; Fig. 2c). However, the second-best model for
 303 neighbor similarity did not include the interaction between the tidal event and SITE (Neighbor similarity:
 304 $\Delta AIC_{Tidal} = 0.08$); suggesting the evidence for different effects across sites might be limited.

305 *Prediction of individual rates of aggression*

306 Models provided evidence that neighbor similarity and proximity to competitors were important
 307 factors explaining individual rates of aggression in all three years (Table 1). Increasing neighbor
 308 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).

330 **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 angustirostris*, 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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439 This study was funded by a Durham Doctoral Studentship awarded to author AB.

440 **CONFLICT OF INTEREST**

441 Author AB declares she has no conflict of interest. Author PP declares that he has no conflict of interest.

442 Author ST declares that he has no conflict of interest.

443

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608 **Figure Captions**

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

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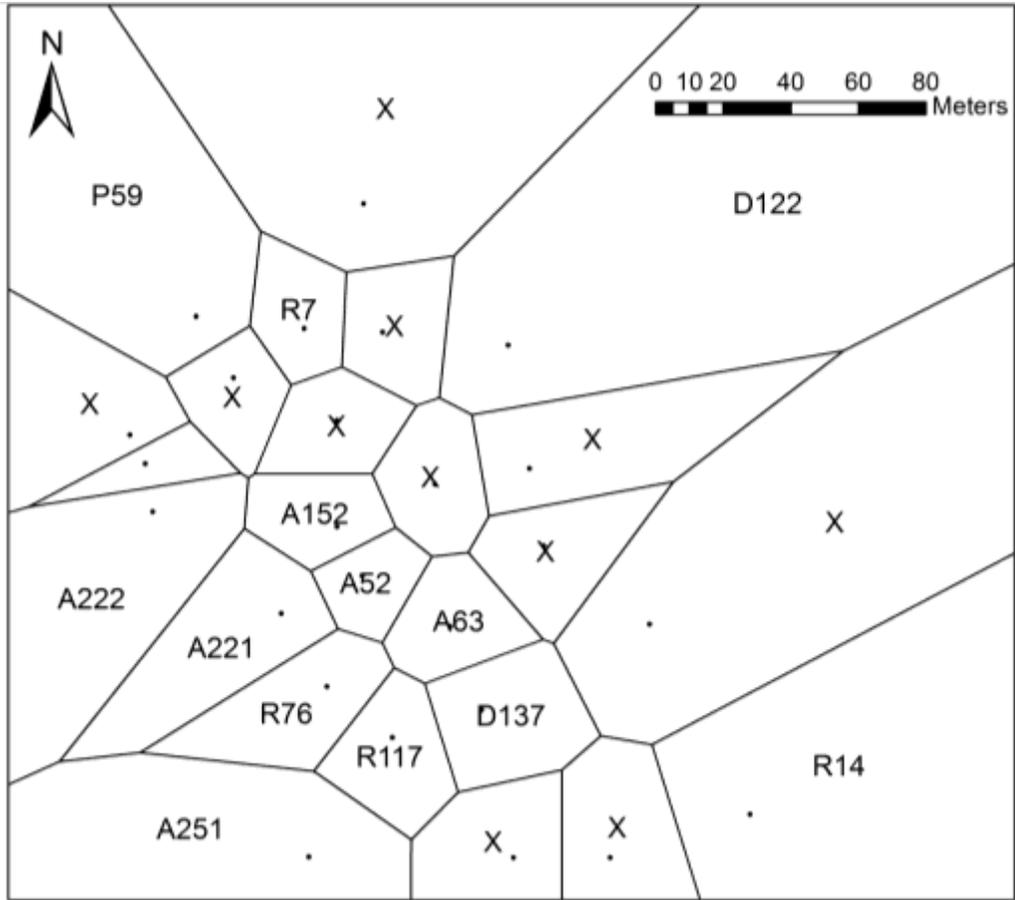
614 **Fig. 2** The differences in (a) mean daily distance (m) to nearest male (DNM); (b) distance (m) to nearest
615 female (DNF); and (c) neighbor similarity (NJSI, 0 = unstable, 1 = stable) at the RAF and PUB site pre
616 and post tidal event in 2011 (Day of year 330). Boxes represent the interquartile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

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620 **Fig. 3** The effects of (a) neighbor similarity (NJSI: 0 = unstable, 1 = stable); (b) distance (m) to nearest
621 male (DNM); (c) distance (m) to nearest female (DNF); and (d) Elo dominance score (DayEloN) in 2011,
622 2012 and 2013 on an individual males’ frequency of AIs daily. If there was an interaction effect of the
623 tidal event, separate responses are differentiated as pre-tidal event (Pink) and post-tidal (Blue). Similarly,
624 if SITE interacted the responses are differentiated as RAF (green) and PUB (orange). (Shaded area is
625 95% CI)

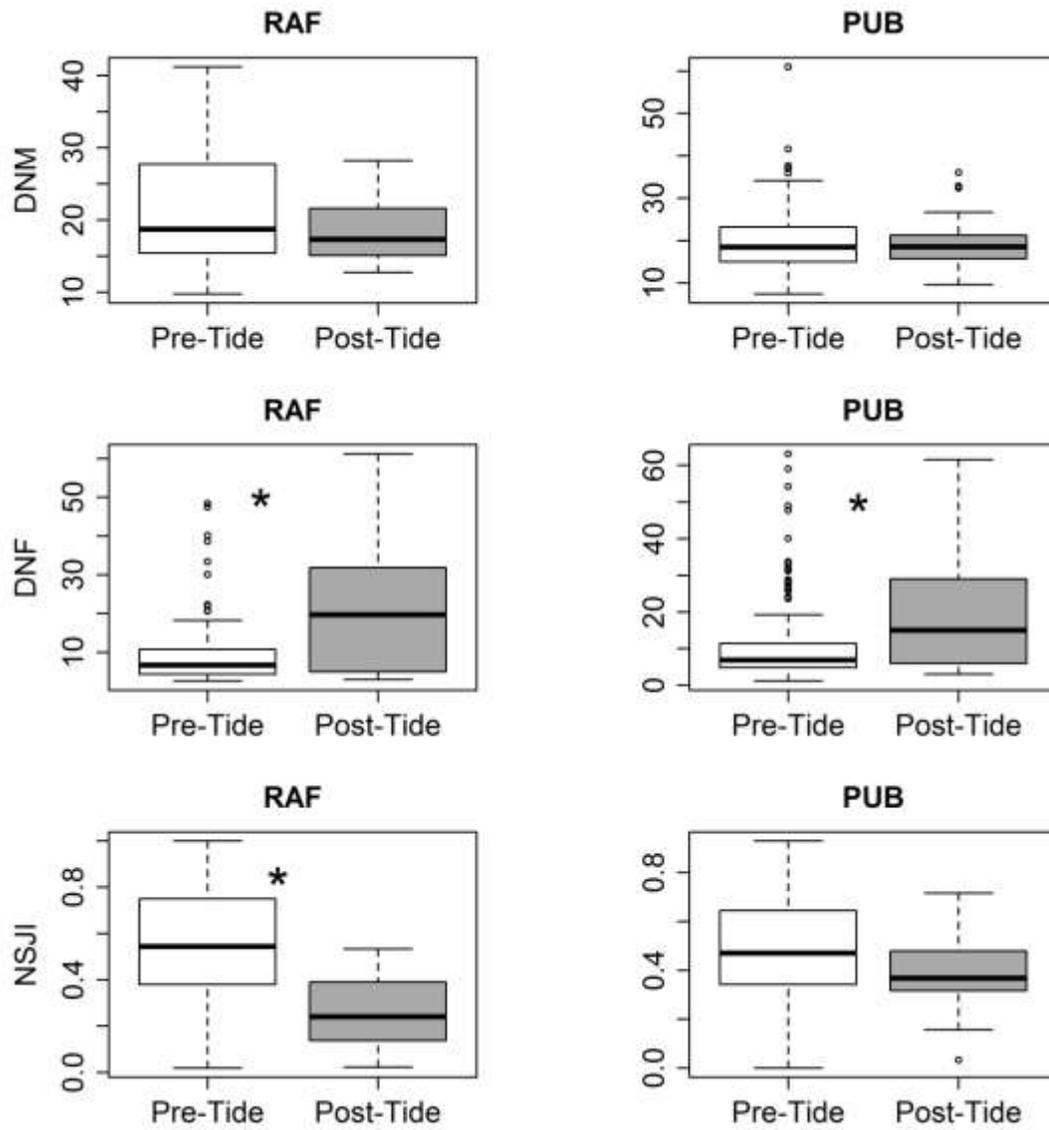
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627 **Fig. 4** The effects of (a) neighbor similarity (NJSI: 0 = unstable, 1 = stable) and (b) distance (m) to
628 nearest male (DNM) in 2011, 2012 and 2013 on the probability of a male engaging in a contact AI on a
629 given day. When SITE was retained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



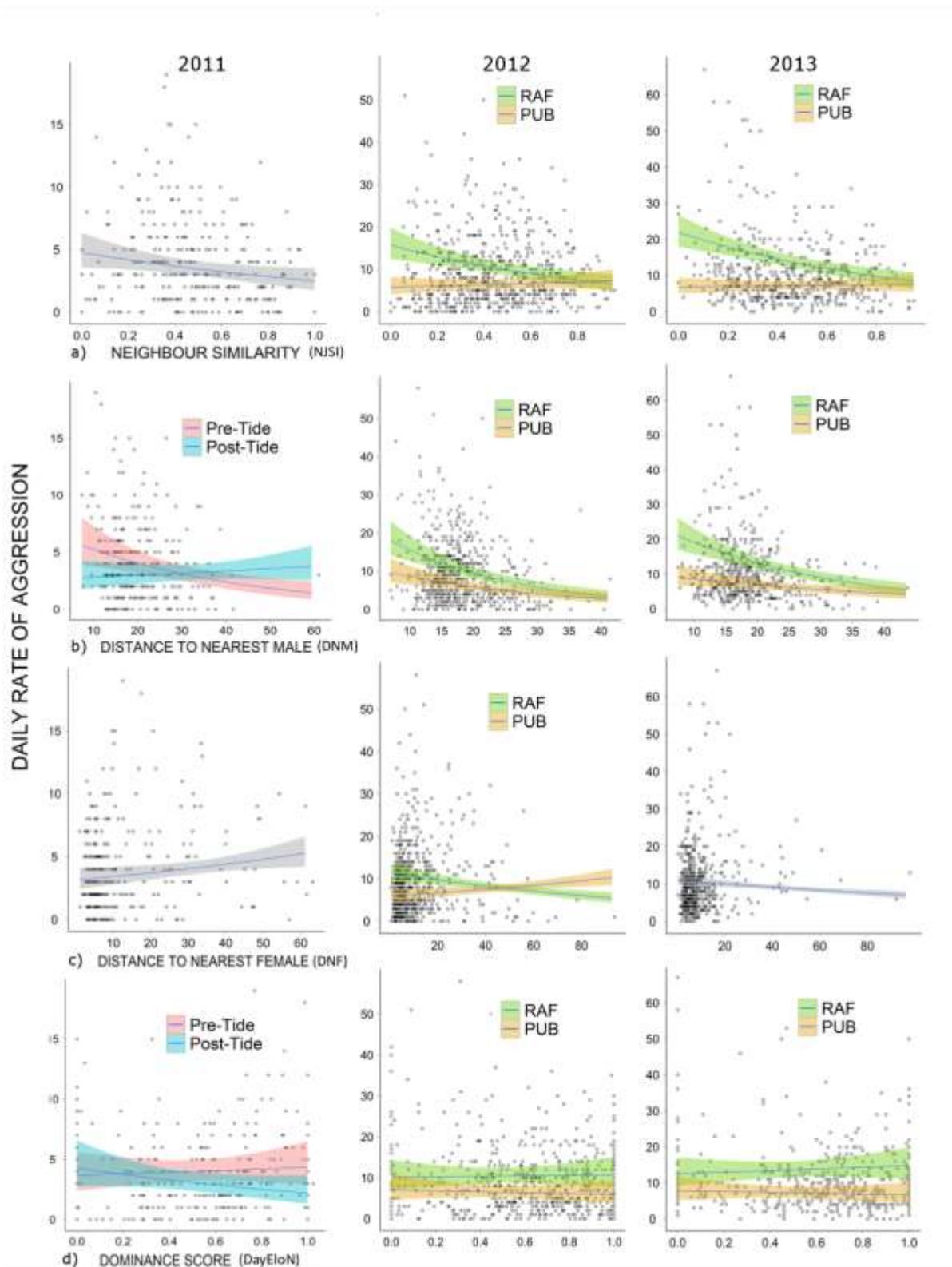
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632 **Fig. 1**

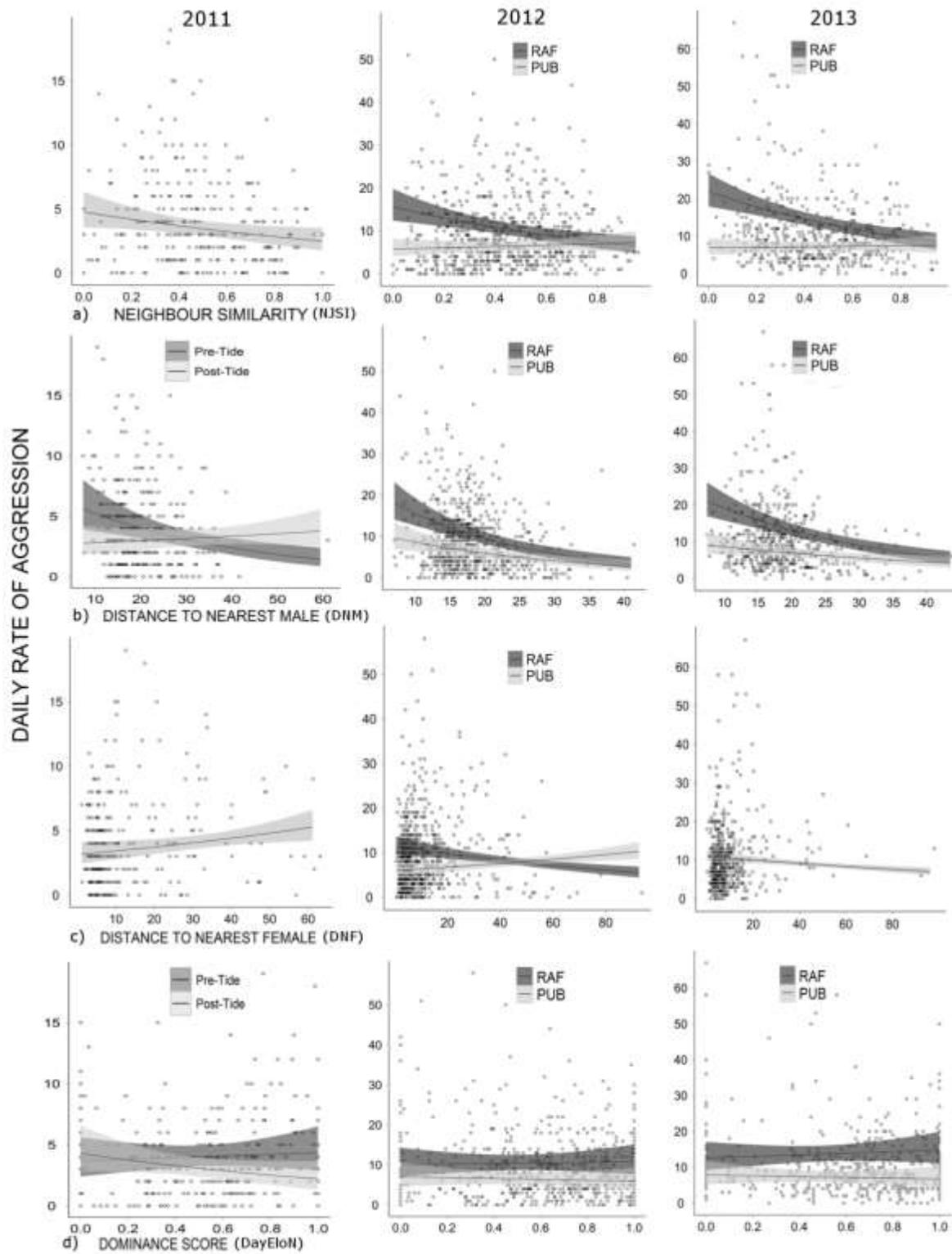


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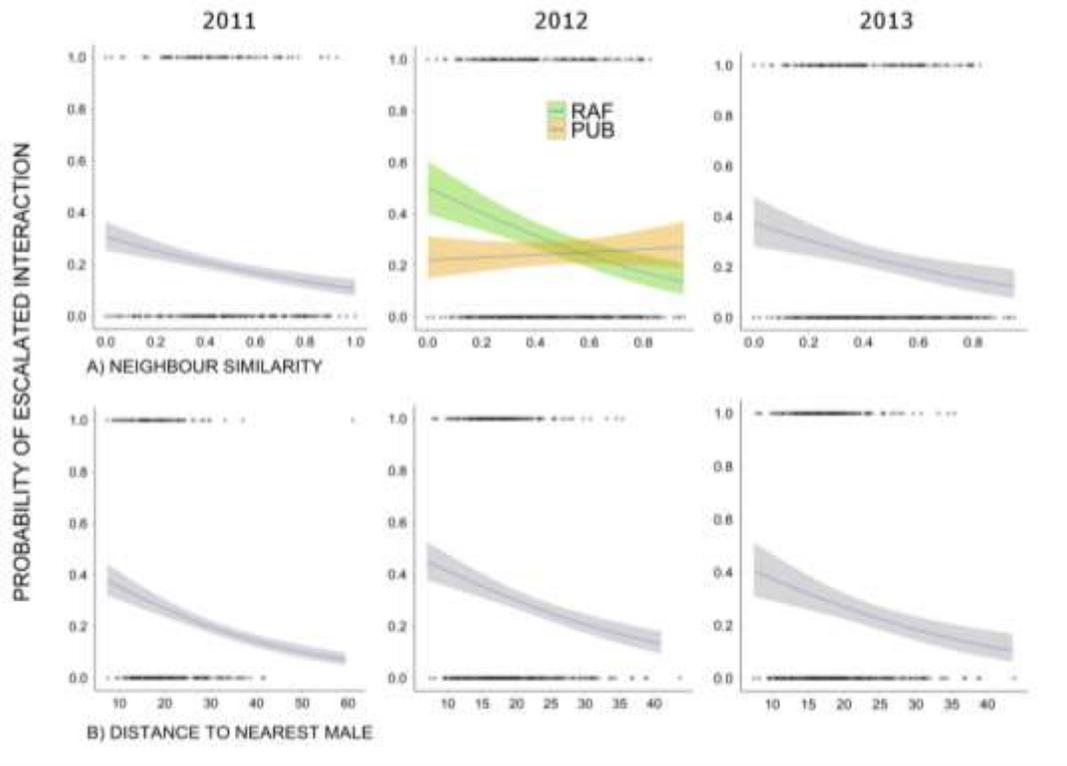
634 **Fig. 2**



635 Fig. 3



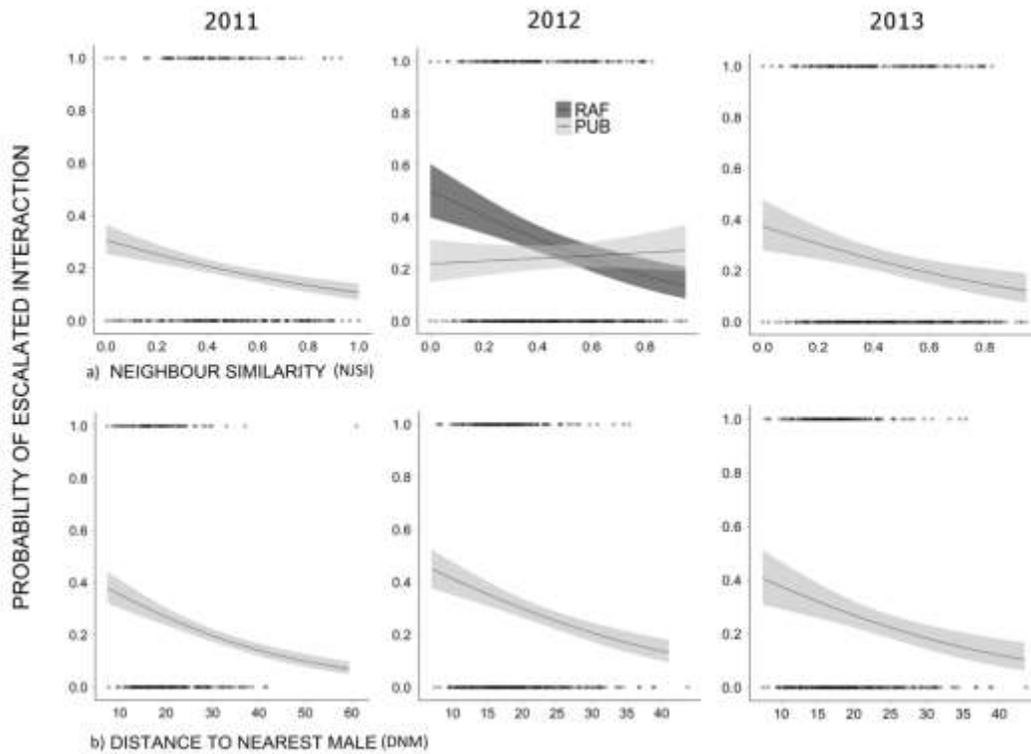
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Fig. 4

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Fig. 4 (grayscale)

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

YEAR	AICc	ΔAIC	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

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

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

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

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 ($\Delta AIC = 0$;
 698 Table 3). All continuous predictor variables are averages per day

YEAR		Coefficient Estimate	Standard Error	P-value
2011	<i>Intercept</i>	0.50	0.57	0.38
	<i>NJSI</i>	-1.42	0.63	0.02
	<i>DNM</i>	-0.04	0.02	0.04
	<i>ELO:PRE TIDE</i>	0.64	0.45	0.16
	<i>ELO:POST TIDE</i>	-0.70	0.64	0.28
2012	<i>Intercept:RAF</i>	1.63	0.63	0.01
	<i>Intercept:PUB</i>	-0.25	0.58	0.001
	<i>DNM</i>	-0.05	0.02	0.01
	<i>NJSI:RAF</i>	-2.06	0.72	0.004
	<i>NJSI:PUB</i>	0.30	0.70	0.67
	<i>DNF:RAF</i>	-0.04	0.01	0.005
	<i>DNF:PUB</i>	0.01	0.02	0.39
2013	<i>Intercept</i>	0.75	0.55	0.16
	<i>NJSI</i>	-1.62	0.52	0.002
	<i>DNM</i>	-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 \geq 330 in 2011 only

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