# Intra-seasonal temporal variation of reproductive effort for male grey seals

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# Abstract

Reproductive skew in polygynous mating systems leads to variation in the mating strategies, or the tactics within strategies, adopted by individual males. For example, variation in the timing of reproductive effort might reflect trade-offs between maximizing access to receptive females and minimizing interactions with competitors. For capital breeding grey seals (*Halichoerus grypus*), male mating success has been positively linked to total duration of tenure, but without differentiation of intra-seasonal changes in reproductive effort. The aims of this study were to identify tactics within the Tenured male strategy based on the timing of social dominance as a metric of reproductive effort, and to compare mating success across identified tactics. Our results confirm that duration of stay on the colony explained the most variation in mating success, but effect strength was reduced for tenures longer than 10 days. Additionally, there was evidence that timing of reproductive effort within a breeding season also contributed to observed variation in mating success. Males that maximized their dominance score at or after the peak in female attendance achieved greater mating success, relative to those who were dominant earlier in the breeding season. Males who timed their reproductive effort earlier in the season still achieved some mating success, but it was reduced. Individuals' tactics were flexible across years, and we found no evidence to support the hypotheses that timing of reproductive effort before or after the peak in female attendance was utilized by smaller Tenured males, or to avoid conflict. These results highlight that understanding temporal scheduling of individual reproductive effort within a breeding season, relative to the availability of resources, constraints of fasting, and intra-male competition, is a key aspect to consider when differentiating individual tactics in long-lived, capital, polygynous breeders.

**Highlights**

- Tenured male grey seals' dominance scores shift throughout the breeding season
- Date of peak dominance was used as a proxy for timing of reproductive effort (RE)
- Prolonged length of stay increased mating success non-linearly
- Timing peak RE at or after peak female attendance also increased mating success.
- Tenured male grey seals were flexible in their mating tactics across years

## Introduction

Mating patterns arise as a function of the spatial and temporal distribution of the limiting sex and the ability to monopolize mating opportunities (Emlen and Oring 1977). In polygynous mating systems, due to the increased conflict and competition for access to females, males often have exaggerated characteristics such as size (Jarman 1983, Carlini et al. 2006, Crocker et al. 2012), ornamentation (Brodsky 1988, Sneddon et al. 1997) or behavioural displays (Clutton-Brock and Albon 1979, Sanvito et al. 2006) that enhance individual fitness. The high reproductive skew in these systems also selects for variation in the mating strategies adopted by individual males (Smith 1982, Gross 1996, Shuster and Wade 2003, Lifjeld et al. 2011, Lidgard et al. 2012).

In spatially and temporally discrete breeding systems, length of stay has been positively correlated with male reproductive success, and so the evolutionary stable strategy is generally agreed to be 'come early, stay long' (Smith and Price 1973, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005, Nagy et al. 2012). Males adopting this strategy are typically referred to as 'dominant' or 'Tenured' and gain the highest reproductive success (Boness and James 1979, Ellis 1995). Alternatively, peripheral or 'Transient' males unable to hold territories or maintain access to females may engage in scramble competition. In these cases, mating opportunities are gained through opportunistic sneaky copulations, or intercepting females (Sandell and Liberg 1992, Lidgard et al. 2004, Huffard et al. 2008, Franco-Trecu et al. 2014, Meise et al. 2014).

Across both of these strategies, timing of arrival and reproductive effort for polygynous males can have implications for mating success (Clutton-Brock et al. 1979, Hoffman et al. 2003, Meise et al. 2014). Early arrival for males is often associated with long tenure and increased mating success (Twiss 1991, Arnould and Duck 1997). Late arrival can result in reduced mating opportunities if fewer sexually receptive females remain (Parker and Maniscalco 2014), or it can reduce costs by targeting periods when male-male competition is less intense (Mason et al. 2012). For example, peak reproductive effort for prime-aged male red deer (*Cervus elaphus*) coincides with female oestrus, and while younger males are present throughout the season, they peak in reproductive effort later (Mysterud et al. 2008). Young male alpine chamois (*Rupicapra rupicapra*) also exhibit greater reproductive effort in the later part of

56    the breeding season, presumably when competition with dominant, older males is reduced (Mason et

57    al. 2012).

58          The mating patterns of many pinniped species are characterized by moderate to extreme

59    polygyny and spatially and temporally discrete breeding seasons (Bartholomew 1970, Fitzpatrick et al.

60    2012, González-Suárez and Cassini 2014). Across most pinniped species, Tenured males that are larger

61    and more dominant tend to stay for longer periods of time, and the duration of an individuals' length of

62    stay within a breeding season shares a strong positive relationship with mating success (Anderson and

63    Fedak 1985, Twiss 1991, Arnould and Duck 1997, Lidgard et al. 2004, Carlini et al. 2006, Pörschmann

64    et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Franco-Trecu et al. 2014, Meise et al. 2014, Parker

65    and Maniscalco 2014). However, variation of alternative mating tactics within the Tenured strategy,

66    particularly with regard to timing of reproductive effort relative to female abundance, is less well-

67    understood. Studies often generalise timing of reproductive effort to pre- or peak-reproductive periods,

68    based on arrival (Meise et al. 2014) or implicitly assume within-individual reproductive behaviours are

69    uniform over-time and could be averaged across the breeding season (Twiss 1991, Twiss et al. 2006,

70    Lidgard et al. 2004, Franco-Trecu et al. 2014, Parker and Maniscalco 2014).

71          The tendency to select a coarse resolution for these investigations may be due to logistical

72    difficulties associated with quantifying within-individual and within-season variation in reproductive

73    effort. For example, mass loss is a common proxy for reproductive effort in ungulate studies (Mason et

74    al. 2012) and in studies of capital breeding pinnipeds (Anderson and Fedak 1985, Pomeroy et al. 1999b);

75    but such measures are typically calculated from one early capture and one late capture (Crocker et al.

76    2012), or at most using 3-4 captures throughout the season (Twiss 1991). This approach provides gross

77    seasonal changes, but is intrusive, and provides limited insight into continuous within-season variability

78    in reproductive effort. Quantifying changes in individual reproductive effort within a breeding season

79    might be approached using behavioural metrics that can be collected at a fine temporal resolution. One

80    such metric is dominance. Highly dominant Tenured male pinnipeds tend to have higher energetic

81    expenditures suggesting dominance can be a proxy for reproductive effort (Twiss 1991, Crocker et al.

82    2012). Additionally, dominance status relative to others on the colony is not uniform throughout an

83    individuals' tenure (Bishop et al. 2015b), and modern dominance-score calculation techniques such as

84 Elo scores (Neumann et al. 2011) that follow the sequence of outcomes of aggressive interactions for

85 individuals across time, can track these changes in social dominance at a daily temporal scale within a

86 breeding season. Being able to describe this variation in the scheduling and expression of dominance

87 within a season could therefore be a useful proxy for intra-seasonal variation in reproductive effort.

88      Grey seals (*Halichoerus grypus*) are an ideal study species to investigate the intra-seasonal

89 variation in timing of male reproductive effort. Grey seal breeding colonies form annually, typically at

90 remote offshore island sites, when females aggregate on shore to give birth to and nurse a single pup,

91 then mate with a male before weaning their pup and returning to sea (Boness and James 1979, Pomeroy

92 et al. 1999, Twiss et al. 2006). Traditionally, individual grey seal males are broadly classified into two

93 strategies: Tenured (present on the breeding colony for $\geq 2$ consecutive days and involved in $\geq 10$ male-

94 male aggressive interactions) or Transient (present for $< 2$ consecutive days; Boness and James 1979,

95 Boness 1984, Anderson and Fedak 1985, Twiss 1991). The Transient strategy is sometimes adopted by

96 younger males until a size/age threshold is met for Tenure (Twiss 1991, Lidgard et al. 2012), and several

97 different tactics within the Transient strategy have been described including: sneaking copulations,

98 failed attempts at Tenured strategies, and aquatic mating (Worthington Wilmer et al. 1999, Lidgard et

99 al. 2001, 2004, 2005, Twiss et al. 2006).

100      Although length of stay is positively correlated with mating success for grey seals (Anderson

101 and Fedak 1985, Twiss 1991, Lidgard et al. 2004, Lidgard et al. 2012), there is still considerable

102 variation in male reproductive success, aggressive behaviours, and timing of activities within breeding

103 seasons that has not been examined. Therefore, the aims of this study were to explore within the Tenured

104 male grey seal breeding strategy the role of within-season scheduling of dominance, as a proxy for

105 reproductive effort, and assess if timing of dominance can explain some of the variation in individual

106 mating success for male grey seals. We tested whether Tenured males who time their peak dominance

107 to synchronize with peak female availability achieved greater mating success or if timing provided no

108 additional benefits relative to length of stay. We predict that within the Tenured male strategy,

109 individuals who cannot achieve the maximum durations of stay (e.g. smaller males) will time their RE

110 early or later in the season to gain mating success. While this tactic has been suggested as a mechanism

111 for smaller males to avoid conflict with larger males (Mysterud et al. 2008, Mason et al. 2012), we

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112    predict that males peaking early or late in the season will engage in a greater frequency of aggressive

113    interactions as sex-ratios during these periods are male-skewed. Further, we examined if individuals

114    exhibited inter-annual consistency in their timing of reproductive effort to suggest the presence of

115    alternative male mating tactics within the Tenured strategy. By assessing the consistency in male's

116    tactics across consecutive years, this will provide initial insights into how flexible Tenured males are in

117    their responses to intra and inter-annual changes in resource availability.

118

## Methods

120    **Ethical Note**

121    This study was observational in nature, and all work was approved by Durham University

122    Animal Welfare Ethical Review Board and complied with ASAB ethics guidance and UK Home Office

123    legislation.

124    **Observational methods**

125    Fieldwork was carried out at the Donna Nook grey seal breeding colony on the mainland North

126    Lincolnshire coast, eastern England, 53.47ºN, 0.15ºE (Bishop et al. 2014). The habitat at the Donna

127    Nook colony is a mixture of shallow dunes, sand flats and marsh grass. Two main breeding aggregations

128    of females form within the Donna Nook colony: one at the waters' edge, and one at the dune line,

129    approximately 1 mile inland from the water's edge. All observations were conducted at the inland

130    aggregation. The breeding season at Donna Nook spans from late October through December with peak

131    pupping occurring around 23 November. Observations in the field were conducted 27 October -14

132    December 2012 (d = 49); and 27 October - 12 December 2013 (d = 47), during all available daylight

133    hours for an average of 8h 48m of observations daily. Observations were conducted from observational

134    hides at two locations within Donna Nook approximately 500m apart, and separated by a bend in the

135    dune line (Hide 1: 53.474° N, 0.155° E, Hide 2: 53.476° N, 0.148° E). Two observers alternated between

136    the two hides daily, allowing for full coverage of the site. A weekly walkthrough census was carried

137    out in both years by the head warden from the Lincolnshire Wildlife Trust, during which the total

138    number of adult females, adult males, and pups present were counted. Counts were used to generate

attendance pattern curves (Figure 1) that describe the relative timing of female and male attendance and pup production within and between years. Individual females remain ashore for 18-20 days, during which they give birth to a single pup, and wean the pup after approximately 18 days of nursing (Pomeroy et al. 1999b). Peak female attendance occurred on Julian Day 327 (Figure 1). Oestrus for female grey seals occurs during a very short window circa 16 days postpartum (Boness and James 1979, Pomeroy et al. 1999, Twiss et al. 2006). While the count of peak female attendance is comprised of females with pups that range in age from new-born through to almost weaned, it is evident from these attendance curves (Figure 1) that after JD 327 the number of females departing (and therefore not available for Tenured males to mate with) exceeds the number of arrivals and female attendance sharply declines, suggesting that peak female attendance is a conservative estimate of peak resource availability for Tenured males.
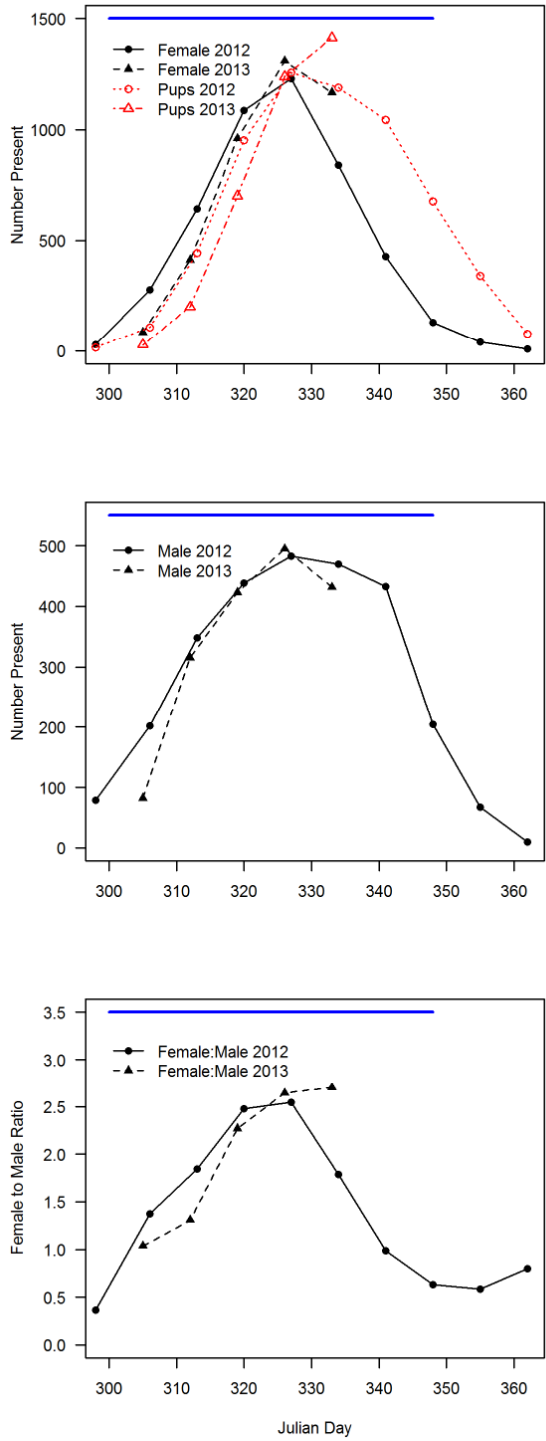
**Figure 1:** Weekly census counts for females and pups (a); males (b), and the female to male ratio (c) at Donna Nook in 2012-2013. Blue lines represent the extent of observations. Data past Julian Day 333 in 2013 (November 29) were not available due to atypical storm surge limiting capacity to conduct weekly counts of the entire colony. Data from: Lincolnshire Wildlife Trust

156    All males within the study areas were individually identified daily via pelage patterns and scars

157    in the field (Twiss et al. 1994), or *post hoc* from high-resolution pictures taken with a Canon EOS 30D,

158    100–400 mm lens. Locations of all males were mapped hourly on printed aerial photos of the colony

159    (Twiss 1991, Twiss et al. 1994, Bishop et al. 2015a, b). Incidences of aggression involving at least one

160    identified male were recorded by the observer with notation of participants' IDs and start and end times

161    (Bishop et al. 2015b). Aggressive interactions are attention grabbing and sufficiently rare, allowing all

162    occurrences to be recorded while performing other observations (Altmann, 1974). Male grey seals in

163    this study engaged in an average of 12 aggressive interactions per day (±0.6 se). The outcome of each

164    interaction was noted as either a Draw or Win-Loss. A male was determined to have won an encounter

165    if his opponent moved away or was chased away and lost his position amongst females; otherwise the

166    aggressive interaction outcome was defined as a draw (Anderson and Fedak 1985, Twiss 1991, Twiss

167    et al. 1998, Bishop et al. 2015b). Draws were included in this assessment because the key components

168    of maintaining position on the colony for grey seals are winning male-male contests, and engaging in

169    interactions that result in draws (Anderson and Fedak 1985). The average daily rate of aggression was

170    calculated for each male (Bishop et al. 2015b). Body length is a significant predictor of mass (Twiss

171    1991), and was used as our proxy for male size.  Photographs collected throughout the season were used

172    to calculate multiple estimates of standard length (nose-to-tail: range 166.1-240.3 cm ± 0.5-10.9 cm

173    SE) for each male using photogrammetry (Jacquet 2006, Bishop et al. 2015a). This method utilized

174    established formulas describing the linear relationship of how the ratio of the known length of an object

175    (cm) to the width of the object in a photograph (pixels) changes as distance from the camera increases

176    (Bishop et al. 2015a). Maximum estimated standard lengths for each male were used in this analysis.

177    For sexual activities, each copulation event was recorded as either an attempted copulation or

178    copulation, dependent on the absence or presence of intromission respectively. Copulations were also

179    sub-classified into successful or unsuccessful. 'Unsuccessful' copulations, where the male achieved

180    intromission but lost contact with the female after a short period of time due to factors such as female

181    aggression, have been shown to last no longer than 7 min on average (average total duration of a

182    'successful copulation' = 20min, Twiss 1991, Twiss et al. 2006). Therefore, we conservatively defined

183    a 'successful copulation' as a male remaining in the copulatory position for a minimum of 10 min

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184 without disturbance. With this criterion, we observed 313 instances of intromission but omitted 37

185 observations where the copulation was determined to be unsuccessful. As the timing of ejaculation is

186 unknown for this species, this definition might be underestimating individual reproductive success if

187 ejaculation occurs immediately following intromission. However, Twiss et al. (2006) found that over

188 80% of assigned paternities agreed with observations of the sexual behaviour, thus suggesting our

189 criterion provides a valid, if conservative, estimate of mating success from behavioural observations.

190 **Identifying timing of Dominance: a proxy for Reproductive Effort**

191 For comparability with previous studies on dominance and mating success for this species only

192 males present for ≥2d and who participated in >10 aggressive interactions were included in dominance

193 calculations (2012 $n = 74$, 2013 $n = 103$) as this ensures males were considered Tenured and engaged

194 in a sufficient number of interactions to calculate a dominance score (Boness and James 1979, Twiss

195 1991, Twiss et al. 1998, Bishop et al. 2015b).  Differences in the number of males between 2012 and

196 2013 are not a product of sampling effort, as duration and frequency of observations were identical

197 across these years, but likely reflect different male activity patterns. We calculated dominance as an Elo

198 score, a metric which estimates an individual's dominance along a sequence of aggressive interactions

199 (Porschmann et al. 2010, Neumann et al. 2011). The parameters of the Elo calculations were set with a

200 starting score of 1000 for every male and a $k$ of 200, where $k$ is the amount a male's score will shift

201 with a win, loss, or draw (0.5 * k) and is weighted by the score of his opponent (Neumann et al. 2011).

202 The constant $k$ can be set at any value between 16-200 (Neumann et al. 2011). Since not losing is key

203 for mating success and dominance for grey seals (Anderson and Fedak 1985), we set $k$ to maximise the

204 penalty for losing. Elo scores were updated following every aggressive interaction with another known

205 male. In the UK, tenured male grey seals that return to breed across multiple years exhibit site fidelity

206 and males do not shift in average dominance scores substantially between years (Twiss 1991, Twiss et

207 al. 1994). Therefore, we based Elo calculation on a continuous consecutive assessment across all years

208 males were observed to take into account previous season's reproductive success (Neumann et al. 2011).

209 To confirm that this did not disadvantage males starting with lower scores in their second year, we

210 calculated the mean Elo score for individuals in each season separately and found the difference in the

211 two calculations was an average of 18.75 (3.6% of total range). Scores were averaged daily (Figure 2)

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212     and the date on which the average score was greatest within a breeding season was used as our metric

213     for timing of high dominance: Peak Elo Day.

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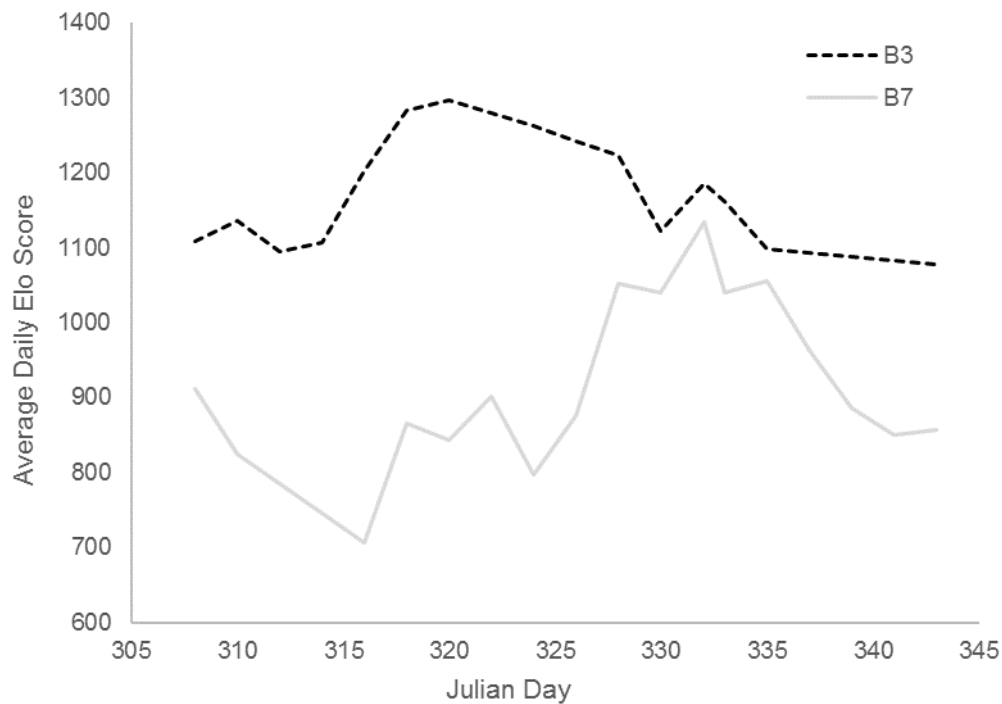


215

216     **Figure 2**: Examples of two males' dominance patterns within a breeding season; points represent the

217     males' average Elo score on a given day. "B3" peaked in dominance on Julian Day 320 after which his

218     score gradually declined, whereas "B7" started with a low Elo score, and then surged and peaked on

219     Julian Day 332.

220          **Statistical Analyses**

221          We first assessed if timing of peak dominance or duration of stay for male grey seals was

222     associated with specific size-classes or was a mechanism for conflict-reduction (Mason et al. 2012).

223     Our prediction was that males timing reproductive effort before or after peak female attendance would

224     be smaller, but both early and late males would have a higher average number of aggressive interactions

225     per day as at the start and end of the season there are relatively more males per female (Figure 1, Boness

226     et al. 1995) and social structures are less stable (Bishop et al. 2015b). We used generalized linear mixed-

227     effects models, GLMMs, with Poisson distributions (link=log) to test if males' estimated body length

228     and average number of aggressive interactions per day were predictors of timing of peak dominance

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229  (response variable = Peak Elo Day relative to date of peak female attendance on the colony), or duration

230  of stay (response variable = total number of days observed). Male ID and year were included as random

231  effects to account for pseudoreplication and observations within years being correlated (n = 150 records

232  with standard length estimates, 127 IDs, 2 Years). These models were fit using R package {lmer4}.

233      We then examined how timing of reproductive effort (via peak dominance) and duration of stay

234  contributed to the variation in observed mating success for Tenured males by fitting a generalized

235  additive mixed effects model (GAMM) with Poisson distribution that included Male ID and Year as

236  random effects to account for individuals present in multiple years and interannual variation (n = 177

237  observations, 153 IDs, 2 Years). These models were fit using R package {gamm4}. We chose to use a

238  GAMM as we predicted mating success would have a non-linear relationship with timing of peak

239  dominance, and GAMMs allow for fitting a mixture of linear and smoothed relationships. Our response

240  variable was the number of observed successful copulations, and predictor variables were all initially

241  set as smoothed-term factors: timing of peak dominance (Peak Elo Day), intensity of dominance

242  (dominance rank based on relative Elo score achieved on Peak Elo Day) and duration of stay (total

243  number of days observed on the colony). If the model output indicated that the estimated degree of

244  freedom for one of the covariates was 1.00 then the smoother function for that covariate was replaced

245  as a linear term (Ingram et al. 2007). Arrival date was considered for inclusion in the model but it shared

246  a positive co-linearity with length of stay and was therefore omitted. Our model selection criteria

247  incorporated $AIC_C$, a bias-corrected version of Akaike's Information Criterion that accounts for small

248  sample sizes. We use ΔAIC to denote the difference between the $AIC_C$ values of each model relative to

249  the lowest AICc value calculated, such that the 'best' $AIC_C$ model has ΔAIC = 0. Our final model set

250  included those models with ΔAIC < 6 that were not nested versions of simpler models. These criteria

251  prevent the selection of overly complex models (Richards 2008).

252      There were 24 Tenured males who were seen in both 2012 and 2013. To examine inter-annual

253  consistency in dominance partitioning and duration, males present across both breeding seasons were

254  examined for repeatability across years. Spearman's correlations between 2012 and 2013 were

255  calculated for Length of Stay, Arrival Date and Peak Elo Day.

# Results

**Male timing of dominance and length of stay**

Timing of peak male dominance score ranged from Julian Day 301 (October 28th) to 346 (December 12th), (median = 323) and appeared to have a bimodal distribution with greatest frequency of peaking at Julian Day 315, and then a secondary peak at Julian Day 330 (Fig.3a). On average, males peaked in dominance 7.8 days ± 0.7SE after arrival (range 0-39) (Fig.3b). Males stayed on the colony for a mean of 8.7 days ± 0.5SE (range 2-29).



N = 177  Bandwidth = 3.641          N = 177  Bandwidth = 3.074
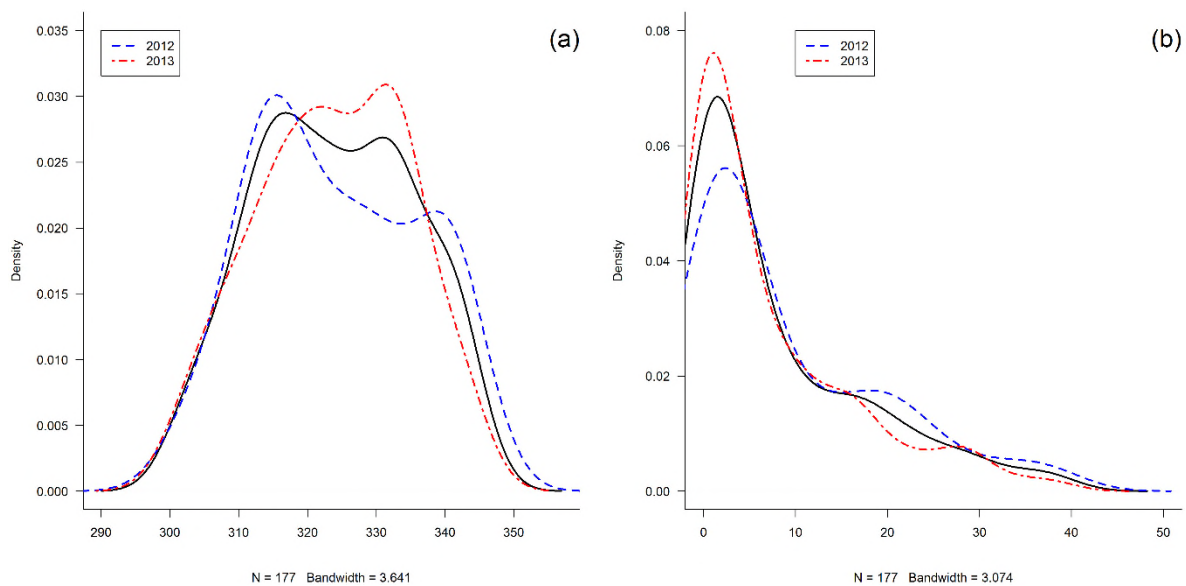
**Figure 3:** Kernel density plot representing the distribution of the date of peak Elo score (a) and of the number of days after arrival individuals peaked in dominance (b), across both years and all Tenured males combined (solid black line). Density for 2012 (n=74) and 2013 (n=103) are shown as blue and red lines respectively. Bandwidth represents the standard deviation of the smoothing kernel.

Both size and aggression were retained as predictors of a male's total length of stay (Table 1). Larger males stayed on the colony for longer and males with a greater average number of aggressive interactions per day stayed on the colony for a shorter duration (Table 1). Size and aggression were not significant predictors of timing of peak dominance (Table 1).

276 **Table 1:** Effect size (standard error), AIC$_c$, ΔAIC, and model weight from GLMMs predicting Peak Elo

277 Day (relative to peak female attendance, Julian Day 327) and length of stay on the colony. The null

278 model was best for predicting Peak Elo Day and the full model was best under selection criteria for

279 predicting days on colony. All models included male ID and year as random effects, (n = 150

280 observations, 127 IDs, 2 Years).

| Response | Model | SL (se) | DAI (se) | AIC$_C$ | ΔAIC | weight |
|---|---|---|---|---|---|---|
| Peak Elo Day (relative to peak female attendance) | Null | | | 1030.3 | 0 | 0.412 |
| | 1a | -0.0041 (0.0035) | | 1031.0 | 0.74 | 0.285 |
| | 1b | | -0.0054 (0.0078) | 1034.1 | 1.63 | 0.182 |
| | Full | -0.0040 (0.0035) | -0.0050 (0.0077) | 1037.1 | 2.47 | 0.120 |
| | | | | | | |
| Days on Colony | Full | 0.018 (0.003) | -0.030 (0.007) | 970.7 | 0 | 0.999 |
| | 1a | 0.017 (0.003) | | 984.4 | 13.6 | 0.001 |
| | 1b | | -0.027 (0.007) | 992.8 | 22.0 | 0 |
| | Null | | | 1002.5 | 31.8 | 0 |

*SL= estimated maximum standard length, DAI = Average number of aggressive interactions per day, se = standard error*

281

282 **Mating success**

283 Average male mating success was 1.56 ± 0.2 SE (range = 0-14). Length of stay and timing of

284 peak dominance were both retained as non-linear predictors of observed mating success (Table 2, Figure

285 4a). Intensity, the relative dominance rank achieved on day of peak Elo, had an estimated degree of

286 freedom of one in the full model. All models were re-run with this factor as a linear term but this did

287 not improve model performance and intensity was not retained. From the visualization of the smoothed

288 relationship between observed mating success and length of stay (Figure 4a), length of stay had an

289 initial positive relationship with observed mating success, but this effect became weaker for stays longer

290 than 10 days (Fig. 4a). Timing of peak dominance also shared a general trend of a positive relationship

291 with observed mating success (Figure 4b). Males peaking between Julian Day 308-318 (November 4-

292 14) had lower than average mating success, while males peaking between Julian Day 326-342

293 (November 22-December 8) had greater than average mating success (Fig.4b).

294

295 **Table 2:** Estimated degrees of freedom (smoothed-terms (s)), estimate and standard error (linear-terms),

296 AIC$_C$, ΔAIC, weight, and R-squared (R-sq) from the GAMMs predicting observed mating success. The

13

model with cubic splines of Peak Elo Day and Days on Colony was best under our selection criteria of

a model having a ΔAIC < 6 and not being a more complicated version of a nested model (Richards

2008). All models included male ID and year as random effects (n = 177 observations, 153 IDs, 2

Years).

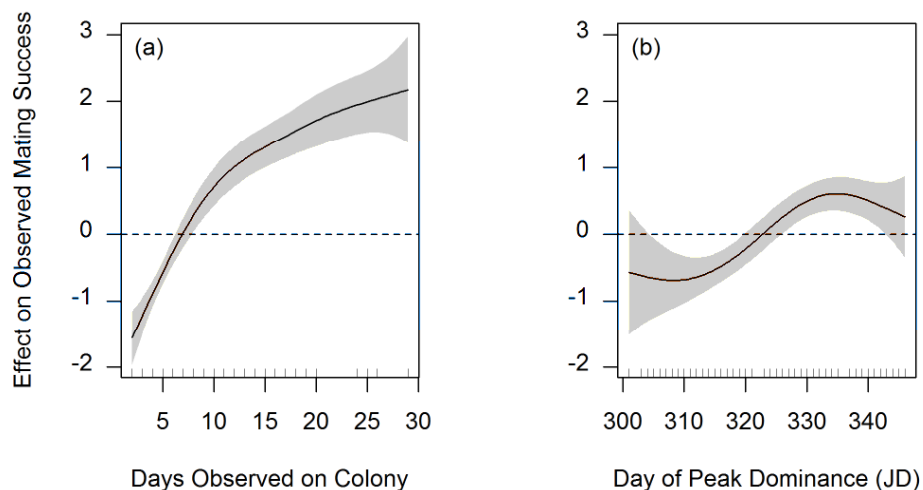| Model | s(Peak Elo Day) | s(Days on Colony) | Intensity | AIC$_C$ | ΔAIC | weight | R-sq |
|---|---|---|---|---|---|---|---|
| | Estimated Degrees of Freedom | | Estimate (se) | | | | |
| 1a | 3.085 | 3.041 | | 476.9 | 0.0 | 0.867 | 0.541 |
| Full | 3.179 | 2.959 | -0.02 (0.02) | 480.6 | 3.8 | 0.133 | 0.537 |
| 1b | | 3.296 | | 494.6 | 9.1 | 0.000 | 0.447 |
| 1c | | 3.298 | 0.01 (0.02) | 498.7 | 12.9 | 0.000 | 0.441 |
| Null | | | | 626.2 | 149.4 | 0.000 | - |



**Figure 4:** Estimated smoothing curves for GAMM describing the effect (a) Duration of Stay on the

Colony and (b) Timing of Peak Dominance (JD = Julian Day) have on observed mating success. The

solid black line indicates the smoothing curve, while the grey shaded area represent the approximate

95% confidence intervals. On the y-axis, 0 corresponds to no effect of the covariate, values >0 indicate

positive correlation and values < 0 indicate negative correlation. The effect, relative to the mean mating

success (dashed line), for a particular value of a covariate can be obtained as the natural anti-logarithm

of the corresponding y-axis value (sold black line).

**Consistency of individual's tactics**

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320        For the 24 males seen in both seasons, there was no consistency in timing of peak dominance

321    (*Spearman's Rank Correlation* r = 0.16, df = 22, *P* = 0.46), date of arrival (*Spearman's Rank*

322    *Correlation* r = 0.226, df = 22, *P* = 0.2865) or length of stay (*Spearman's Rank Correlation* r = -0.09,

323    df = 22, *P* = 0.66) between 2012 and 2013.

## Discussion

325        Timing of reproductive effort and its effect on mating success has been examined in several

326    species (Mysterud et al. 2008, Mason et al. 2012, Parker and Maniscalco 2014), but for species where

327    handling or repeat captures are difficult, assessments of within-season individual variation of timing of

328    reproductive effort have been limited. Additionally, prior to this study the general characteristic of

329    Tenure for grey seals has been that longer stays are positively associated with greater mating success

330    (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2004, Lidgard et al. 2012). By using

331    intraseasonal variation in dominance as our proxy for reproductive effort, we refine this understanding

332    and show using observational methods that within the generalized strategy of "Tenure", males that

333    timed their reproductive effort during or after peak female attendance had increased mating success,

334    and that timing reproductive effort later in the season resulted in more success than exerting high

335    reproductive effort early in the season. We found that larger males stayed longer and males with greater

336    rates of aggression had shorter stays, but contrary to our prediction, there was no evidence to suggest

337    that timing reproductive effort early or later in the season was associated with smaller males or greater

338    rates of aggressive interactions. Timing of reproductive effort for individuals was also not consistent

339    across the two years of the study, suggesting there may be individual behavioural flexibility or that

340    males might respond to shifts in localized conditions.

341        Assessing differences in attendance duration and timing of reproductive effort across

342    individuals enabled us to first examine if there were any patterns to the types of males exhibiting specific

343    temporal or attendance tactics. Our results indicated that individuals with greater size and fewer

344    aggressive interactions had longer lengths of stay. This matches previous work that has shown that, for

345    many polygynous species, the total energy available for fasting and the adoption of mechanisms that

346    reduce energetic expenditure are positively associated with mating success (Clutton-Brock and Albon

347    1979, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2001, McElligott et al. 2001, Lidgard et al.

348    2004, Twiss et al. 2006, Pörschmann et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Meise et al.

349    2014). With regards to timing however, we found no evidence to suggest size or rates of aggression

350    were predictive of male timing of reproductive effort. Late timing of reproductive effort has been

351    considered a conditional tactic that young or smaller individuals use to avoid costly interactions with

352    other larger males (Gross 1996, Mysterud et al. 2008, Mason et al. 2012), but may result in a greater

353    number of aggressive interactions between similar size/age class individuals as male-female sex ratios

354    draw closer to equivalent (Boness et al. 1995, Twiss et al. 1998).  It is possible we did not capture this

355    shift in size or aggression in our sampling window as our observations concluded approximately 15-20

356    days before all males had left the colony. However, our study captured the majority of the female

357    attendance duration and the associated decline in female:male ratios late in the season as females

358    departed, which is when we would have expected to see shifts in aggression (Fig 1). Future work

359    targeting this late period could help clarify the apparent absence in size-related associations with timing

360    of reproductive effort and would also provide the opportunity to look for other alternative tactics that

361    could be linked to timing of reproductive effort, such as inter-colony dispersal (Robertson et al. 2006).

362    For male grey seals, inter-colony movements are possible due to differences in breeding timing across

363    the UK (Coulson 1981) and could be tracked via observational methods and photo-ID networks (Hiby

364    et al. 2012, Patterson et al. 2013).

365        We found mating success had positive relationships with both duration of stay and timing of

366    reproductive effort. In contrast to previous work which suggested a linear relationship between male

367    duration of stay and mating success (Twiss 1991), we found that the relationship between length of stay

368    and mating success was non-linear, with a stronger effect when increasing tenure from 2-10 days,

369    followed by a reduced effect when males stayed for longer than 10 days. Winning, or more precisely

370    not losing, aggressive interactions is required to establish and maintain a position amongst females, and

371    increases an individual's dominance score (Anderson and Fedak 1985, Twiss et al. 1998), but

372    maintaining access to females can be costly in terms of metabolism (Copeland et al. 2011), stress

373    (Lidgard et al. 2008) or physical injury. Donna Nook is characterized by relatively high individual rates

374    of aggression and closer male-male proximity than observed on off-shore UK colonies such as North

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375 Rona (Twiss 1991, Bishop et al. 2015b). This may explain the discrepancy between previous findings

376 of a linear relationship between length of stay and mating success and the findings of the present study.

377 Our findings could suggest that at Donna Nook, the costs and risks associated with increased aggression

378 would be worthwhile early in a males' tenure on the colony as the marginal benefits of mating increase

379 substantially for each day longer they can remain. Then, as marginal benefits diminish with increasing

380 length of stay, other mechanisms might become more important to facilitate conservation of energy

381 instead of risky behaviours that could result in losing position. For example, it has been shown that

382 males which maintained local social stability through engaging in low-cost threat behaviours with

383 neighbours had fewer daily aggressive interactions on average, but that dominance score shared no

384 relationship with rate of aggression (Bishop et al. 2015b). In the present study, we found that males

385 with lower rates of aggression stayed longer, and length of stay positively predicted mating success.

386 Therefore, winning or maximizing dominance score is not the key driver in this system, but how

387 individuals achieve a balance in the trade-off between behaviours and energetics (fighting and fasting)

388 within a breeding season is important to consider in terms of predicting male fitness. It will be

389 informative for future work to examine of how differences in colony dynamics, topography, and

390 demography influence this apparent trade-off between aggression and fasting within breeding seasons.

391      Timing of peak dominance did share a relationship with mating success, with males peaking in

392 reproductive effort just before or during peak female attendance achieving a greater number of observed

393 copulations. A similar pattern has been observed for Steller sea lions (*Eumetopias jubatus*). Males in

394 centrally located territories, who maintained positions throughout female pupping had the greatest

395 relative mating success across years, but males that held sub-optimal territories and timed their arrival

396 to just prior to peak female attendance still achieved some mating success (Parker and Maniscalco

397 2014). In the present study, males who peaked in their reproductive effort early had poor mating success.

398 This finding is somewhat in contrast to other systems with spatially and temporally constrained breeding

399 seasons where early arrival and territory establishment is often associated with greater reproductive

400 fitness (Pomeroy et al. 1999, Smith and Moore 2005, Cordes and Thompson 2013). Some early breeding

401 female phocid seals have greater reproductive investment in their offspring and greater fitness than later

402 arrivals at breeding colonies (Boness et al. 1995, Cordes and Thompson 2013). We found a relatively

403  low number of copulations associated with the tactic of peaking early, so while males that express high

404  reproductive effort early might be targeting higher quality females, without a moderate length of stay

405  they could be experiencing greater risks of losing access to females before any mating success is

406  achieved.

407         Interannual variability in female arrival and reproductive phenology could further increase the

408  risks of early reproductive effort tactics if males experience temporal mismatch between timing their

409  reproductive effort and availability of their resource, oestrus females (Crick et al. 1997, Forrest and

410  Miller-Rushing 2010, Cordes and Thompson 2013). Nesting date for birds in the UK (Crick et al. 1997),

411  ringing date for seabirds (Møller et al. 2006), and pupping date for harbour seals, *Phoca vitulina*,

412  (Cordes and Thompson 2013) have shown advances over time which can be attributed to various factors

413  such as climate change, the North Atlantic Oscillation, or population density respectively. In our study,

414  female attendance and pup production in 2013 was approximately 5-7 days later than observed in 2012.

415  When species are exposed to variable environments, alternative mating tactics enable males to maintain

416  high levels of fitness across unpredictable fluctuations (Gross 1996, Meise et al. 2014). Populations

417  able to cope with disturbances are those that contain some portion of behaviourally flexible individuals

418  and such inter-individual variation can have profound consequences for how populations respond to

419  stress (Bolnick et al. 2003, Araújo et al. 2011, Carrete and Tella 2011, Violle et al. 2012). Across our

420  two study years, male grey seals did not appear to be consistent in their tactic in regards to arrival, peak

421  reproductive effort, or duration of stay; which could suggest their behavioural mechanisms for

422  optimizing mating success are reactive to local current conditions. Longitudinal data over a much longer

423  time period would be necessary to confirm if the differences we observed in individual, interannual

424  patterns of reproductive effort are in response to natural fluctuations in weather (Meise et al. 2014) and

425  phenological shifts in resources and mates (Forrest and Miller-Rushing 2010), or if any individuals

426  within the population are fixed in their behavioural tactics within the Tenured strategy (Twiss et al.

427  2012).

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