



Intraseasonal temporal variation of reproductive effort for male grey seals



Amanda M. Bishop^{a,*}, James E. Stewart^b, Patrick Pomeroy^c, Sean D. Twiss^a

^a Department of Biosciences, Durham University, Durham, U.K.

^b College of Life and Environmental Sciences, University of Exeter, Exeter, U.K.

^c Sea Mammal Research Unit, St Andrews University, St Andrews, Fife, U.K.

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Reproductive skew in polygynous mating systems leads to variation in 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 intraseasonal 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 used 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 intermale competition, is a key aspect to consider when differentiating individual tactics in long-lived, capital polygynous breeders.

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Mating patterns arise as a function of the spatial and temporal distribution of the limiting sex and the ability to monopolize mating opportunities (Emlen & 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 (Carlini, Poljak, Daneri, Marquez, & Negrete, 2006; Crocker, Houser, & Webb, 2012; Jarman, 1983), ornamentation (Brodsky, 1988; Sneddon, Huntingford, & Taylor, 1997) or behavioural displays (Clutton-Brock & Albon, 1979; Sanvito, Galimberti, & Miller, 2006) that enhance individual fitness. The high reproductive skew in these systems also selects for variation in the mating strategies adopted by individual males (Gross, 1996; Lidgard, Bowen, & Boness, 2012; Lifjeld et al., 2011; Shuster & Wade, 2003; Smith, 1982).

In spatially and temporally discrete breeding systems, length of stay has been positively correlated with male reproductive success, and so the evolutionarily stable strategy is generally agreed to be 'come early, stay long' (Anderson & Fedak, 1985; Lidgard, Boness, Bowen, & McMillan, 2005; Nagy, Knörnschild, Voigt, & Mayer, 2012; Smith & Price, 1973; Twiss, 1991). Males adopting this strategy are typically referred to as 'dominant' or 'tenured' and gain the highest reproductive success (Boness & 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 (Franco-Trecu, Costa, Schramm, Tassino, & Inchausti, 2014; Huffard, Caldwell, & Boneka, 2008; Lidgard, Boness, Bowen, McMillan, & Fleischer, 2004; Meise, Piedrahita, Krüger, & Trillmich, 2014; Sandell & Liberg, 1992).

Across both of these strategies, timing of arrival and reproductive effort for polygynous males can have implications for mating

* Correspondence: A. M. Bishop, Alaska SeaLife Center, 301 Railway Avenue, Seward, AK 99664, U.S.A.

E-mail address: amybi@alaskasealife.org (A. M. Bishop).

success (Clutton-Brock, Albon, Gibson, & Guinness, 1979; Hoffman, Boyd, & Amos, 2003; Meise et al., 2014). Early arrival for males is often associated with long tenure and increased mating success (Arnould & Duck, 1997; Twiss, 1991). Late arrival can result in reduced mating opportunities if fewer sexually receptive females remain (Parker & 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 (Myserud et al., 2008). Young male alpine chamois, *Rupicapra rupicapra*, also exhibit greater reproductive effort in the later part of the breeding season, presumably when competition with dominant, older males is reduced (Mason et al., 2012).

The mating patterns of many pinniped species are characterized by moderate to extreme polygyny and spatially and temporally discrete breeding seasons (Bartholomew, 1970; Fitzpatrick, Almbro, Gonzalez-Voyer, Kolm, & Simmons, 2012; González-Suárez & Casini, 2014). Across most pinniped species, tenured males that are larger and more dominant tend to stay for longer periods, and the duration of an individual's length of stay within a breeding season shares a strong positive relationship with mating success (Anderson & Fedak, 1985; Arnould & Duck, 1997; Carlini et al., 2006; Crocker et al., 2012; Franco-Trecu et al., 2014; Lidgard et al., 2004, 2012; Meise et al., 2014; Parker & Maniscalco, 2014; Pörschmann, Trillmich, Mueller, & Wolf, 2010; Twiss, 1991). However, variation in alternative mating tactics within the tenured strategy, particularly with regard to timing of reproductive effort relative to female abundance, is less well understood. Studies often generalize timing of reproductive effort to pre-reproductive or peak reproductive periods, based on arrival (Meise et al., 2014) or implicitly assume within-individual reproductive behaviours are uniform over time and could be averaged across the breeding season (Franco-Trecu et al., 2014; Lidgard et al., 2004; Parker & Maniscalco, 2014; Twiss, 1991; Twiss, Poland, Graves, & Pomeroy, 2006).

The tendency to select a coarse resolution for these investigations may be due to logistical difficulties associated with quantifying within-individual and within-season variation in reproductive effort. For example, mass loss is a common proxy for reproductive effort in ungulate studies (Mason et al., 2012) and in studies of capital breeding pinnipeds (Anderson & Fedak, 1985; Pomeroy, Fedak, Rothery, & Anderson, 1999); but such measures are typically calculated from one early capture and one late capture (Crocker et al., 2012), or at most using three to four captures throughout the season (Twiss, 1991). This approach provides gross seasonal changes, but is intrusive, and provides limited insight into continuous within-season variability in reproductive effort. Quantifying changes in individual reproductive effort within a breeding season might be approached using behavioural metrics that can be collected at a fine temporal resolution. One such metric is dominance. Highly dominant tenured male pinnipeds tend to have higher energetic expenditures, suggesting dominance can be a proxy for reproductive effort (Crocker et al., 2012; Twiss, 1991). Additionally, dominance status relative to others in the colony is not uniform throughout an individual's tenure (Bishop, Pomeroy, & Twiss, 2015), and modern dominance score calculation techniques such as Elo scores (Neumann et al., 2011) that follow the sequence of outcomes of aggressive interactions for individuals across time, can track these changes in social dominance at a daily temporal scale within a breeding season. Being able to describe this variation in the scheduling and expression of dominance within a season could therefore be a useful proxy for intraseasonal variation in reproductive effort.

Grey seals, *Halichoerus grypus*, are an ideal study species to investigate the intraseasonal variation in timing of male reproductive effort. Grey seal breeding colonies form annually, typically at remote offshore island sites, when females aggregate on shore to give birth to and nurse a single pup, then mate with a male before weaning their pup and returning to sea (Boness & James, 1979; Pomeroy, 1999; Twiss et al., 2006). Traditionally, individual grey seal males are broadly classified into two strategies: tenured (present on the breeding colony for ≥ 2 consecutive days and involved in ≥ 10 male–male aggressive interactions) or transient (present for < 2 consecutive days; Anderson & Fedak, 1985; Boness, 1984; Boness & James, 1979; Twiss, 1991). The transient strategy is sometimes adopted by younger males until a size/age threshold is met for tenure (Lidgard et al., 2012; Twiss, 1991), and several different tactics within the transient strategy have been described, including sneaking copulations, failed attempts at tenured strategies and aquatic mating (Lidgard, Boness, & Bowen, 2001, 2004, 2005; Twiss et al., 2006; Worthington, Allen, Pomeroy, Twiss, & Amos, 1999).

Although length of stay is positively correlated with mating success for grey seals (Anderson & Fedak, 1985; Lidgard et al., 2004, 2012; Twiss, 1991), there is still considerable variation in male reproductive success, aggressive behaviours and timing of activities within breeding seasons that has not been examined. Therefore, the aims of this study were to explore within the tenured male grey seal breeding strategy the role of within-season scheduling of dominance, as a proxy for reproductive effort, and assess whether timing of dominance can explain some of the variation in individual mating success for male grey seals. We tested whether tenured males who time their peak dominance to synchronize with peak female availability achieved greater mating success or whether timing provided no additional benefits relative to length of stay. We predicted that, within the tenured male strategy, individuals who could not achieve the maximum duration of stay (e.g. smaller males) would time their reproductive effort early or later in the season to gain mating success. While this tactic has been suggested as a mechanism for smaller males to avoid conflict with larger males (Mason et al., 2012; Myserud et al., 2008), we predicted that males peaking early or late in the season would engage in a greater frequency of aggressive interactions as sex ratios during these periods are male-skewed. Furthermore, we examined whether individuals exhibited interannual consistency in their timing of reproductive effort to suggest the presence of alternative male mating tactics within the tenured strategy. By assessing the consistency in male's tactics across consecutive years, this will provide initial insights into how flexible tenured males are in their responses to intra- and interannual changes in resource availability.

METHODS

Ethical Note

This study was observational in nature, and all work was approved by Durham University Animal Welfare Ethical Review Board and complied with ASAB/ABS ethics guidance and U.K. Home Office legislation.

Observational Methods

Fieldwork was carried out at the Donna Nook grey seal breeding colony on the mainland North Lincolnshire coast, eastern England, 53.47°N, 0.15°E (Bishop, Lidstone-Scott, Pomeroy, & Twiss, 2014). The habitat at the Donna Nook colony is a mixture of shallow dunes, sand flats and marsh grass. Two main breeding aggregations of females form within the Donna Nook colony: one at the water's

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