Behavioural mechanisms of conflict and conflict reduction in a wild breeding polygynous pinniped

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Behavioural mechanisms of conflict and conflict reduction in a wild breeding polygynous pinniped

By

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Abstract

Aggressive interactions arise as a means of resolving access to resources such as food, habitat or mates, but these interactions are often costly in time, energy, or physical damage. Therefore, natural selection favours social systems, spatial organisations and behavioural mechanisms which can balance the trade-offs between conflict and increasing fitness. The diversity of behaviours associated with animal conflict has been investigated in a variety of species; however, rarely are these investigations done in wild systems or with consideration of geographic and intra-seasonal variation in environmental factors, resource availability or social dynamics.

Therefore, the aim of this thesis was to examine the behavioural mechanisms underpinning population and individual conflict and conflict reduction at a variety of temporal and spatial scales. I focused my investigation on a particular form of animal contest, male-male breeding aggression, and used the colonial, wild grey seal (*Halichoerus grypus*) as my model. Specifically, I studied males at Donna Nook, an atypical breeding colony, in order to: (1) update our current knowledge of grey seal breeding systems by comparing the behavioural patterns at recently expanding mainland colony to previously examined, offshore colonies, (2) investigate the information present in a geographically isolated behaviour used in male grey seal conflict, (3) identify the variation in assessment strategies used by individuals in grey seal conflict and conflict reduction, (4) examine how environmental, anthropogenic, and social environments shape individual variation in aggression, and (5) assess the individual variation in decision-making processes such as mating strategies within- and across seasons.

Draws were identified as a common conflict outcome for male grey seals, and the acceptance of draws represented a behavioural mechanism which can promote conflict reduction. Assessment strategies relied on individual energetics when costs of conflict were high, but mutual assessment was used in low-cost contexts. Activity budgets were relatively conserved across colonies, and social stability played a key role in mediating conflict. These findings all demonstrate the trade-offs between conserving energy for reproductive activities and expending energy to ensure exploitation of resources. Methodological approaches which accounted for variation in individual partitioning of aggression and reproductive effort within- and between-seasons revealed that the relative importance of dominance as a driver of conflict, the use of specific aggressive behaviours, and broad assessment and mating strategies were all context-dependent at a variety of temporal and spatial scales.

Overall, these findings have provided new insights into the evolution of conflict and conflict reduction within polygynous mating systems. This work highlights the importance of incorporating the natural environmental variation and social dynamics into models of individual behaviours. Such approaches not only reveal the plasticity or consistency in how individuals deal with tradeoffs, but they also allow for observing the importance of behavioural mechanisms such as draws, which might have been ‘artificially selected out’ in controlled, laboratory settings. Finally, by using the grey seal breeding system as a model, this work has contributed to our knowledge of this species’ behavioural repertoire, and the role of topography in the evolution of polygyny and aggression in pinnipeds.

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported here has been conducted by the author unless stated otherwise.

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List of Abbreviations

Abbreviation: Definition (page first used/defined)

AI Aggressive interaction, can be Non-Contact or Contact (29)

BSP Presence of Body Slap behaviour in an aggressive interaction, present = 1 or absent= 0 (136)

CAM Cumulative assessment model (120)

CSL Centred standard body length, absolute value of maximum standard body length minus X cm (133)

CLA Centred body lateral area, absolute value of maximum lateral area of body minus X cm^2 (133)

CLUSTER The categorization of a male based on his duration and timing of dominance, 3 categories (183)

DAYEloN Normalized Elo dominance score (range 0-1); calculated using 3 year approach (150)

DAI Daily rate of aggression, number of AI per 8 h (35)

DN Donna Nook, England, breeding colony (60)

DNM Distance from focal male to nearest male in meters, calculated in ArcGIS 10 (52)

DNF Distance from focal male to nearest female in meters, calculated in ArcGIS 10 (52)

DOS Day of season, 27 Oct = 0 (1298)

DOY Day of Year, 0-365 (55)

DS David's score for dominance, calculated across an entire breeding season (95)

DURDRAW Duration of contest where outcome is a draw (127), definition o

DURTOT Total duration of a contest from first aggressive behaviour until end; contact or non-contact AI (127)

DURCT Duration of only the contact phase of a contact AI (127)

DurDom50% Duration (d) that a male's dominance score remained about his 50% threshold (181)

HDM Hourly distance moved in meters, distance between two hourly mapped points for focal male (70)

LRHP Loser's Resource Holding Potential (128)

$LRHP_0$ Resource holding potential of 'smaller' male in a draw, smaller being MSL is farther from 205 cm (129)

MSL Maximum standard body length in cm, estimated from photogrammetric measures (38)

MLA Maximum lateral area in cm^2, estimated from photogrammetric measures (38)

NJSI Neighbour Jaccard's similarity index, average similarity of neighbours between hours per day (152)

NR North Rona, Scotland, breeding colony (60)

OMT Open mouth threat aggressive behaviour (29)

PF Probability of engaging in a contact AI (fight) on a given day; 0 = none, 1 = at least one fight (166)

PK Prior knowledge, if two individuals in a contest have been observed previously engaging (128)

PUB The study site at Donna Nook with tourism, characterized by grassy dunes and wallows (22)

RAF The study site at Donna Nook closed to tourism characterized by flat sandy beach (22)

RE Reproductive effort; in this study, RE was defined by duration and timing of dominance (178)

RHP Resource holding potential, as the characteristics determining the outcome of a fight (3)

SI Sable Island, Canada, breeding colony (60)

TDEV Tidal event in 2011; 0 = pre tidal event; 1 = post tidal event (153)

WHRP Winner's Resource Holding Potential (128)

$WRHP_0$ Resource holding potential of 'larger' male in a draw, larger being MSL is closer to 205 cm (129)

Chapter 1

Introduction

1.1 The evolution of animal conflict

Much of our current knowledge of evolution and animal conflict began with the ponderings of Darwin in his *On the Origin of Species* (1859). In this, he argued that conflict arises in animal systems due to limited resources or limited access to resources. Since that initial hypothesis, a multitude of studies have investigated the selection of individual strategies, and how animals reduce costs while maximizing benefits towards their individual fitness (Darwin 1859, Maynard-Smith and Price 1973, Maynard-Smith 1979, Maynard-Smith and Harper 1988, Shuster and Wade 2003, Hardy and Briffa 2013). For example, Maynard-Smith and Price (1973) subsequently followed up much of Darwin's initial research by modelling the types of strategies animals might adopt in conflict situations and how selection acts on them in nature; their research produced the foundation on which a multitude of studies have since been conducted. At present, the role of conflict and conflict reduction, in particular the role conflict plays in breeding systems, has been studied across numerous taxa and across a variety of mating patterns in an attempt to better understand the selection pressures driving individuals in competition for resources (*Pinnipeds*: Anderson and Fedak 1985, Haley 1994, Twiss et al. 1998, Lidgard et al. 2005, Carlini et al. 2006, Pörschmann et al. 2010; *Cervids*: Dunbar et al. 1990, McElligott et al. 2001, Vannoni and McElligott 2008, *Primates:* Setchell et al. 2006, *Fish:* Johnsson and Forser 2002, *Invertebrates*: Kotiaho et al. 1997, Graham and Herberholz 2009, Painting and Holwell 2014, Palaoro et al. 2014). Here I examine the role of conflict and conflict reduction in a wild animal system which exhibits a polygynous breeding pattern, assess how individuals minimize costs while maximizing fitness, and investigate the social and environmental factors and behavioural mechanisms which contribute to the variation in individual aggression. First, I will review the current knowledge and provide a rationale for the specific aims of my research.

1.1.1 Total vs. limited wars

Species which have relatively high rates of aggression often exhibit phenotypes with weaponry (*e.g.*, the antlers on red deer, *Cervus elaphus;* or the horns of beetles (reviewed in Emlen 2008)), extreme size (*e.g.*, male elephant seals, *Mirounga sp.*) or stereotyped fighting styles (*e.g.*, fighting fish *Betta splendens*) (Maynard-Smith and Price 1973). Based on these phenotypes and the benefits of gaining access to resources, one might assume that animals in systems with highly contested resources should exhibit a 'total war' strategy, where fighting commences until one opponent is completely defeated (to the death). Yet, in natural observations, most aggressive encounters between individuals are settled with low-cost behaviours which involve minimal physical damage (Clutton-Brock and Albon 1979, Jennings et al. 2002, Boness and James 1979); death is exceptionally rare.

Group selection theorists would argue this form of 'limited war' is selected to benefit the species as a whole by not reducing population sizes; however, Maynard-Smith and Price (1973) considered this scenario under the constraints of individual level selection and found that 'limited-war' was also an evolutionarily stable strategy of individuals. In their paper on 'the Logic of Animal Conflict', Maynard-Smith and Price (1973) first considered the game theory model of a Hawk-Mouse scenario (later termed the "Hawk-Dove" model in Maynard-Smith 1979), where individuals either adopt low cost tactics or dangerous, costly tactics. Hawks were described as individuals that always adopted dangerous tactics while the mouse/dove strategist always displays low cost behaviours until faced with the possibility of receiving costs from facing a Hawk competitor, at which point the mouse/dove will retreat. The simulations confirmed that fighting to the death was not a stable strategy for individuals, but that they should escalate if presented with an opponent escalating (Maynard-Smith and Price 1973). Furthermore, selection favoured individuals which adopted mixed-strategies depending on competitor asymmetries, as this would provide pay-offs of saving time and energy and avoiding fatal damage, thus increasing individual fitness (Maynard-Smith and Harper 1988). Maynard-Smith and Price's work not only provided evidence for why total wars are not observed in nature, but set the foundations for examinations into individual strategies in animal conflict and for exploring the diversity of phenotypes and forms of conflict in nature.

1.1.2 Strategies within animal contests

Maynard-Smith and Price (1973) admitted their Hawk-Dove model was an over simplified version of actual animal conflict. In natural contexts, individuals exhibit extensive variation in not only the type of strategy but in the skill and intensity of the performance. This variation in fighting styles and decision making in contests became of increasing interest to animal behaviourists, and formed the basis for the study of animal assessment (Parker 1974, Maynard-Smith and Harper 1988, Taylor and Elwood 2003, Arnott and Elwood 2009). Under assessment theory, three main strategies were suggested through which animals make decisions concerning escalation and retreat during contests, and for which selection could still generate variability. The first was the war of attrition or an 'all-out fight' (Maynard-Smith 1974, Maynard-Smith and Harper 1988). In this scenario, there is no correlation between the resource holding potential (RHP), defined by Parker (1974) as a characteristic determining the outcome of a fight such as size, and winning. Instead, each individual has a threshold point for disengaging based on time or injury they are prepared to suffer. There are no signals of RHP exchanged between combatants. Secondly, the 'size game' (Maynard-Smith and Harper 1988) refers to contests settled by a size or weaponry. In this scenario, contests are won by the larger combatant and signalling of RHP may occur between individuals. The third model was termed ‘badges of dominance’ (Parker 1974, Maynard-Smith and Harper 1988). In this model, bigger individuals do not necessarily win, but combatants’ behaviours or phenotypes provide information regarding aggressiveness or RHP. Subsequently, the opponent with the relatively smaller RHP can back down without engaging or with minimal costs. An example of this would be the plumage colouration of birds signalling the likelihood of an individual winning a contest (Maynard-Smith and Harper 1988, Payne and Pagel 1997). Since the initial investigation and definition of these models by Maynard-Smith and Harper (1988), the models of assessment have changed in name from “war of attrition” to self-assessment, “size game” to cumulative assessment, and “badges of Dominance” to mutual assessment (Taylor and Elwood 2003, Arnott and Elwood 2009), but the definitions remain essentially the same. In Chapter 5, I further investigate the recent work on conflict assessment, the current state of the three models, and the variation in strategies across contexts.

1.1.3 Mating patterns as specialized forms of conflict

When mates are the contested resource, individuals engage in agonistic interactions to gain access to mating and reproductive opportunities (Emlen and Oring 1977). The distribution of mates spatially and temporally determines the ease of monopolization, and sexual selection will favour individual attributes that allow for monopolization of breeding opportunities (Emlen and Oring 1977, Shuster and Wade 2003). Therefore, the ecological constraints on monopolization are what determine the intensity of sexual selection and ultimately the ‘mating pattern’ (Shuster and Wade 2003). The three main categories of mating patterns are ‘polygynous’ in which males mate with multiple females, ‘polyandrous’ in which females mate with multiple males, and ‘monogamous’ in which both sexes only mate with a single individual within a breeding season (Shuster and Wade 2003).

While these terms provide some basic structure to the concept of mating patterns, there is still considerable variation within these categories in relation to the relative mating success of individuals. For example, in a system which exhibits the polygynous mating pattern some males will mate with multiple females, but others will achieve mating success with only one or perhaps no females. Therefore, this thesis will consider the differences in how individuals balance the trade-offs between energetically costly behaviours and the potential fitness benefits, and how the relative importance of different mechanisms of conflict and conflict reduction vary within broad mating patterns at the scale of the individual.

1.1.3.1 Types of polygyny

Polygynous mating patterns are typically used as models for examining male-male conflict as these mating patterns arise when female distributions are clustered spatially and access to the ‘resource’ is contested (Orians 1969, Emlen and Oring 1977). Male strategies within polygynous patterns can be broadly classified into three types of defence (Emlen and Oring 1977). In resource defence polygyny, males monopolize and defend resources or territories that are desired by females (Gemmell et al. 2001, Stamps and Krishnan 2001, Van Parijs et al. 2003, Wolf et al. 2007). An example of this would be the territorial scorpionflies (*Panorpa sp.*) in which males defend food (Thornhill 1981) and subsequently mate with females when they arrive to eat. The second sub-category of polygyny is female defence polygyny, or harem defence in which males sequester groups of females that are clustered (Emlen and Oring 1977, Haley 1994, Haley et al. 1994, Kelly 2006, Ang and Manica 2010). In this system, females are typically defended from intruding males but also prevented from leaving the harem. The model example of this strategy is the elephant seal (Le Boeuf 1974, Haley 1994), in which harem sizes can reach in excess of 200 females (Carlini et al. 2006) and intricate male alliances are formed to assist in the defence (Le Boeuf 1974). The final type of polygyny is the ‘Lek’: an extreme form of dominance polygyny exemplified by male black grouse (*Tetrao tetrix*). In leks, males are the contested resource, and female mate preferences are strongly based on male quality, as assessed through their relative positions in the lek group (Emlen and Oring 1977, Widemo and Owens 1995).

1.1.3.2 Characteristics of polygynous mating patterns

In both female and resource defence polygyny, competition and aggression occur as males attempt to gain direct or indirect access to females and secure mating opportunities with direct fitness benefits (Emlen and Oring 1977, Lindenfors et al. 2002). While aggression and conflict can help in attaining successful mating and individual fitness, such aggressive behaviours are not without costs. The allocation of time and energy into individuals’ aggressive behaviours should reflect how the marginal benefits (reproductive success) outweigh the costs; that is, a behavioural mechanism should be selected only if it achieves higher fitness *in relation* to the current next best alternative (Sandell and Liberg 1992). This is particularly relevant in polygynous species which are also capital breeders, such as the phocid seals, as energy available to expend on reproductive and aggressive behaviours is constrained by body condition on arrival (Anderson and Fedak 1985, Twiss 1991).

Due to the high potential for male-male conflict in systems with polygynous mating patterns, many species exhibiting female and resource defence are sexually dimorphic, with male phenotypes typically characterized as larger or “equipped” with more developed weaponry than females (Jarman 1983, Bartholomew 1970, Modig 1996, McElligott et al. 2001, Lidgard et al. 2005, Carlini et al. 2006, Milner et al. 2010). Additionally, dominance hierarchies, display behaviour, and conspicuous weaponry are selected for to facilitate the reduction of conflict and the probability of costly escalation (Krebs and Dawkins 1984, Preuschoft and Schiak 2000, Setchell et al. 2006, Vannoni and McElligott 2008, Arnott and Elwood 2009, Lifjeld et al. 2011). For example, high dominance rank is associated with increased mating success in many systems with polygynous mating patterns (Twiss 1991, Drews 1993, Anderson and Fedak 1985, Haley et al. 1994, Twiss et al. 2006, Herberholz et al. 2007, Gerber et al. 2010), but the formation and maintenance of dominance hierarchies often relies on mechanisms such as signalling, in which individuals are able to assess their potential opponent's RHP or dominance remotely and decide whether to engage or retreat (Maynard-Smith and Price 1973). Signalling can take the form of complex behavioural displays (Jennings et al. 2002), morphological structures (Parker 1974, Miller and Boness 1979, Haley et al. 1994, Vreys and Michiels 1997, Lidgard et al. 2005) or other sensory cues (Kotiaho et al. 1997). In this way, signalling provides a conventional way of resolving conflict and facilitating assessment of dominance relationships without entering 'total-war' scenarios (Maynard-Smith and Price 1973).

Social and environmental contexts can also mitigate or drive conflict and the probability of escalation in polygynous systems (Haley 1994, Tinker et al. 1995, Twiss et al. 1998, Millner et al. 2010). For example, the formation of stable territories, coupled with the behavioural mechanism of individual recognition, facilitates the emergence of the Dear Enemy Phenomenon as a form of conflict reduction (Jaeger 1981). Other spatial-social contexts such as increased group density and male-skewed sex ratios increase the rate of aggression in a mating pattern, as these factors can directly impact the degree of polygyny experienced (Tinker et al. 1995, Twiss et al. 1998). While the social, individual and environmental drivers of conflict and conflict reduction each have had some research attention, this thesis will address specific questions regarding: (1) the fine-scale environmental and social determinants of how and when interactions occur between individuals, (2) what assessment strategies individuals utilise during contests to address marginal costs and benefits of interacting and (3) how behavioural strategies for contests within the mating system correlate with individual fitness measures. Such information can help discern the evolution of conflict and conflict reduction within and across species (Arnott and Elwood 2009).

1.1.4 Evolution of polygynous, pinniped mating patterns

Due to the varying levels of polygyny across and within species, pinnipeds have been used frequently as a model for examining the evolution of conflict and conflict reduction. Male strategies within the polygynous mating pattern vary between phocids, otariids, and odobenids and may be described as resource defence, female defence, scramble, or lekking (Bartholomew 1970, Twiss et al. 1994, Gentry 1998, Carlini et al. 2006, Boness et al. 2006). The polygynous mating pattern in general, seen in pinnipeds today, evolved through their unique physiological, morphological and ecological adaptations to both terrestrial parturition and marine foraging (Bartholomew 1970, Emlen and Oring 1977, Lindenfors et al. 2002). For marine foraging, pinnipeds have morphological adaptations such as fusiform bodies for movement in water. As top predators with the ability to dive to considerable depths, both sexes of all pinnipeds have large surface-area to volume ratios (Bartholomew 1970). The insulating layer of blubber doubles as an energy source during the breeding season for both sexes, especially in the capital breeding phocids. This selection for large body size and the varying degrees of sexual dimorphism in many pinniped species (González-Suárez and Cassinni 2014) are both important drivers in polygynous mating species, as they allow males to fast while monopolizing females for long periods (Bartholomew 1970). Additionally, due to the relatively reduced mobility on terrestrial or ice substrates, and the temporally restricted pupping and breeding window, pinnipeds demonstrate spatial and temporal gregariousness in the terrestrial environment, which in turn promotes high levels of sexual selection acting on males competing for monopolization of spatially clustered females (Bartholomew 1970). While elephant seals and the northern fur seal (*Callorhinus ursinus*) both exemplify these driving selection pressures for sexual size dimorphism and extreme polygyny, there is still considerable variability in the expression of these factors amongst other pinniped species which seems to depend on the degree of terrestrialization and breeding site topography (*e.g.*, ice vs. land). For example, phocid species which still mate aquatically such as the harbour seal, *Phoca vitulina*, are considered some of the least size dimorphic of the pinnipeds and are not known to have high apparent polygyny (Bartholomew 1970, van Parijs et al. 2003, Boness et al. 2006). This inter- and intra-species diversity in the degree of polygyny, size dimorphism, and breeding habitats (Anderson and Harwood 1985, Tinker et al. 1995) exemplifies why pinnipeds are excellent study species for investigating the evolutionary pressures driving contest and conflict behaviours and individual fitness.

1.2 Approaches to studying male conflict and conflict reduction

A wide range of study animals, systems and methodologies are available to researchers investigating various aspects of animal contests (reviewed in Hardy and Briffa 2013). Studies often utilize captive animals, in laboratory controlled environments, to test specific hypotheses such as: the effects of audiences on aggression (Leiser 2003, Fitzsimmons and Bertram 2013), opponent familiarity (Dzieweczynski et al. 2012, Granroth-Wilding and Magurran 2013), the role of size in aggression (Poulos and McCormick 2014, Painting and Holwell 2014), signalling of RHP (Briffa et al. 1998), eco-physiological variables (Ganem and Nevo 1996) and many others. The controlled environment approach provides the utility of holding potentially conflicting variables constant (Briffa et al. 1998, Leiser 2003, Höjesjö et al. 2004, Booksmythe et al. 2010), which in turns allows for specific questions to be addressed. As contests consist of an interaction between two or more players, laboratory trials investigating male-male conflict typically take the form of 'arena tests' (Leiser 2003, Goessmann et al. 2000, Höjesjö et al. 2004, Kelly 2006, Booksmythe et al. 2010) where data on outcomes, durations or changes in behaviours (contest dynamics) can be recorded (Hardy and Briffa 2013).

While arena tests are useful tools, contests occur in the wild under a variety of environmental and social contexts which each might change within and between years. Furthermore, it has recently been argued that fitness predictions of growth or survival which were based on laboratory assessments of consistency and flexibility might not be suitable for extrapolation across the natural environmental contexts (Adriaenssens and Johnsson 2010). Thus studies investigating individual plasticity in behavioural phenotypes and mechanisms of conflict reduction would ideally be conducted *in situ.* This, however, presents challenges. Due to logistic constraints, finding systems and model taxa from wild populations that are suitable for examining questions regarding mating patterns, conflict and conflict reduction is a difficult task. Many studies which investigate conflict and conflict reduction in wild populations have utilized populations of ungulates (Ozoga 1972, Clutton-Brock and Albon 1979, Clutton-Brock et al. 1979, Jennings et al. 2012) or pinnipeds (Sullivan 1982, Haley 1994, Haley et al. 1994, Wolf et al. 2007, Gerber et al. 2010, Pörschmann et al. 2010, Crocker et al. 2014) likely due to their highly stereotyped sexual dimorphism, high apparent polygyny, and stereotyped contests between males in competition for access to females. Less extensive coverage has been given to other wild systems. For example, many studies on contest behaviour in crustaceans have been conducted in laboratories (see: Hardy and Briffa 2013) but wild *Uca sp.* have been used to look at short term effects of prior residence (Milner et al. 2011) or predation risk (Reaney and Backwell 2007). Examples from other species include: eavesdropping in wild little blue penguins, *Eudyptula minor* (Mouterde et al. 2012), and the extensive work with Caribbean anoles (*Anolis aeneas*) done by Stamps and Krishnan (1995). In both the penguin and anole examples, researchers investigated wild systems but still used experimental manipulations in the form of acoustic playbacks or release of juveniles into patches of habitat respectively. A comprehensive review of the prevalence and extent of wild versus laboratory studies investigating animal conflict and contest behaviour is beyond the scope of this chapter or thesis, but these examples highlight the overarching paradigms for the methods and systems most commonly used to address questions regarding animal contests.

While less common than laboratory studies, studies utilizing behavioural observations of wild populations with or without experimental manipulations have contributed considerable information to the present knowledge of mating patterns and animal conflict. Natural variation in breeding site topography and environments has been linked to variation in individual rates of aggression (Fabiani et al. 2004, Bohórquez et al. 2014) and as mentioned previously, much of our knowledge on the ‘Size Game’ (Maynard-Smith and Harper 1988) has been derived from species such as elephant seals (LeBoeuf 1974, Haley et al. 1994, Sanvito et al. 2007a, b). However, due to the lack of control of external variables in many *in situ* studies and the methodological or statistical constraints in the past, factors such as male size, dominance, aggression and mating success were sometimes analysed as averages across discrete breeding seasons or at the level of an individual within a breeding season (Anderson and Fedak 1985, Twiss 1991, Haley et al. 1994, Lidgard et al. 2005, Pörschmann et al. 2010). While this method has likely been adopted due to logistic or methodological constraints, it ignores how individuals respond to immediate, environmental fluctuations at a fine temporal or spatial scale. Thus, this thesis will use fine-scale *in situ* approaches to examine how individual aggression, mating success, reproductive effort, dominance or spatial distributions vary at a fine-temporal and spatial scale, and if individual factors and behaviours are constrained by broader longer term strategies or selection pressures.

1.3 Grey seals as a study system for animal contest behaviour

Many studies investigating polygynous mating patterns and animal conflict have focused on elephant seals due to their relatively exaggerated sexual dimorphism (Miller and Boness 1979, González-Suárez and Cassini 2014) and extreme female defence and apparent polygyny (Haley 1994, Haley et al. 1994, Carlini et al. 2006). These factors make the elephant seals good case studies, but also present complications in extrapolating findings to other species.

In contrast, grey seals (*Halichoerus grypus*) are also long-lived and can be individually identified by natural markings, but they breed on a wide range of substrates, do not assort into clearly defined dominance hierarchies, do not form the clear territories seen in Otariid species (Riedman 1990), and are not as distinctly sexually dimorphic as the closely related elephant seals (Anderson and Harwood 1985, Miller and Boness 1979, Tinker et al. 1995, Twiss et al. 1994, Twiss et al. 1998). The mating patterns of grey seals are closely linked to resource distribution; for example, female grey seals on breeding colonies such as North Rona (Scotland) distribute according to the availability of pools of water on the colony (Twiss et al. 2007, Culloch 2012, Stewart et al. 2014). Therefore, due to the responsiveness of females to environmental fluctuations, the apparent polygyny or potential for sexual selection has been shown to vary in relation to spatial and temporal environmental fluctuations for grey seals (Twiss et al. 2007). Furthermore, not only are there considerable differences between individuals for behaviours such as aggression and time spent alert (Boness 1984, Twiss 1991), but there is also evidence of consistent individual differences indicative of behavioural types within populations (Twiss and Franklin 2010). These factors make grey seals an ideal study system for the focus of this thesis: examining individual variation in mating patterns and aggression in response to the social and ecological environment. It also allows for the examination of questions about how male-male conflict is mediated and moderated in this less ‘exaggerated’ system, relative to the model elephant seal system.

1.3.1 Grey seal breeding ecology

Grey seals are widely distributed in the North Atlantic and Baltic Sea. Characterisation of grey seal breeding habitat varies geographically and between populations, and may include sandy beaches, rocky shorelines, grassy knolls and land-fast ice (Cameron 1967, Twiss et al. 1994, Tinker et al. 1995). The timing of the breeding season also varies geographically, with breeding occurring in the winter in the Western Atlantic and Baltic (Boness 1984) and in the autumn in the Eastern Atlantic (Coulson 1981). As capital breeders, the breeding season for both male and female grey seals is mutually exclusive to foraging (however; see Lidgard et al. 2003 for some evidence of foraging during the breeding season).

Otariid males such as the northern fur seal often arrive on breeding grounds prior to the start of pupping to establish territories (Gentry 1998). For grey seals, male and females begin to arrive on shore at relatively the same time; however, there is considerable variation in attendance timing and duration between individuals (Twiss et al. 1994). Females give birth to a single pup and remain on the breeding colony for the duration of nursing (15-18d) (Anderson et al. 1975, Kovacs 1987). Oestrus typically occurs on day 16-18, at which point a female will mate, and subsequently return to the sea (Kovacs 1987, Pomeroy et al. 1994, Twiss et al. 2006). As the breeding season usually lasts approximately 6-8 weeks, this results in a turnover of females throughout the season (Pomeroy et al. 1994). Reproductively active males can stay on the colony for up to 60 days to maximize access to females and are primarily thought to fast during this time (Boness and James 1979, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2003) but there is some evidence of apparent foraging trips during the breeding season at certain colonies (Lidgard et al. 2003).

The apparent decoupling of foraging and breeding behaviours for both sexes simplifies the assessment of trade-offs between performing behaviours which might increase reproductive benefits, such as defending positions or vigilance, and the associated energetic and physical costs. Since for males, duration of stay on the colony is positively correlated to reproductive success, energy conservation becomes essential for individual fitness (Anderson et al. 1975, Twiss et al. 1994). For example, males on the North Rona (Scotland) breeding colony spend only 13% of their time in active behaviour (Anderson and Fedak 1985). Even on colonies with relatively high rates of aggression, aggressive behaviours only comprise 6.2% of male activity budgets (Boness 1984, Twiss et al. 1998). The proportion of time male grey seals spend resting is only exceeded by one other pinniped species, the northern elephant seal *Mirounga angustirostris* (Boness 1984).

1.3.2 Male grey seal mating and reproductive success

The mating pattern of grey seals is somewhat unusual in that males do not defend discrete territories or harems, nor do they aggregate in leks (Anderson et al. 1975, Boness and James

1979), and the degree of polygyny also varies across colonies within the species (Twiss et al. 1998). Instead, males appear to defend non-exclusive territories in which they attempt to maintain positions within shifting groups of females (Anderson et al. 1975, Boness and James 1979, Anderson and Fedak 1985, Tinker et al. 1995, Twiss et al. 2007). Consequently, the grey seal mating pattern has lacked clear categorization, but research has provided evidence suggesting the degree of polygyny in this system is dependent on factors such as sex ratio skew (Twiss et al. 1998), degree of female spatial clustering (Twiss et al. 2007), social context (Ruddell et al. 2007, Poland et al. 2008), and environmental conditions (Coulson 1981, Twiss et al. 2007).

Within the grey seal system, many studies have focused on male mating behaviours and the links to individual fitness (Anderson et al. 1975, Anderson and Fedak 1985, Twiss et al. 1994, Worthington-Wilmer et al. 1999, Lidgard et al. 2005, Twiss et al. 2006, Twiss et al. 2007). For example, different male mating strategies, or behavioural phenotypes, have been examined for their reproductive success and ultimately, their impact on individual fitness. Length of stay on the colony has been positively correlated with male reproductive success, and so the evolutionary stable strategy (ESS; a strategy which, if members adopt it, no other strategies can arise which yield higher fitness) is generally agreed to be ‘come early, stay long’ (Maynard-Smith and Price 1973, Anderson et al. 1975, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1994, Lidgard et al. 2005). Males adopting this strategy are typically referred to as ‘dominant’ or ‘tenured‘ and gain the highest reproductive success (Boness and James 1979). Behavioural observations have characterized male grey seals that adopt the alternative strategy of roaming as ‘transients’ (Boness and James 1979). These males often remain on the periphery of the colony, attempt to sneak into the colony, and will attempt to mate with females as opportunities arise or will intercept females *en-route* to sea (Lidgard et al. 2001, Lidgard et al. 2004, Lidgard et al. 2005). Additionally, similar to other species of phocid seals like the harbour seal, there is some evidence of aquatic mating for grey seals, and with advances in genetic analysis, there is debate as to the extent to which aquatic mating comprises a third mating strategy for grey seals and other pinnipeds (Worthington-Wilmer et al. 1999, Gemmell et al 2001, Twiss et al 2006, Lidgard et al. 2005).

1.4 Research aims

As noted in **1.2**, investigations into individual variability in aggression, mating success, reproductive effort, dominance or spatial distributions have been conducted for a variety of species, including the grey seal, but less often are these investigations done in wild systems, or at a fine-temporal scale with consideration of intra-seasonal variation in environmental factors, resource availability or social dynamics. Therefore, the aim of this thesis is to investigate inter-male aggression by using a colonially breeding, wild pinniped system to examine the behavioural mechanisms driving individual conflict and conflict reduction at a variety of temporal and spatial scales. These investigations will assess the behaviours expressed by grey seals at a newly formed, mainland colony for the study site, but they will also answer specific questions regarding the role of environmental conditions, social structure, and selection pressures driving conflict in systems with polygynous mating patterns. Due to the diverse nature of this thesis, the specific rationale and aims of each of these studies are thoroughly explained and discussed in the individual chapters. Here, I will briefly discuss the types of knowledge gaps driving the research covered in this thesis and the overarching rationale.

Section 1: Geographic variability in behaviour within a species (Chapter 3).

In their paper, Anderson and Harwood (1985) investigated how the topographic differences between breeding sites might account for observed variations in behaviours; Twiss (1991) also did some cross-colony comparative work, but no updates have been made to these predictions and assumptions through the inclusion of mainland colonies which differ in topography, sex-ratios, and environmental conditions. The study site where my research was conducted was the Donna Nook breeding colony along the East coast of England (**Chapter 2.1**). This area of grey seal distribution is somewhat atypical in comparison to colonies used for past studies in that the breeding aggregations are not on offshore islands (Anderson and Harwood 1985), but instead, many colonies are forming along the mainland coast. Furthermore, this region has been experiencing incredible population growth since the 1980s (Duck and Morris 2010). Thus, there is an increased potential for un-intentional and intentional human-wildlife interactions at breeding sites like Donna Nook through activities such as wildlife tourism, industrial, or military training activities.

Due to the lack of attention to these growing colonies, what is presently known about the broad-scale variation in grey seal breeding behaviours needs to be updated to include mainland colonies, both in respect to topography and anthropogenic activities. Therefore, this chapter will first consider:

1) *Where do behavioural measures for individuals breeding at Donna Nook fit within the known spectrum of male breeding behaviours for grey seals?*

Since humans are a component of the environment at mainland colonies, this chapter will also answer the question:

2) *Does the amount of time males spend in Non-Active and vigilance behaviours vary across colonies which are exposed to varying levels of anthropogenic activities and topography?*

Section 2: Signalling in agonistic interactions (Chapter 4).

When conducting behavioural observations *in situ*, research questions and opportunities that were not previously planned for might arise. The original aims of this thesis were to focus on the inter-individual variation in male aggression; however, upon conducting research at the Donna Nook colony, it was apparent that a behaviour not noted in ethograms from other study sites was being regularly performed by males during agonistic interactions: the Body Slap. Upon further investigation, it was apparent that this behaviour was characteristic of only males, and only from breeding colonies along the Eastern Coast of England. Signalling during animal contests is considered one way individuals can minimize costs by displaying their own RHP, and assessing their opponents' RHP prior to engaging or escalating (Arnott and Elwood 2009). Signals can take the form of air-borne acoustic cues (Vannoni and McElligott 2008), chemical cues (Schneider et al. 2001), tactile cues (Briffa et al. 1998) or visual cues (Tyack and Miller 2002, Sanvito et al. 2007a). Grey seal threat behaviours have previously been described as less conspicuous than other closely related phocids (Miller and Boness 1979), and although the behaviour in question had been known anecdotally for more than 15 years, no academic endeavours had been taken to examine its form or function. Therefore, I sought to investigate this behaviour in as much depth as possible. In **Chapter 4**, I will seek to define the pattern of the Body Slap behaviour and ask:

1) *Is the Body Slap an aggressive or submissive display?*
2) *Are seismic components of the Body Slap reliable indicators of male RHP?*
3) *Does variation in the ususal substrate characteristics alter the seismic component of the Body Slap?*

Section 3: Fine-scale factors leading to inter-individual variability in contest assessment, rates of aggression and reproductive effort (Chapters 5-7).

Across broader taxonomic groupings, much research has been invested in determining the decision-making processes during contests (Arnott and Elwood 2009), but these studies are often focused either on non-mammalian systems in laboratory settings (exceptions being some ungulate species *e.g.*, Jennings et al. 2012) or have ignored or omitted contests with ambiguous outcomes (Herberholz et al. 2007, Colléter and Brown 2011). Also, while a great deal is known about broad scale determinants of male, pinniped aggression (Anderson and Harwood 1985, Twiss et al. 2007, Pörschmann et al. 2010, Bohórquez-Herrera et al. 2014), due to past methodological constraints, it has been difficult to examine what conditions promote the frequency of individuals escalating into contact fights or engaging in aggressive interactions at a fine temporal scale (*e.g.* within a season). Individuals have also previously been assumed to expend constant rates of reproductive effort (RE) daily across the duration of a breeding season, even though sex-ratios, attendance and environmental variables are known to vary at much finer temporal and spatial scales (Twiss et al. 1994, Twiss et al. 2007). Therefore, through the use of new methodologies, interdisciplinary techniques, and fine-scale temporally and spatially explicit behavioural data I will investigate:

1) *What assessment strategy is predominant in individual contests for grey seals?* (**Chapter 5**)

2) *What assessment strategies are found in contests with ambiguous outcomes, in which neither opponent retreats?* (**Chapter 5**)

3) *At a fine temporal scale, do individual dominance scores, social or environmental variables explain the inter-individual variation in rates of aggression?* (**Chapter 6**)

4) *Does duration or timing of male reproductive effort explain the inter-individual variation in mating success for tenured males?* (**Chapter 7**)

Chapter 2

General field methods

2.1 Study colony

2.1.1 Donna Nook

Fieldwork was carried out at the grey seal breeding colony of Donna Nook, on the north Lincolnshire coast, eastern England, just south of the Humber Estuary (53.47°N, 0.15°E), (Figure 2.1). The site is managed as a part of the Lincolnshire Wildlife Trust's wildlife refuge system and spans the Defence Infrastructure Organisation's Air Weapon Range (AWR) Donna Nook training range.

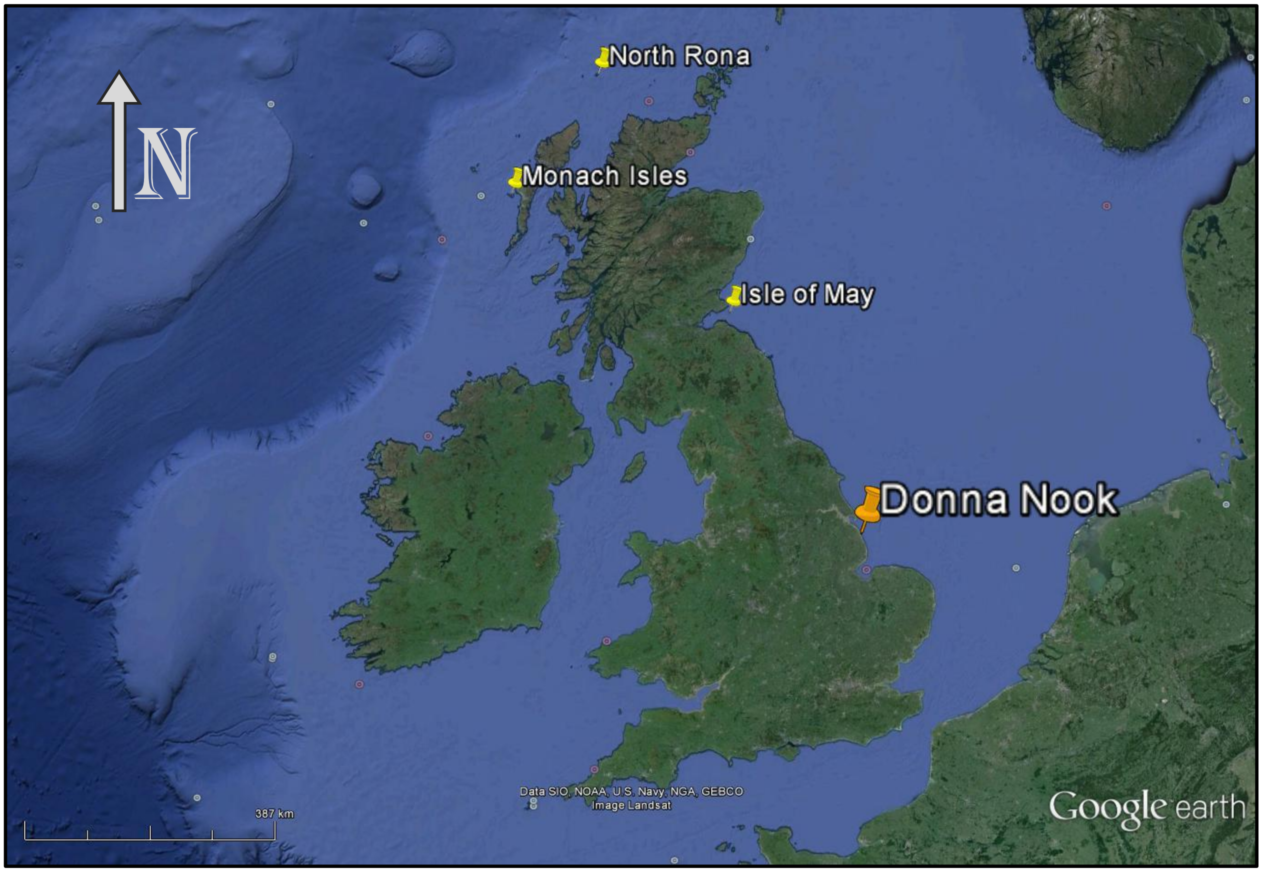


Figure 2.1: Donna Nook, England with other grey seal breeding colony locations in the UK that have long term, comparable datasets for reference. [*Image © Google Earth]*.

Donna Nook is characterized by tidally influenced, estuarine topography. To the north, tidal marshes transition into a mixture of grassy dunes, muddy wallows and man-made paths consisting of primarily tamped sand. The remainder, and vast majority, of the colony is a sand-flat with little to no topographic variation or vegetation. Seaward, there are no discrete access points from the ocean to the beach making it broadly accessible, and the entire colony is bordered on the south/western extent by high dunes and thick vegetation. During the breeding season, two aggregations form: the outer aggregation along the shoreline and the inner, or main, breeding aggregation which is distributed farther landward with clustering near the dune-line (Figure 2.2). Seals often use tidal channels to move from the sea to locations across the sand flats. All observations for this study were conducted at the inner/main aggregation.

While most grey seal colonies form on offshore islands and in remote locations (Anderson et al. 1975, Boness and James 1979, Anderson and Harwood 1985, Twiss et al. 1998), Donna Nook is located on the mainland coast of England where it is exposed to various levels of anthropogenic activity (Duck and Morris 2010). For example, the northern section of the colony is open to public viewing access. Visitors gather during the breeding season to view and photograph the seals. Physical contact with the seals and the extent to which visitors can enter the colony is limited by a double wooden fence (Figure 2.2) and by Wildlife Trust wardens (see: *http://www.lincstrust.org.uk/donna-nook*). Due to the presence of the AWR Donna Nook, the southern extent of the colony is off-limits to visitor access, and terrestrial-based anthropogenic disturbance is limited to operational necessities. The colony as a whole is exposed to anthropogenic noise in the form of military training exercises, usually consisting of periodic jet or helicopter flyovers. Jet flyovers typically occurred between 10:00 and 15:00; passed by at five to ten minute intervals, and could last from one to three hours. Helicopters were less predictable.

2.1.2 Study sites within Donna Nook

Observations were conducted from observational hides at two locations within Donna Nook which spanned the available topographic and anthropogenic variation (Figure 2.2). The first hide location was on the restricted access RAF site (53.474° N, 0.155° E); south of a break in the dune line that allows entrance to, and exit from, the RAF base by vehicle. This hide was placed on the dunes to allow for slight elevation of view point (0.5-1m). The average distance from the hide to the closest seals was 10m, and seals could fully access the hide location. The hide on the public access portion of the colony (PUB; 53.476° N, 0.148° E) was positioned approximately 25m from the closest seals and the fence line. Though this distance was farther back than the hide at the RAF site, the PUB hide had to be positioned on a dune with substantial elevation (approx. 2-3m) to allow for a higher vantage point. During the season, large groups of visitors would congregate along the fence-line. If the hide was placed lower down and closer to the fence, they would disrupt the observers' line of sight; thus a vantage point farther back, but elevated, was selected. Views from this site included grassy dunes just north of the fence-line, wide expanses of grass and sand flats, a number of wallows and low dunes, and in the eastern portion of the study site, the beginnings of the sand-flats which predominate to the south/east.

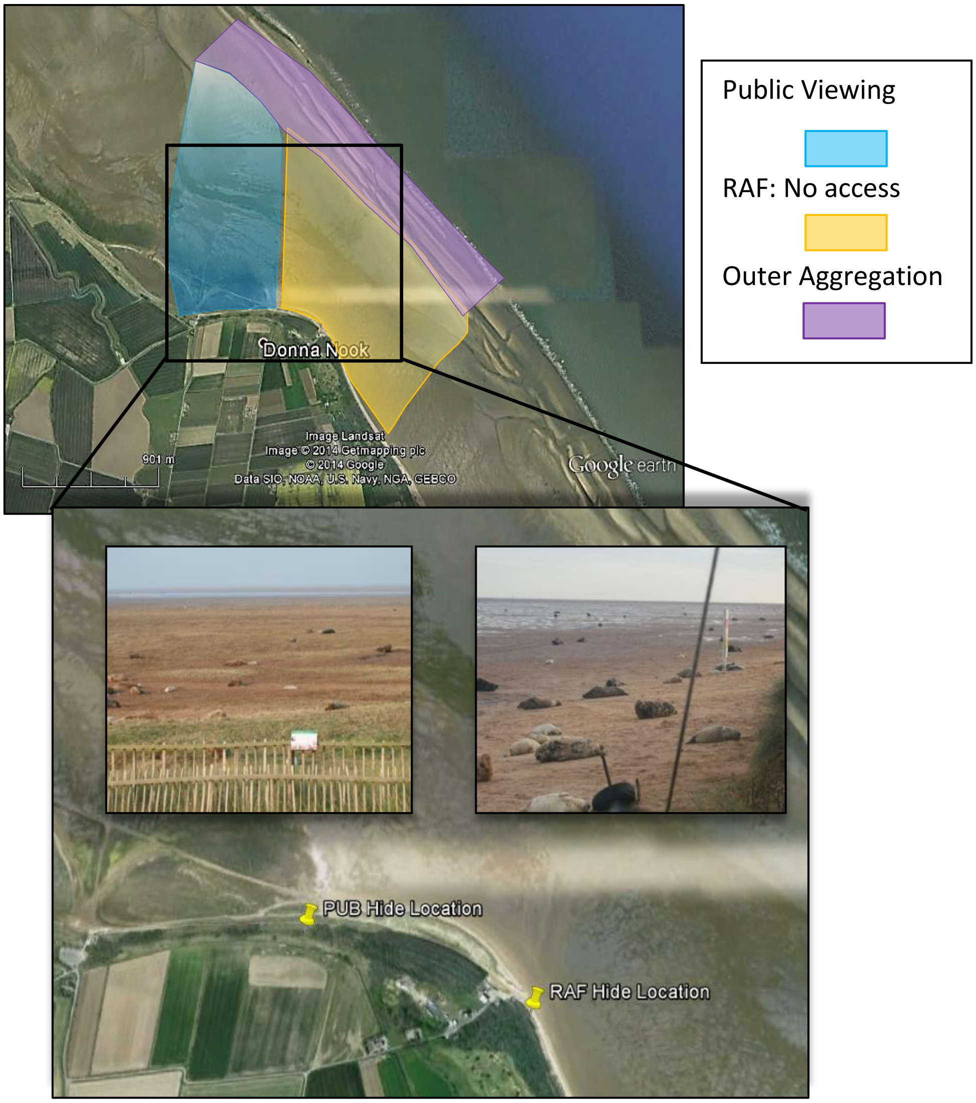


Figure 2.2: The top image is of the entire Donna Nook wildlife refuge/ DOI training range. The colony is split into three regions; Blue = visible to public via footpath; Yellow = off limits to visitor access; Purple = outer aggregation of breeding seals along waterline where visitation is discouraged but does occur occasionally. The lower image shows the location of hides at PUB (Left) and RAF (Right) sites at Donna Nook, with inserts showing the view from the respective hides. [*Base images © Google Earth; Inserts: A.Bishop).*

2.2 Field dates and observations regime

2.2.1 Observer ID

Fieldwork spanned 3 years (2011-2013). In all three years, AB was the primary observer (referred to as such henceforth). In 2012 and 2013, a secondary observer, JS, also conducted field observations so that observation periods could be conducted at both the RAF and PUB site simultaneously. Preliminary analyses investigated considerations of observer bias (**3.3.1**).

2.2.2 Observational dates and times

The breeding season at Donna Nook spans from late October through December, with peak pupping occurring around 23 November (**2.4**). Observations in the field were conducted 3 November 2011 through 10 December 2011 (38 d); 27 October 2012 through 14 December 2012 (47 d); and 27 October 2013 through 12 December 2013 (41 d) during all available daylight hours for an average of 8h 48m of observations daily. In 2011, the primary observer alternated daily between the two hide locations. In 2012, the primary observer alternated from 27 October – 3 November, after which the secondary observer arrived and also alternated between the two, allowing for full coverage of both the RAF and PUB sites thereafter. 2013 followed a similar pattern, with the primary observer alternating from 27 October – 6 November, followed by full coverage until 30 November. After 30 November, the primary observer left the field and the secondary observer alternated between sites until 6 December. On 6 December 2013, a tidal surge struck Donna Nook and much of the eastern English coast. During the event, the observational hide at the RAF site was lost (the dune was eroded during the night), rendering observations at this site impossible for the remainder of the season. As such, from 6 December 2013 to 12 December 2013, observations were only conducted at the PUB site.

2.3 Individual identification

The individual-based approach of this thesis necessitated repeat observations on individuals throughout the breeding season and between years. Grey seals have unique pelage patterns of cream, brown and black patches that are stable among years (Boyd et al. 1962, Anderson and Fedak 1985, Hiby and Lovell 1990, Twiss et al. 1994, Pomeroy et al. 2000, Figure 2.3). Additionally, from aggressive interactions, many male grey seals have scarring along their muzzles, flanks and necks. Scarring is not as stable between seasons; new scars can change the shape of older marks and some scars can fade among seasons, so these marks were predominantly used as secondary forms of identification.

In the field, on the first sighting, new males were given a temporary alphanumeric ID and photographs were taken of all visible sides using a Canon DSLR EOS 30D or 40D with a 100-400mm zoom lens. This temporary ID was then cross-referenced with known males in the photo-ID catalogue for false negatives and false positives. If no matches were found, the alpha-numeric ID was retained and the male was also given a unique male ID (e.g., 201101). The most common causes of false-negatives were: the male was initially only visible from one side; the pelage condition (wet or dry) obscured the pelage patterns, or excessive amounts of sand and mud in the pelage masked marks. A thorough cross-reference was conducted post-season each year, in which each male was manually compared to the remainder of the catalogue to check for false-negatives and false positives. Even with careful inspection, marks might have been missed, or males' pelage conditions in photographs might restrict ability to rule out false-negatives. Therefore, analyses were typically restricted to males that had both sides photographed. The final catalogue of definitive males included 170 males in 2011; then increased to a total of 287 males in 2012; and finally the cumulative total was 398 males in 2013.

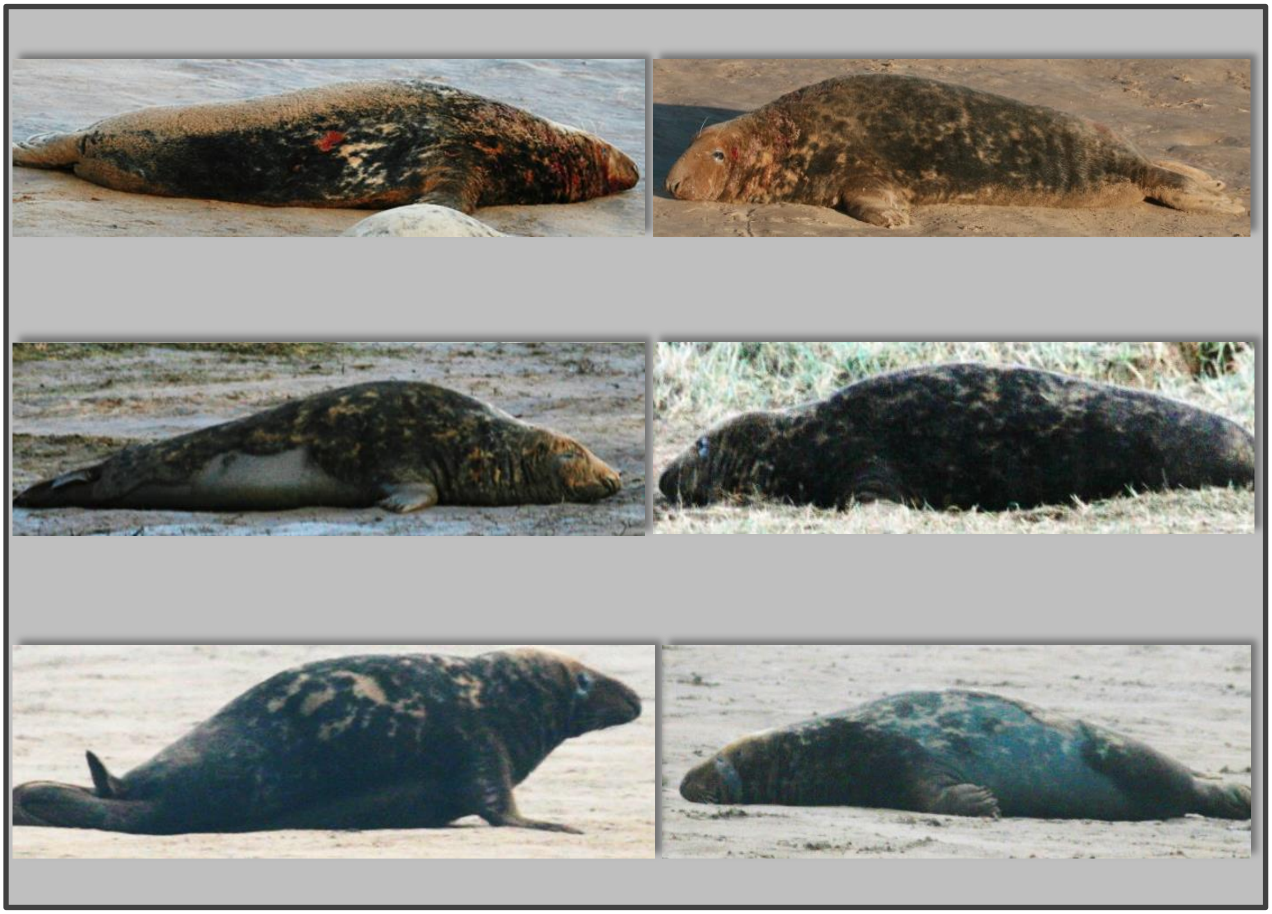


Figure 2.3: Unique pelage markings used for ID for three different males (Top to Bottom: D44, B7, A53).

2.4 Attendance patterns of males, females and pups, and sex ratios

Weekly census of female and pup numbers at Donna Nook were carried out for all three seasons by Rob Lidstone-Scott (RLS), the head warden from the Lincolnshire Wildlife Trust. These values were used to generate attendance pattern curves (Figure 2.4) to describe the relative timing of female and male attendance and pup production within and between years (**Chapter 7**).

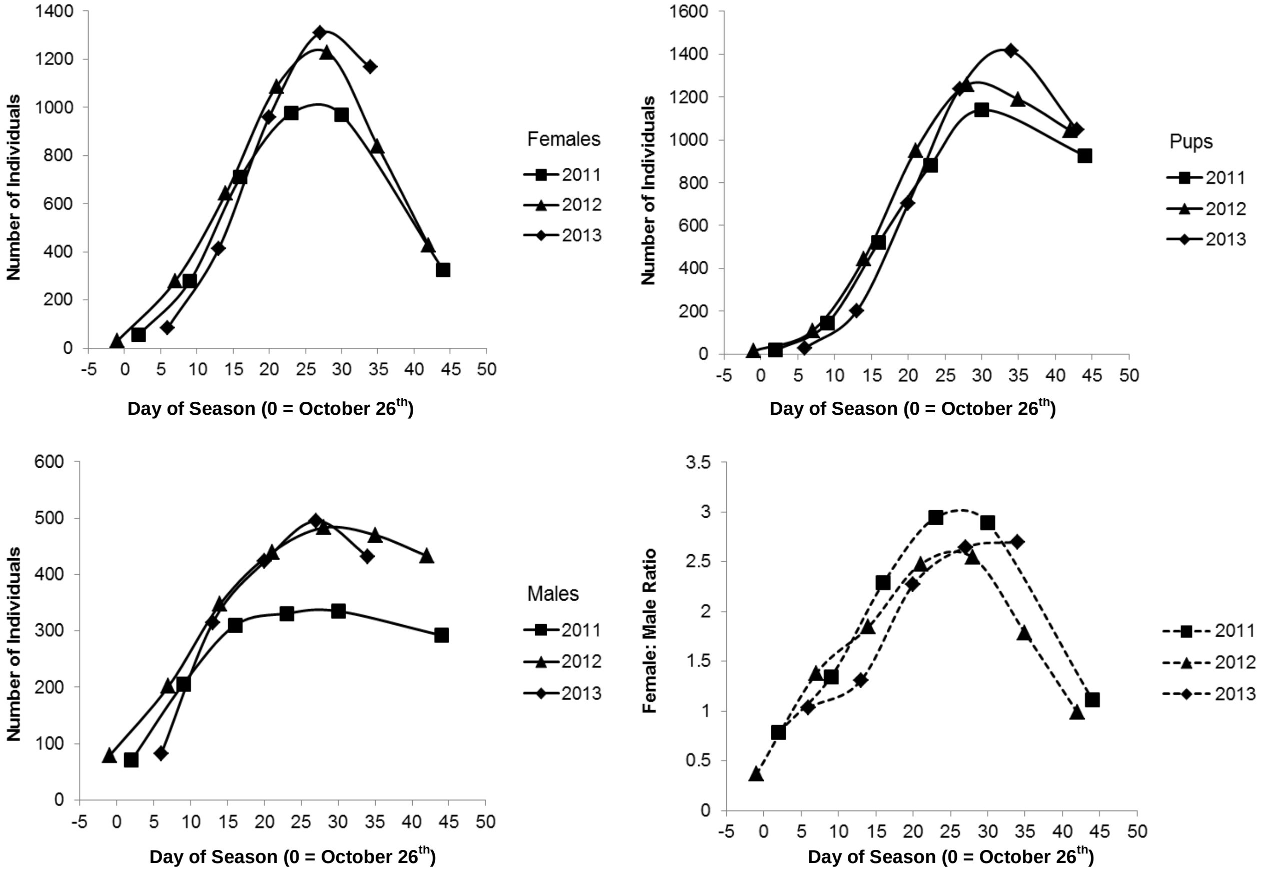


Figure 2.4: Census count attendance patterns for females (top left); pups (top right); and males (bottom left), and the female-to-male ratio (bottom right) at Donna Nook in 2011-2013. Weekly counts come from Lincolnshire Wildlife Trust data (RLS).

2.5 In-field mapping

Locations of all males were mapped hourly on printed aerial photographs of the colony (Twiss 1991, Twiss et al. 1994, Culloch 2012) with the identity of known males and males with new temporary IDs noted. Topographic features were used at the public site to assist in mapping; however, the RAF site was relatively uniform. Thus, to improve accuracy in mapping at both sites, a Nikon laser 550 rangefinder (6x21), with accuracy of 0.5 m up to 100m and ±1m at >100m distance, was used in conjunction with horizon reference points (military targets) to position the distance and direction of males. Females and pups were mapped once daily on the first map of the day, with differentiation noted for the age class of pups (Kovacs and Lavigne 1986). Sex ratios were calculated based on female-to-male numbers during the first hour of observations for each site, and overall colony sex ratios were calculated from weekly census counts conducted by the Lincolnshire Wildlife Trust (personal corr. RLS, 2011-2013). *Post-hoc*, the location data for the hourly maps were georectified using ArcInfo (ESRI) and the images were digitized to the Ordinance Survey Great Britain (OSGB) coordinate system.

2.6 Behavioural observations protocol

2.6.1 Behavioural ethogram

Mutually exclusive and broad categories for behaviours were defined for consistency and to allow comparisons between this study and previously-conducted behavioural assessments of male grey seals (Boness and James 1979, Anderson and Fedak 1985, Twiss 1991, Lawson 1993, Twiss et al. 1998):

A) Aggressive Interaction: Aggressive interactions (AIs) were defined as any agonistic interaction between two or more males involving the use of aggressive behaviours (Sandegren 1976, Boness and James 1979, Twiss 1991, Lawson 1993). AIs can be defined as Non-Contact (consisting of only threat behaviours) or Contact (where part of the interaction has escalated to lunges and biting). Contact AIs usually consist of both a Non-Contact threat period followed by bouts of escalated physical fighting.

Aggressive Behaviours

A.1 Approach male: A sub-group of general locomotion, the male under observation moves directly towards another male. It is possible the distance at which movement evokes a response from a conspecific might differ by size of the individual. With this caveat in mind, to ensure that no incidental movement was misclassified as an approach, distance was required to be less than 20m between males as this reflected movements were closer than the average distance between males (Table 3.6). Additionally, the movement was typically accompanied by another aggressive behaviour such as an OMT, further ensuring the aggressive context of the locomotion (A.2).

Figure 2.5: Male performing an Open Mouth Threat (OMT)

A.2 Open Mouth Threat (OMT): This is a threat display which consists of a male opening his mouth to wide gape and does not engage in contact with conspecific (Figure 2.5). Sometimes a slight hiss or huff can be heard, but no vocalization. Orientation can be towards opponent, perpendicular or in cases following a departure, directed away from an opponent (Twiss 1991, Lawson 1993). In some studies, differentiation is made between high and low OMT based on the elevation of the head off the substrate (Anderson and Fedak 1985); however, no differentiation was made for this study. Records of the conspecific to which the behaviour is directed (female, male, or pup) were included with each observation of this behaviour.

A.3 Aggressive Flippering: This behaviour involves a male vigorously waving his fore-flippers at an opponent and/or slapping his own side in a clearly aggressive (defensive or offensive) manner during an AI. Contact is often made between opponents but not exclusively. This behaviour is seen often at the end of a Contact interaction where one male, usually the loser of the interaction, ‘rears’ back with high OMT and aggressive flippering; the ‘victor’ continues to maintain close proximity and performs low OMTs.

A.4 Lunge: An attempt to bite without making contact.

A.5 Bite: A singular bite made though a singular lunge (Figure 2.6). This behaviour is sometimes associated with a vigorous shaking of the head laterally while maintaining grasp of opponent, but can also be described as a prolonged ‘hold’ without thrashing. A subcategory of this behaviour is Bite Hind Flippers (BHF) where male grasps his opponents’ hind-flippers or tail with his mouth. BHF usually, but not exclusively, is the final behaviour in a Contact AI.

Figure 2.6: Male on right biting the neck of opponent, with female and pup in foreground.

A.6 Fight/Contact AI: The broad term for an AI during which contact is made by one or both males. The physical engagement is usually preceded by a threat period during which males exchange Non-Contact threats. Leading up to contact, males typically, though not exclusively, will begin to position themselves closer and parallel to each other until one engages the other in contact. This segment of an AI is thus characterized by series of lunges, bites and bouts of 'wrestling' behaviour (see: Twiss 1991). Both males attempt to manoeuvre towards his opponent's hind flippers/tail. A Fight/Contact AI typically ends with one male chasing the other away, but in some cases both males simply cease to engage in contact and resume threat behaviours, with no change to the *status quo* regarding position or access to females resulting from the AI.

Figure 2.7: Male on right chasing opponent at end of an aggressive interaction.

A.7 Chase: Chases can be an exclusive form of an AI if no threats or contact are made, or can be a segment of an AI which occurs when the winner chases the loser following threats and/or contact (Figure 2.7). Chases cover distances of 10-20m on average, though occasionally they will persist to over >50m. They often will begin between two males, but in fleeing the activity sometimes attracts the attention of other males; resulting in additional individuals engaging in the chase, while others may cease chasing.

A.8 Roll: The motor-pattern of the roll consists of a male spinning along his longitudinal axis in either a full 360° spin or in some cases, rolling 180° and then returning back to starting position in the same direction. Usually seen after a fight or chase, and suggested to be a victor returning to where he came from (a 'victory roll' Twiss 1991). From personal observations at Donna Nook, this behaviour has also been seen between two males engaging in OMT or in close proximity when neither is a clear 'winner'. As the chest is shown to the opponent during this behaviour, when performed in Non-Contact threat bouts, a roll is possibly a visual display of chest width, and might signal body-size. Alternatively, this behaviour could be a form of locomotion which might have reduced energetic costs.

If any of these 'aggressive behaviours' were directed at a female, it was considered under the behavioural category of 'Female Aggression' (Agg Fem).

B. Reproductive or Male-Female Behaviours

B.1 Approach Female: A subgroup of general locomotion, approach refers to direct movement of a male towards a female. Distance between male and female must be less than 20m to ensure context of locomotion, or the approach accompanied by additional aggressive behaviours such as OMT. Direct contact is not necessary but this behaviour can involve touching of noses or examination of female posterior end.

B.2 Attempted copulation (At Cop): Attempted copulations begin when a male attempts to get his fore-flippers on the female's back and grabs the dorsal side of her neck with his jaws. Often at this point the female will respond in an agitated/aggressive manner, with intensity diminishing as females approach oestrus. If the female aggression does not initially deter the male, the male will then swing his rear end around to line up with the female's and attempt intromission. His body can be positioned dorsally or laterally to hers. This behaviour has also been called a mount (Boness 1984).

B.3 Copulation (Cop): Following the attempted copulation/mounting behaviour, the male will attempt intromission. If successful, this is the point in which actual copulation commences. If the copulatory embrace post-intromission persists for a minimum of 10 min the copulation is classified as 'successful' (see **2.6.3**, Figure 2.8).

Figure 2.8: Male in copulatory embrace with female. Position consists of the male biting the female's neck and grasping her body with his fore-flippers.

B.4 Unsuccessful copulation: Copulations which do not last for longer than 10 min post intromission are considered unsuccessful (**2.6.3**). In some cases, after intromission the female will ‘shake off’ the male with aggression or movement, the pair will be interrupted by another seal, or the male will not maintain his grip and ‘fall off’ the female—in these cases the copulation is termed ‘unsuccessful’.

Other categories:

C. Rest: Non-active state. Head down, eyes may be open or closed.

D. Comfort-move (CMV): A comfort move is defined as a male repositioning without change in geographic location, or a male scratching his body. Head may be up but not demonstrating any alert behaviour directed at a conspecific. This is often considered a sub-category of resting (Twiss 1991).

E. Alert: All cases where a male is clearly observant, head raised, and looking around or engaged in a directed gaze at a conspecific. Twiss (1991) differentiated between Alert and Alert-male (when a male’s gaze was directed at another male); however, for this study the two are not distinguished.

F. Locomotion: Movement around the colony without directed approach towards a female or male. Change in geographic location.

G. Out of Sight (XOOS): This ‘behaviour’ is where a male is not visible from the hide (due to topography or range of view) but is known to still be present in the study site.

2.6.2 Male-male aggression

Male-male agonistic interactions were defined as any agonistic interaction between two or more males (**2.6.1**, Bishop et al. 2014) and will be referred to as AIs, aggressive interactions, or agonistic interactions, in all further chapters. Incidents of aggression involving at least one identified male were recorded by the observer with notation of participants' IDs, start and end times, and coarse details of behaviours performed. Agonistic interactions are highly attention grabbing and sufficiently rare, allowing all occurrence records to be kept while performing other observations (Altmann, 1974). For aggressive interactions, the record was labelled as Non-Contact or a Fight (Contact) (Table 1) and the outcome was noted as either Draw or Win-Loss (WL). A male was determined to have won an encounter if his opponent moved away or was chased away and lost his position amongst females; otherwise the AI outcome was defined as a draw (Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998). When there was a clear winner and loser, the duration of an AI was defined as the interval between the onset of the first aggressive behaviour and the end of the final aggressive behaviour. In draws there is not always a discrete ending from which to calculate duration as the display of aggressive behaviours (*e.g.*, OMT) might continue intermittently by a single contestant while the other has stopped responding. I followed the general criteria for determining the end of ambiguous AIs described in Boness et al. (1982), but in addition, if the interval between successive aggressive behaviours was greater than the AI average duration (2.6 min) they were recorded as two separate AIs. This provided a conservative estimate for differentiating interactions and calculating durations (Bishop et al. 2014).

Two metrics were calculated to quantify the amount and rates of aggression on the colony. First, the total number of aggressive interactions (TAI) was calculated for each male. This metric combined both Non-Contact interactions and Contact interactions. Due to variation in the number of days individual males were present, I also calculated the average daily number of aggressive interactions (DAI) for each male. While this standardized across the number of days observed, there was still the potential for unequal observation times within days due to males arriving and departing, or moving out of sight (*e.g.,* 2 vs. 8 hours of observation). Thus, the number of aggressive interactions observed in a day for each male was divided by the number of hours he was present to get a rate of aggression per hour, per day. This metric was then converted to a rate per 8 hours and rounded to the nearest whole number to allow for comparison to published data from other colonies (Twiss 1991, Twiss et al. 1998). To minimize potential bias due to extrapolation (*e.g.,* if a male partook in a large number of AIs observed over a short time period), for each male, only the days in which he was observed for a minimum of 4 hours were used in analyses (**Chapters 3, 6, 7**).

In addition to in-field data, video records were kept for a sub-sample of the total AIs to allow for in-depth analysis of behaviours, sequences of behaviours and outcomes of aggressive interactions *post-hoc*. Video recording was conducted with Canon DC40 digital camcorder in all years (specifications: 10x optical zoom, 35mm field of view, 4.29 megapixel DVD). A Panasonic HC-V520 digital camcorder (specifications: 62x optical zoom, 35mm field of view, 1920 x 1080p HD video recording) was used in 2013 for a subset of the video records. Each video was a discrete AI and included in-field commentary providing details of date, time and male IDs as well as any information on conditions leading up to the video-captured behaviours. Sampling was targeted to capture the maximum number of contact aggressive interactions and a pseudo-random selection of Non-Contact AIs across a wide range of individuals, seasonal and social patterns. This resulted in a total of 279 videos of 908 observed AIs in 2011 (142 RAF, 137 PUB), 464 videos of 4,288 observed AIs in 2012 (222 RAF, 242 PUB) and 499 videos of 5,598 observed AIs in 2013 (313 RAF, 186 PUB) for an average of 16.8% of AIs videoed per year.

2.6.3 Reproductive activities

For sexual activities, each event was recorded as either an attempted copulation or copulation (**2.6.1**). Attempted copulations could then be further classified as unsuccessful if the male did not achieve intromission. If the male achieved intromission the interaction was re-classified as copulation. Copulations were also sub-classified into successful or unsuccessful (**2.6.1 B3-4**). 'Unsuccessful copulations' indicate the male achieved intromission but lost contact with the female after a short period of time, and the cause of the interruption was recorded (*e.g.*, female aggression). Copulations for grey seals last on average 20 min (Twiss 1991), but the timing of ejaculation is unknown. Longer durations of intromission could be a strategy to stimulate ovulation; however if ejaculation occurs immediately, longer durations could instead be a form of mate guarding. Direct observations have noted the female's ventral muscles 'contracting' towards the end of long intromissions, possibly indicating late ejaculation (Twiss 1991). It is further thought to be unlikely that insemination will occur during copulations lasting for very short durations, as short durations are typically associated with increased female aggression or the male leaving to engage a competitor (Twiss 1991). Twiss (1991) found that copulations which were interrupted only lasted on average 5-7 min. With this information in mind, I decided that for this study, in order to provide a conservative estimate of mating success (Twiss et al. 2006), a 'successful copulation' was defined as a male remaining in the copulatory embrace for a minimum of 10 min without disturbance. This resulted in the exclusion of 29 out of 374 copulations with observed intromission.

2.6.4 Activity budgets

Using the behavioural definitions in **2.6.1,** the primary observer in 2011 and 2012 conducted instantaneous scan sampling of all identified males at 5 min intervals while in the field (Twiss 1991). The order in which males had their behaviours recorded was consistent between scans. Throughout the season a range of 5-20 males could be sampled at a time, but even when peak numbers were scanned, the process of recording all males' behaviours took less than 1 min (mean = 50s). Both of these considerations ensured that the interval between any given male's samples stayed consistent at 5 min. Activity budgets were then calculated from the scan samples to quantify the proportion of time each male spent in each distinct behavioural category. Observations were only conducted during daylight hours. Recent work on female grey seal day-night observations has suggested certain behaviours, particularly those which rely on visual signals, might be reduced at night relative to daytime (Culloch et al. 2015). Limited, previous studies on male grey seals have suggested that night and day activity budgets do not differ for male grey seals (Anderson 1978); and daylight observations of mating success were strongly correlated with assigned paternities (Twiss et al. 2006). As such, until a more comprehensive assessment of how male behaviours do or do not change from night to day, the underlying assumption of this thesis is that the behaviours addressed and measured here represent the daily activity budgets, rates of aggression and mating success for males.

Many males were only scanned for brief periods or for a single day. To restrict the potential for these records to skew overall averages, the protocol of previous behavioural studies was followed; activity budgets were only calculated for males that had >200 scan records (approximately 2 d of observation; Twiss 1991). These males would be classified as 'Tenured' (Boness 1984, Twiss 1991). For initial analyses, some behaviours were combined to investigate the proportion of time spent in the broad behavioural categories of 'Rest' (rest + comfort move), 'Aggression' and 'Sexual activities' (**2.6.1**). Furthermore, 'Non-Active' was the combination of Rest, Comfort Move and Alert; while 'Active' was the time spent in combination for all other behavioural categories. Broad comparisons were done at both the whole colony level and individually for the RAF and PUB sites. Results were compared to published activity budgets from other grey seal colonies in the UK (Twiss 1991, Twiss et al. 1998) and Canada (Twiss 1991) to determine relative similarities. Male activity budgets were also available for Sable Island from Boness (1984); however, the protocol followed varied from the methods used in Twiss (1991) and in this study; therefore, the findings of that report will not be considered for direct analysis in this thesis.

2.7 Photogrammetric assessment of morphology

2.7.1 Standard length

Standard length (cm) and lateral area (proxy for mass) were used as morphological measures of male RHP. For male grey seals, the links between male mass and RHP suggests that mid-sized males have the highest mating success, likely due to trade-offs between mass and manoeuvrability (Lidgard et al. 2005, Twiss 1991). Lidgard et al., (2005) also found a positive relationship between standard length and length of stay, the latter of which is a known positive correlate of mating success for males adopting the primary ‘tenure’ strategy (Twiss, 1991). Finally, Anderson and Fedak (1985) found that larger males lost fewer male-male encounters than smaller males by mass, again suggesting that size is positively associated with RHP.

Seals cannot be handled at Donna Nook, so to determine morphological features associated with RHP, photogrammetric estimation techniques similar to that used by Jacquet (2006) and McFadden et al. (2006) were adopted. Standardized photographs at a fixed camera height of 1 m above the ground were taken of known males lying prone and perpendicular to the photographer using a Canon EOS 40D digital SLR with 100-400mm Canon Lens (Figure 2.9). Distance to the male in the photograph was determined using a Nikon Laser Range Finder 550 with +/- 0.5 m (up to 100 m) accuracy. Multiple photographs were taken of individual males throughout the season. Each photograph was assessed for quality across the following criteria: the extension of the male's neck, the angle of offset from perpendicular, and if the tail was visible (Jacquet 2006, McFadden et al. 2006). Only photos which scored a 1 (1= good, 2= moderate, and 3= poor) for all of these categories were used for analysis.

Distance correction calibration formulae (Eq. 2.1) for each of the four zoom levels used (100, 200, 300, 400mm) were generated following the methods of Jacquet (2006). A formula was then generated from the linear relationship describing how the ratio of the known length of an object in cm (SL) to the width in pixels of that object in a photograph (P) changes as distance from the camera increases (D) (Jacquet 2006). In the example formula (Eq. 2.1), at 400mm zoom, the 0.0015 was derived from the slope of the regression line and 0.0038 represents the intercept. The R^2 values for the best fit lines for each zoom level were all 0.99. These formulae were then used to calculate nose to tail standard lengths (SL) for each male from photographs.

$$SL = [(0.0015 * D) + 0.0038] * P \tag{2.1}$$

2.7.2 Lateral area

McFadden et al. (2006) found that for weaned monk seals (*Monachus schauinslandi*) values of lateral area (LA), girth perimeter (GP) and lateral perimeter (LP) calculated from photographs were highly correlated with measured values for body mass. Also, for northern elephant seals (Haley et al. 1991) and southern elephant seals (*Mirounga leonina*) (Bell et al. 1997) lateral area was a strong predictor of body mass. To estimate mass from our photographs, the LA of the seal was calculated using methods similar to McFadden et al. (2006). A digitized outline of the seal, including hind-flippers, was generated in ArcMap 10 and the area of the polygon was calculated in pixels^2 (Figure 2.9b). Using quadratic versions of the distance correction calibration formulae used to estimate SL (Eq. 2.1), where D was again distance to the seal, and P^2 was the area of the seal, in pixels squared, from the photograph, LA was then estimated in cm^2 (Eq. 2.2).

$$LA = \left[(0.000002 * D^2) + (0.00004 * D) - (0.0013)\right] * P^2 \tag{2.2}$$

No quantification of accuracy between actual morphometric and photogrammetric values was possible due to seal handling restrictions. However, the range of generated lengths, 166.1 to 240.3 cm (±0.5 – 10.9 cm SE per male), were well within the range of known grey seal sizes (Twiss 1991, Twiss et al. 2000, Lidgard et al. 2005). To account for the remaining uncertainty resulting from off-angle positioning or lack of neck-extension, both of which would under-estimate length or area, I only used the photograph resulting in the maximum SL and the photograph with the maximum LA for each male in my analyses. Year appropriate measures were used whenever possible, but if no value was calculated during a particular year the next closest year's value was used instead (Table 2.1).

Table 2.1: An example of the decision making process for choosing a photogrammetric data source. If males were sampled in multiple years, the year appropriate photographs were used. However, if a sample was not collected in a given year, but in the previous or following year a photograph was acquired, this measurement as used to fill in any years that were not sampled. This was done for SL and LA.

Male ID	2012	2013	Decision Process
A152	✓	X	Use 2012 for both
R76	✓	✓	Use year appropriate
B18	X	✓	Use 2013 for both

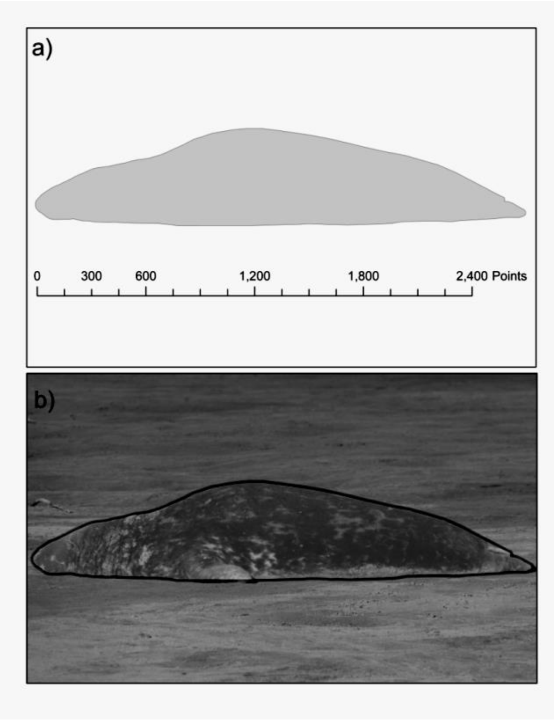


Figure 2.9: Example of photogrammetric positioning and digitizing of image to calculate: a) nose to tail standard length (SL; 1 point unit = 1 pixel) and b) lateral area (LA) for an individual male (Bishop et al. 2015a).

2.8 Environmental data

Environmental data were recorded *ad libitum* in the field. Estimates of cloud cover in tenths, wind speed (none, slight, moderate, strong), and rain (none, mist, fog, light, moderate, heavy) were recorded at the start of every observation period and periodically as conditions changed. Quantitative weather data were downloaded from the UK Meteorological Office; Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current) via the NCAS British Atmospheric Data Centre. The stations selected were Donna Nook 2 (Src ID 405) for hourly weather measurements and North Somercotes (Src ID 3784) for daily rain fall (mm). Hourly weather measurements include: air temperature (C°), wind speed (knots), wind direction, and relative humidity (%). Data for 10 years prior to the study (2003-2013) were also extracted to provide a baseline for this site.

Chapter 3

Geographic variation in male grey seal breeding behaviour

Revisiting Anderson and Harwood (1985) with inclusion of recently expanded, mainland breeding colonies

Manuscripts from this Chapter:

Bishop AB, Pomeroy PP, Twiss SD (In Review) Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity. Marine Ecology Progress Series.

3.1 Introduction

3.1.1 Geographic variation in behaviours

The occurrence of geographic variations in behaviours has been demonstrated across numerous taxa (*Teleosts:* Luyten and Liley 1985; *Aves:* Burnell 1998, Podos and Warren 2007; *Pinnipeds:* Perry and Terhune 1999, Van Parijs et al. 2000, Risch et al. 2007, Bishop et al. 2014, **Chapter 4**). This variability arises as animals adapt to local conditions such as resource availability (El Alami et al. 2012), environmental conditions and topography (Anderson and Harwood 1985), or anthropogenic presence (Pirotta et al. 2014). In some cases, cultural transmission will shape geographic variations as singular behaviours spread through localized social learning; for example, tool usage by bottlenose dolphins (*Tursiops truncatus*) (Krutzen et al. 2005), or clan-specific vocalizations of sperm-whales (*Physeter macrocephalus*) (Rendell and Whitehead 2003). Documenting broad behavioural indices for a species was common practice in the 1970s-1990s (Boness 1984, Goudie and Ankney 1986, Symington 1988, Twiss 1991, Lawson 1993, Shi et al. 2003), and often this was done across a range of geographic distributions within taxa (Anderson and Harwood 1985, Adolph and Porter 1993, Twiss et al. 1998). These early studies not only formed the foundation for subsequent work, but also provided a collection of available data that could be used in further investigations into the selection pressures driving geographic variability in behaviours.

Pinnipeds are ideal for examining broad changes across environmental gradients as they are a widely dispersed taxonomic group. Grey seals in particular occupy a wide geographic range, breed across a variety of substrates, and their behavioural ecology has been well established in the literature since the 1970-80s (Anderson et al. 1975, Boness 1984, Anderson and Fedak 1985, Twiss 1991, Lawson 1993). In particular, investigating male behaviour in grey seals has revealed geographic variations in behaviours (Anderson and Harwood 1985, Twiss 1991). During the breeding season, male mating success is positively correlated with his length of stay (Twiss 1991). Therefore, their behavioural activity budgets should reflect the trade-offs between maintaining access to females and losing energy through costly interactions and behaviours (Boness 1984, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1994). For example, topographic differences between breeding colonies have long been suggested as drivers of variation in male aggression (Anderson and Harwood 1985, Twiss 1991, Twiss et al. 1998). Anderson and Harwood (1985) examined activity budgets between three breeding colonies (Figure 3.1): North Rona and the Monach Islands (Scotland, UK) and Sable Island (Can) and suggested that broad topographic differences likely shaped the broad behavioural patterns. Their comparison of 'topographies' was largely qualitative in nature, but with the expanded usage of geographic information systems (GIS), further studies have since found fine-scale topographic characteristics are linked to variation in breeding behaviours for female grey seals (Twiss et al. 1994, Pomeroy et al. 1994, Twiss et al. 1998, Twiss et al. 2000, Twiss et al. 2001, Twiss et al. 2006, Stephenson et al. 2007).

Figure 3.1: Locations of grey seal breeding colonies and selected studies: Sable Island (Boness and James 1975, Boness 1984, Twiss 1991, Lidgard et al. 2001, Lidgard et al. 2004); North Rona (Anderson et al. 1975, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1994, Twiss et al. 1998, Twiss et al. 2006); Monach Islands (Anderson and Harwood 1985. Twiss et al. 1998); Isle of May (Kovacs 1987); Donna Nook (Bishop et al. 2014, Bishop et al. 2015a, Bishop et al. 2015b, Bishop et al. 2015c).

3.1.2 Geographic variation in human wildlife interactions

Human population growth has been associated with the increase in wildlife/human interactions (Treves and Karanth 2003, Converse et al. 2005). The potential for human-wildlife interactions is particularly of concern in coastal regions. According to the United States 2011 census, in 2010, coastal counties accounted for <10 % of land area (excluding Alaska), but 39% of the population, a 39% increase since 1970 (US census data 2012; NOAA). This overlap of human and wildlife spatial usage not only drives unintentional human-wildlife interactions such as manatee (*Trichechus manatus*) vessel strikes (Jett et al. 2013) or fisheries by-catch (Lewison et al. 2014), but also has a tendency to promote intentional interactions such as wildlife-tourism (Hardiman and Burgin 2010, Velando and Munilla 2011, Curtin 2013, Mustika et al. 2013).

Marine wildlife tourism is a multi-million dollar industry world-wide, particularly in countries with significant coastlines. For example, in 2010, reports from Scotland indicated that marine wildlife tourism had a net economic impact of around £65M (equivalent to $110M US; SGSR 2010). In most cases, organized wildlife tourism operates under the ethos of sustainable, non-invasive and conservation-minded wildlife viewing, and likewise the public responds positively to these measures (Ballantyne et al. 2009). To ensure sustainability and low-disturbance, many government organizations, non-profit organizations or associations of tour operators work with scientists to generate self-enforced viewing guidelines (Hoover-Miller et al. 2013). However, even when ecotourism is promoted under such ‘best intentions’, critics argue that there is potential for cumulative adverse effects to animals’ fitness from these activities (Duffus & Dearden 1990, Williams et al. 2006, Catlin et al. 2011, Christiansen et al. 2013).

One group of animals which has potentially high exposure to human interactions is the phocid seals. Species within this group face exposure to human activities at sea during their foraging (Skeate et al. 2012) and on land during breeding, moulting and resting periods (Perry et al. 2002). Unlike Otariid pinnipeds, as capital breeders, phocids are energetically limited during their time ashore to reserves previously gained during the foraging season. For males in particular, the ability to prolong the length of stay on the colony during fasting is strongly correlated with mating success (Twiss 1991, Lidgard et al. 2005). Therefore, any disturbances during these discrete life history periods could lead to reduced individual fitness. To account for this, in many countries, legislation, such as the Marine Mammal Protection Act of 1972 (MMPA) in the USA, prohibits disturbance of marine mammals through clauses that define ‘harassment’ as any act which, “has the potential to disturb a marine mammal or marine mammal stock in the wild by causing disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering”. In the UK, similar laws prohibit intentional harassment or disturbance of pinnipeds at significant haul-out sites (Marine Scotland Act 2010), while others prohibit direct takes of animals through culling or hunting (Conservation of Seals Act 1970). To uphold these legislative directives, managers must first be able to identify when animals enter periods of disturbance. Therefore, studies have focused on determining effects of disturbance, particularly during critical periods such as pupping or moulting, as altered behavioural states could be placing an energetic cost on seals that might have long-term repercussions or reduced fitness (Suryan and Harvey 1999, Lewis and Matthews 2000, Perry et al. 2002, Engelhard et al. 2002, Stevens and Boness 2003). For example, Perry et al. (2002) examined the exposure of harbour seals and grey seals to sonic booms from concord overflights, and Engelhard et al. (2002) compared the behaviours of southern elephant seals in areas of high and low human presence at the same colony. Both studies found limited or no behavioural effect of anthropogenic presence; however, more studies are needed that address chronic as well as acute responses to anthropogenic activities.

3.1.3 Rationale for study and objectives

Many of the studies investigating the ecology and behaviour of grey seals have been conducted on populations breeding on offshore islands in remote places such as northern Scotland (*e.g.,* North Rona and the Monach Islands, Figure 3.1) or Eastern Canada (Sable Island, Figure 3.1). However, since the mid-1990s, there has been a remarkable expansion of grey seal breeding distributions along the eastern, mainland coast of England and a parallel expansion south along the eastern US coast (Duck and Morris 2010, NEFSC). Haul-sites and breeding colonies are continually appearing in areas of greater human densities, such as around the Thames Estuary near London (Barker et al. 2014). One such breeding colony is Donna Nook (**2.1.1**). While the continuum of behaviours, and the interplay between geography and colony parameters has been addressed across offshore colonies (Anderson and Harwood 1985, Twiss 1991, Lawson 1993, Twiss et al. 1998); no studies to date have included mainland colonies in these assessments. Therefore, this chapter addresses two main objectives: 1) to assess across a wide range of behavioural and spatial metrics, where individual males at Donna Nook fall within the continuum variation already established at offshore breeding colonies for this species, and 2) determine if the mainland location, and the associated increased exposure to anthropogenic activities appears to be influencing the activity budgets of males at Donna Nook, relative to more offshore colonies.

Objective 1: The Donna Nook breeding colony provided the opportunity to document the breeding ecology of mainland colonies and to examine how individuals' behaviours at these locations fit into the known spectrum for this species (Anderson and Harwood 1985). The mainland location is one factor which sets Donna Nook apart, but the flat sandy substrate and dune habitat are similar to colonies such as Sable Island (Canada) or the Monach Islands (Scotland) (pers. corr S. Twiss). In contrast, access to North Rona is restricted to 4 main gullies and the topography once on the main breeding area is composed of grassy and rocky expanses with variation in elevation and slope. As previous work has suggested strong ties between topography and behavioural measures (Anderson and Harwood 1985, Twiss et al. 1998), I predict that behavioural patterns at Donna Nook will align more similarly to those observed at Sable Island than North Rona, regardless of Donna Nook's location on the mainland. To test this hypothesis, and to begin to place mainland colonies within the known spectrum, behavioural and spatial metrics were calculated for males at Donna Nook including: 1) rates of aggression, 2) degree of polygyny, and 3) neighbour proximities for individuals and I compared these to previously published values for males at the North Rona and Sable Island breeding colonies (Twiss 1991).

Objective 2: I compared activity budgets for males breeding on a mainland colony to males at colonies with historically little to no human presence, and determined if there were any behavioural indications of disturbance from human terrestrial activities. Disturbance was here defined as any stimuli which "cause the disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering" (MMPA 1972). Previous studies investigating the effects of human activities on grey seal behaviours have focused on non-terrestrial forms of disturbance; either aircraft noise-pollution (Perry et al. 2002) or vessel-based viewing platforms (Curtin et al. 2009, Strong and Morris 2010) and the results are inconclusive. For example, Curtin et al. (2009) found that when wildlife viewing vessels were in close proximity, groups of grey seals (mixed age and sex-classes) at a haul-out site did exhibit greater rates of alert behaviours; however, Perry et al. (2002) found no evidence that adult male or female grey seals were responding behaviourally to sonic booms during the breeding season. Studies from other animal systems have suggested that the presence of anthropogenic activities, including wildlife tourism, can increase the amount of time animals spend in vigilance and anti-predator behaviours within a population (Frid and Dill 2002). Bottlenose dolphins in the presence of tourism boats had reduced amounts of time and number of bouts of resting and socializing (Lusseau 2003). Harbour porpoises (*Phocoena phocoena*) exposed to geological seismic surveying noise showed reduced vocalizations (Pirotta et al. 2014), and caribou herds (*Rangifer tarandus caribou*) in the presence of tourists were found to spend more time vigilant and standing at the expense of time spent resting (Duchesne et al. 2000). Based on these patterns, if seals at Donna Nook are exhibiting anti-predator disturbance behaviours, one might assume individuals to be more active or vigilant than at the remote colonies. To test this hypothesis, I compared activity budgets for males within Donna Nook at the RAF and PUB sites, and then compared males at Donna Nook to males at North Rona and Sable Island (Twiss 1991); both of which are offshore colonies where the only human presence during the breeding season is research oriented. Specifically, I predict that the time males spend in non-active behaviours will be lowest at the PUB site within Donna Nook, and at Donna Nook across colonies. I also predict time spent alert will be greatest at the PUB site within Donna Nook, and at Donna Nook in comparison to males at North Rona and Sable Island.

3.2 Methods

3.2.1 Observer bias

Data in 2012 and 2013 were collected by two observers (**2.2.1**). The data most prone to observer bias were the records of aggressive interactions (**2.6.2**). Although both observers followed the same protocol for recording all-occurrence records, there is still potential that observations could be missed due to multi-tasking or prioritization, particularly for the more ‘transient’ males who were located at the fringes of the study areas. For males whose dataset comprised data from both observers, I compared the mean rate of aggression when only the observations from the primary observer were used with the mean rate of aggression when only the data from the secondary observer was used (Paired t-test; 2012 n = 49, 2013 n =

71). Another area of potential observer bias was the hourly mapping of individuals. Maps were routinely checked by the primary observer for quality during the field seasons and both observers used the same mapping equipment and techniques; however, spatial mapping was another area in which slight differences in observer accuracy or precision of mapping could have an effect (**2.5**). Differences in the mean distance to nearest neighbour for each male was compared across observers (Paired t-test; 2012 *n* = 49, 2013 *n* = 71). Dominance score calculations were not prone to observer bias due to strict definitions of winner-loser that both observers adhered to with routine cross-checking of data by the primary observer (**2.6.2**). The inclusion of only males that were present for 2 days and had >10 AIs also assisted in ensuring that no anomalous observations from either observer would skew the calculations by restricting the analyses to males with sufficient sample sizes. Activity budgets were only recorded by the primary observer eliminating potential observer bias for this metric (**2.6.4**).

3.2.2 Weather patterns at Donna Nook

Interannual weather patterns and availability of pools on the breeding grounds have been linked to variation in grey seal behaviour (Twiss et al. 2007, Stewart et al. 2014). To examine for such potential confounding differences in weather between the three studied seasons at Donna Nook (2011-2013), mean daily weather variables (**2.8**: Rainfall, Air Temperature, and Wind Speed) were compared across years, and study sites using t-tests or ANOVA tests, with TukeyHSD *post-hoc* tests for specific pairing relationships. Due to inconsistencies in data availability between years, data used for analysis were from 28 October through 6 December in all years. Data were log-transformed when necessary to meet normality assumptions. To examine how individual breeding seasons compared to the long-term average for this site, average daily temperatures for each breeding season of this study were compared to the average daily temperatures from 2003-2013 using a t-test (*e.g.*, the mean for 2003 was compared to the mean for 2004-2013).

3.2.3 Comparisons of anthropogenic presence between years: Donna Nook

Data on visitor numbers at the Donna Nook breeding colony were provided by the Lincolnshire Wildlife Trust. No data were available for North Rona, the Monach Isles or Sable Island. The number of visitors on each day of the weekend (two values per week) was compared across years using an ANOVA due to normality of data (2011 n = 11, Anderson-Darling normality test A = 0.676, P = 0.06; 2012 n = 12 Anderson-Darling normality test A = 0.641, P = 0.07; 2013 n = 11 Anderson-Darling normality test A = 0.678, P = 0.05). The cumulative number of visitors during weekdays (one value per week) was tested for differences across years of the study using non-parametric Kruskall-Wallis tests due to small sample sizes (2011 n = 6, 2012 n =7, 2013 n = 8) and non-normality of data. The presences of other anthropogenic sources of disturbance (jets, tractors, photographers) were quantified to examine changes in seasonality or between year presences.

3.2.4 Activity budgets and rates of aggression comparison analyses

Donna Nook activity budget data were only available for 2011 and 2012 (**2.6.4**) so t-tests were used for comparisons between years and between sites within Donna Nook. I tested for differences across diurnal periods, but due to sampling restrictions, Activity Budgets were examined at a coarse temporal scale using ANOVA tests with TukeyHSD *post-hoc*: Morning (0700-1000), Mid-Day (1001-1300), Afternoon (1301-1700). Data were arc-sine transformed for normality and to account for proportional values. Raw values for Sable Island and North Rona were provided by SDT from the 1988-1989 seasons on North Rona and 1990 season on Sable Island (Twiss 1991). Daily rates of aggression (DAI, **2.5.2**) for all males, and for males who were present for two or more days (Tenured males: Boness and James 1979, Twiss 1991) were compared across years, sites (Twiss 1991), and diurnal categories using t-tests or ANOVA with TukeyHSD *post-hoc* tests; data were log-transformed when necessary to meet normality assumptions.

3.2.5 Apparent polygyny

To assess the degree of polygyny at Donna Nook, I calculated two different metrics: monopolization percentage as a measure of how many males are sequestering a given percentage of the observed copulations, and standardized variance (I_s) of mating success to see how the observed copulations are distributed amongst individuals (Wade and Arnold 1980, Twiss 1991). Monopolization percentage was calculated as the cumulative percentage of observed copulations (**2.6.3**) accounted for by each successive 10% of all identified males who were present for ≥4 hrs (Twiss 1991). The monopolization curves generated for each year and site were compared statistically using Kolmogorov-Smirnov 2-sample tests. Standardized variance is widely used and thus allows for comparisons across various taxa (Wade and Arnold 1980, Shuster and Wade 2003). It is calculated as: $\boldsymbol{I_s} = (\frac{\boldsymbol{s^2}}{\boldsymbol{x^2}})$ where s is the sample standard deviation in mating success, x is the sample mean (again, this was computed for all identified males present for ≥ 4hrs). This calculation results in values increasing from 0, with high values suggesting increased variation of copulation success or higher apparent polygyny. This was done for 2011, 2012 and 2013, and then separately for RAF and PUB sites within each year. Values for North Rona and Sable Island are from Twiss (1991).

3.2.6 Spatial distributions of males and females

Female and male spatial distributions and densities were mapped from the 1300 hr positions (**2.5**) using the kernel density tool in ArcGIS 10 (ESRI) and generated a 1m grid using a 10 or 20 m search radius respectively. I selected only the positions at 1300 hr each day partially because this was one of the times when females were mapped (**2.5**), and also because by afternoon males had typically settled into their locations with minimal activity afterwards (**3.3.4.4**). The size of the radii for which local density was calculated were selected based on protocols used in previous grey seal spatial studies for ease of comparison, and due to the general spacing of males and females on the colony (Table 3.7; Twiss et al. 1994, Pomeroy et al. 1994). In addition, in 2012 and 2013, the densities of aggressive interactions which included a contact phase were mapped for the RAF and PUB site separately (ArcMap 10.1, ESRI). These maps of distributions are included in Appendix 3.

Measures of proximity were also analysed. For each male, the distance to the nearest male in meters (DNM), and the distance to the nearest female in meters (DNF) during each hour of mapping were calculated using the NEAR function in ArcMap 10.1 (ESRI). In order to provide accurate estimates of female-to-male distance, if a male was not present at the hour for which females were mapped, DNF was not calculated for him that day. I identified potential outliers in 2011 (n=1) and 2013 (n=1) where a male had a DNF value more than double the next greatest DNF value from the sample, but found these points were for identified males observed elsewhere on the colony outside of the study sites, and removed them from the sample. DNF and DNM values were then averaged for each individual by day, and separately for an overall seasonal average per male. I tested for differences between sites and between years in the mean distance to nearest male per day, mean distance to nearest female per day, and mean distance moved per hour per day using generalized linear mixed-effects models (GLMM). To avoid pseudo-replication of comparing values from the same male multiple times, ID was included as a random effect. Model selection followed Richards' guidelines (2008), where all models within Δ6 AIC are retained, and any models within this set that are more complex versions of their nested counterparts, but with higher ΔAIC values, are excluded (Richards 2008).

3.2.7 Evidence of behavioural consistencies in activity budgets

Restricting activity budget calculations to males with greater than 200 scans allowed for conservative comparisons across seasons and across study sites; however, there was still high variability among individuals (Figure A1 & A2). While this variation typically gets absorbed into the standard error around the mean, I tested to see if any of the males were consistent in their time allocations for behaviours across years (2011 *vs.* 2012) to determine if there is evidence of behavioural consistency (Twiss and Franklin 2010). To do this, the activity budgets for males who were present with >200 scans in both years (*n* = 25) and males who were highly 'tenured' in that they were present for >500 scans in both years (*n* = 9) were compared across years using inter-class correlations (ICC). ICC is a measure of how strongly units in two groups resemble each other, and can be used to determine the consistency of individual's behaviours across conditions (Twiss and Franklin 2010). In previous studies on grey seals, rates of aggressive behaviours have been found to relate to other variables (*e.g.,* dominance, length of stay: Twiss 1991); however, levels of 'alert' seem to be independent of individual parameters such as size, age, dominance, or tenure (Twiss and Franklin 2010).

3.3 Results

3.3.1 Observer bias considerations

Observer ID did not have a significant effect on average rates of aggression. There were no significant differences in the mean DAI (**2.6.2**) per male in 2012 or in 2013 by observer (2012: Paired t = 1.74, df = 48, P = 0.08, 2013: Paired t = 1.66, df = 70, P = 0.213). For all following analyses, data from both observers were used. Spatial metrics were significantly different across observers; there was an observed 1.03 m difference in the mean nearest male distance between the primary and secondary observer in 2012 (t = 2.01, df = 48, P = 0.09) and a 2.1 m difference in 2013 (t = 1.99, df = 70, P = 0.001). The differences in mapping between observers are partially absorbed by the equipment error of the laser range-finder (±0.5 m up to 100 m; ±1 m > 100 m). Also, the method of placing the positions on the overview maps will have slight errors within observers as well as between. Overall, differences of 1-2 m were considered acceptable, considering the mean distances between males is generally 18-20 m (**3.5.7.3**). Finally, as daily and hourly positions of males fluctuate, the observed differences could reflect true differences in spatial distributions between days and not necessarily observer bias. For these reasons, I chose to use the data from both observers in all further analyses.

3.3.2 Weather and environmental data at Donna Nook

3.3.2.1 Weather variables by year

The 2011 breeding season stood out as a drier and warmer year than 2012 and 2013. Mean daily air temperature was significantly greater in 2011 than 2012 ($F_{2,153}$ = 6.45, P = 0.002) but 2013 did not differ from either year (Figure 3.2). In 2012, the average rainfall per day was significantly greater than in 2011 (Figure 2; $F_{2,140}$ = 3.89, P = 0.02); 2012 also had more rainfall than 2013 but this was not significantly different (P = 0.09). Rainfall in 2011 and 2013 did not significantly differ either. Daily values of wind speed did not differ between years ($F_{2,151}$= 0.73, P = 0.48).

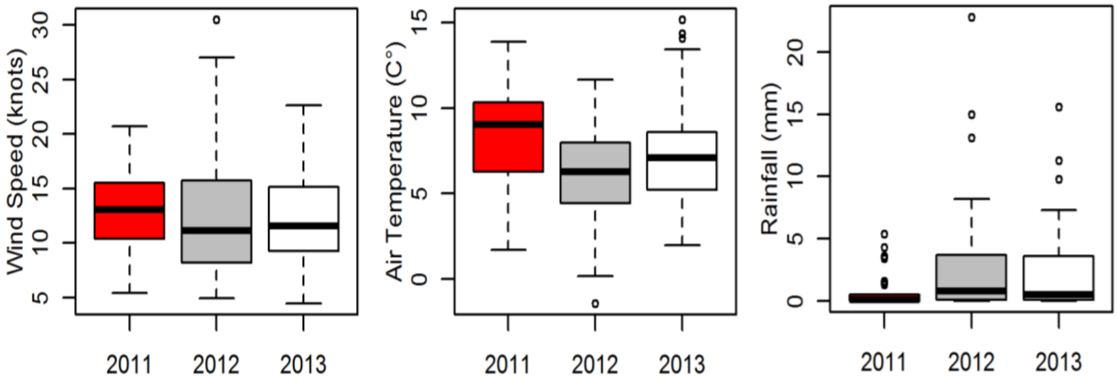


Figure 3.2: The average daily measures for three weather variables at Donna Nook: wind speed (knots), air temperature (C°), and rainfall (mm) from the breeding seasons (Day of Year, DOY 300-340) in 2011, 2012 and 2013. Data from BADC: MIDAS station 405 and 3784. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outlies.

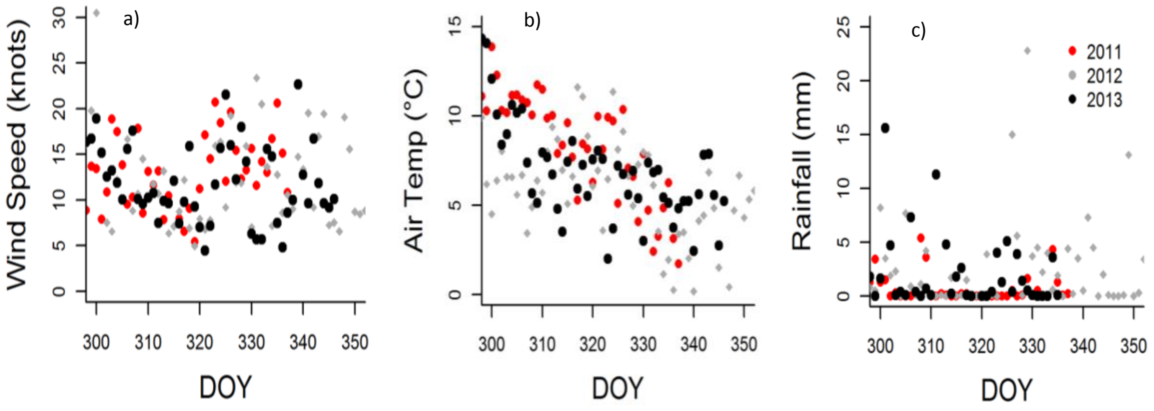


Figure 3.3: Visualization of the variation in the mean daily: a) wind speed, b) air temperature and c) rainfall across Day of Year (DOY 300 = 28-Oct). Data were not available for rainfall after DOY 340 in 2011 and 2013.

3.3.2.2 Within-season variation in weather

Even with the variation between years, the general pattern of weather within seasons was fairly well conserved (Figure 3.3). Wind-speed varied throughout the season similarly in all three years, with a gradual reduction in wind-speed through DOY = 320, then an increase in wind speeds and variation towards the end of the season (Figure 3.3a). Temperature followed a general negative trend across the season for all years; however, in 2012 the initial temperatures for DOY < 310 were significantly lower than the temperatures during that time in the previous year (t = 5.37, df = 23.71, P < 0.0001, Figure 3.3b). Temperatures after this point were not significantly different between years. Rainfall did not appear to follow any set pattern in any of the three years.

3.3.2.3 Historical weather data at Donna Nook

The air temperature data during the breeding season for Donna Nook for the 10 years prior to this study showed that across breeding seasons, the mean air temperature varied from 8.52 (0.37 ±SE) in 2006 to 6.11 (0.70 ±SE) in 2010. Data for 2009 were not available throughout the entirety of the study season preventing an average from being calculated. Results of an ANOVA and *post-hoc* Tukey HSD revealed between year differences ($F_{9,12499}$ = 87.77, P < 0.0001). Temperatures in 2011 were greater than in 2012 (P < 0.001) and 2013 (P

< 0.001) but 2012 and 2013 did not differ (*P* = 0.237). 2006 was an anomalous season with higher average temperatures than any other in this period (*P* < 0.001, Figure 3.4).

The average daily air temperature during the breeding season across all years was 7.3°C 0.3 ±SE (Figure 3.4). Comparing the average daily temperature within a given breeding season to the 13 year average, it appeared that 2003, 2006, and 2011 were on average warmer years for the site, while 2008, 2010, 2012, and 2013 were colder years (Figure 3.4). This comparison is qualitative, but provides a baseline from which to interpret the temperatures observed during this study, and demonstrates the range of the typical temporal fluctuations for Donna Nook.

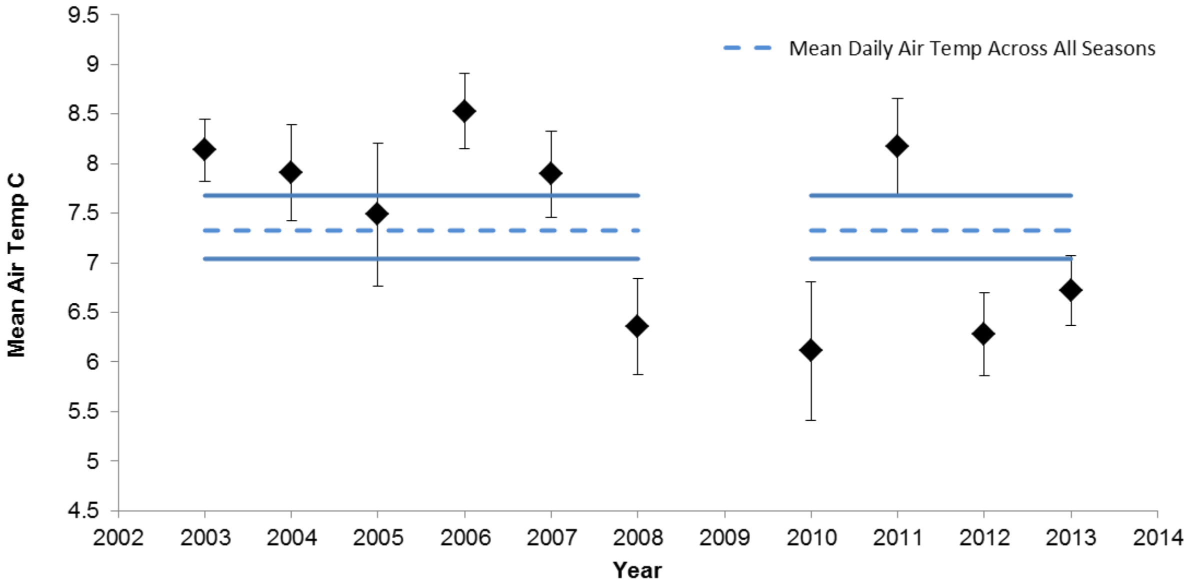


Figure 3.4: The average daily air temperature (±SE) from 27 Oct to 5 Dec for each of the 8 years prior to the study years (2011-2013). Daily mean across all years is represented by dashed line (7.39 °C) with ±SE by the solid lines above and below.

3.3.3 Anthropogenic presence at Donna Nook

3.3.3.1 Visitor numbers at the PUB site

Lincolnshire Wildlife Trust has monitored the total visitor numbers at Donna Nook since 1993 and their data shows a general increasing trend through 2006, with stabilisation and some yearly fluctuations in the subsequent years (Figure 3.5). The tourist visitation patterns exhibited variability within and between the three study seasons with the highest weekend visitation numbers in 2011 but the difference was not significant (Figure 3.6a, Kruskal-Wallis $\chi^2 = 5.3818$, df = 2, $P = 0.067$). Weekend visitation in 2011 averaged 3559 (± 591 SE) visitors each day during peak season (DOY 315-335), while attendance only reached 2175 (± 392 SE) during the same period in 2012, and 2323 (± 338 SE) in 2013 (Figure 3.6a). This was likely due to 2011 being the warmer and drier year. The total number of weekday visitors (summed across five weekdays) did not differ between years (Kruskal-Wallis χ^2 = 0.616, df = 2, $P = 0.73$) and followed the same pattern through the season in each year (Figure 3.6b).

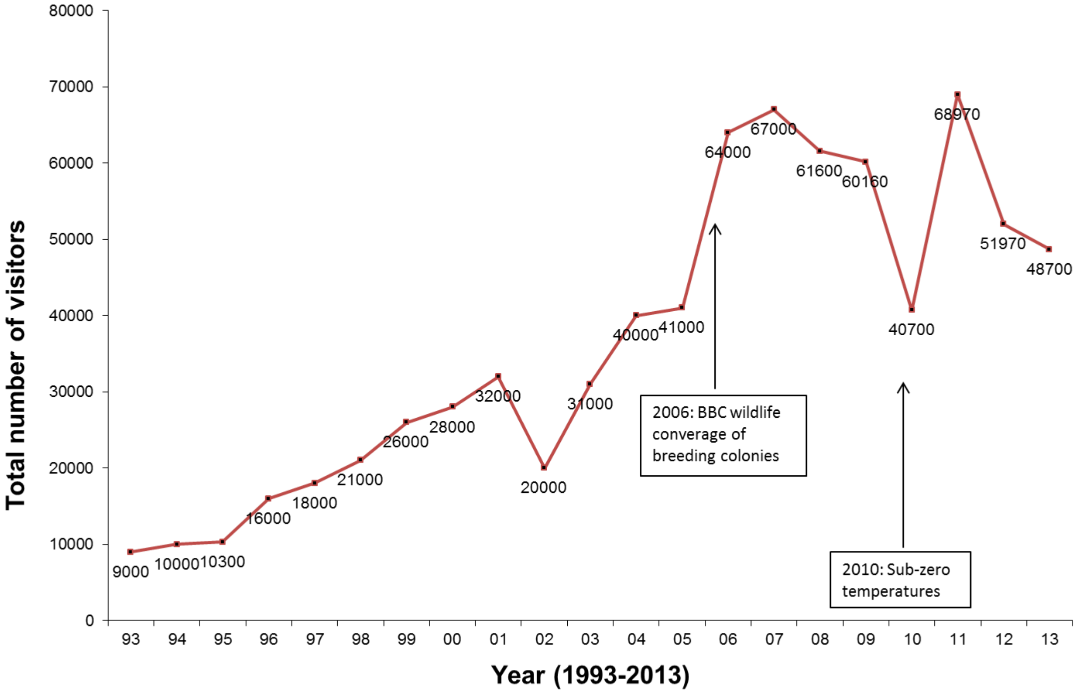


Figure 3.5: The total visitors at Donna Nook during the breeding season (Nov and Dec) each year. Annotations indicate timing of events which correlate with dramatic increases or decreases in visitation numbers (data and annotations from: Lincolnshire Wildlife Trust, RLS).

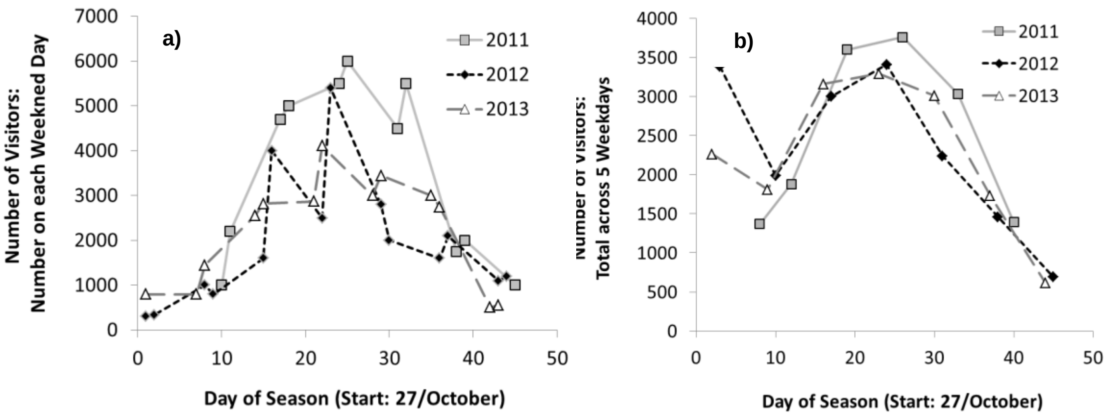


Figure 3.6: Number of visitors on weekend days only for 2011- 2013 at the PUB site (a) and total number of visitors across five week days (b). Note difference in y-axis scales.

3.3.3.2 Other forms of anthropogenic presence

All other forms of anthropogenic presence come from the general operations of the RAF training base. Jets and helicopters are cleared to fly over the space on weekdays. In 2011, 14 of 28 weekdays (50%) had jet or helicopter flyovers observations. This rate increased to 29 of 35 weekdays (83%) in 2012 and to 23 of 29 weekdays (79.3%) in 2013. On all weekdays at the RAF site, a tractor would leave the base around 0800 and return at dusk (~1600) travelling along the length of the beach. Though it had to pass through the seals initially, the tractor would then move in the open space seaward of the main breeding aggregation. Less regularly, a JCB would also travel this route or go straight out from the base toward the sea to service the air-targets. While no formal analysis was conducted, it was observed that male and female seals were alert to the vehicle activities, with rare occasions of individuals moving out of the path. Photographers were seen walking along the dunes early in the season (< DOY 305) at the RAF site in 2012 and 2013, but no other non-RAF activity was recorded at this site. Finally, though a single event each year, for ‘bonfire night’ each year (5-Nov), large bonfires are lit at the RAF base and in the field just behind the dunes at the PUB site. Both fires typically remain smouldering for 5-7 days post lighting.

3.3.4 Activity budgets

3.3.4.1 Averages at Donna Nook and comparison to other colonies

Activity budgets for males at Donna Nook were generally consistent between seasons and demonstrated considerable similarities in comparison to other colonies (Table 3.1). At Donna Nook, the only significant difference in activity budgets between years was that in 2011, males spent less time in agonistic behaviours with females than in 2012 (AggFem: $t = 9.58$, df = 96.32, $P < 0.001$; Table 3.1). Across colonies, when examining the overall Non-Active (Rest + Alert + CMV) activity budgets, there were no significant differences between colonies ($F_{2,208} = 0.60$, $P = 0.55$); however, Sable Island had a slightly reduced amount of time spent in Non-Active behaviours (Table 3.1, Figure 3.7). There were significant differences in the time spent in aggression between all colonies ($F_{2,208} = 11.04$, $P < 0.0001$); Donna Nook males had higher percentages of time spent in aggression than those at North Rona ($P <0.0001$), but spent a similar time in aggression compared to males on Sable Island ($P = 0.91$, Table 3.1). The time males spent resting at Donna Nook was significantly greater than either of the other two colonies ($F_{2,208} = 21.42$, $P < 0.0001$, Table 3.1) and males at Donna Nook spent the least amount of time Alert of the three colonies ($F_{2,208} = 32.06$, $P < 0.00001$, Table 3.1, Figure 3.7).

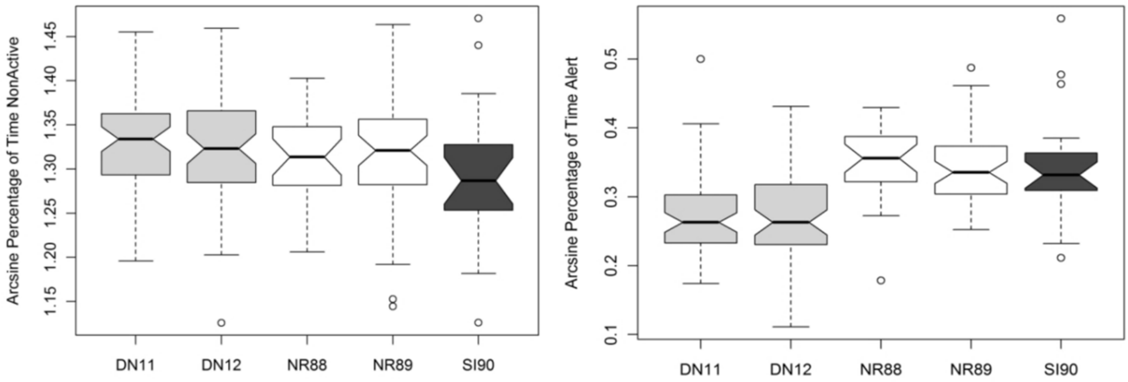


Figure 3.7: Arcsine-transformed percentage of time spent in Non-Active behaviours (left) and arcsine-transformed Percentage of time spent alert (right) at each of the three colonies.at Donna Nook (DN11, DN12), North Rona (NR88, NR89), and Sable Island (SI90). Boxes represent the interquartile range around the median (dark line), with notches displaying the 95% confidence interval around the median. Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outlies.

Table 3.1: Activity budgets for Donna Nook (2011, 2012, DN) and comparison colonies (±SE); percentage of time spent in each activity is the mean across all males with ≥200 scans (or ≥180 scans for North Rona and Sable Island).

	2011 (*n* = 61)	2012 (*n* = 56)	DN (*n =117)*	NR (*n = 73)* *	SI (*n* = 20) *
§Rest	86.5 (0.63)	85.6 (0.65)	86.1 (0.45)	81.6 (0.63)	79.8 (2.02)
§Alert	7.5 (0.45)	7.9 (0.48)	7.7 (0.33)	11.8 (0.42)	11.8 (1.27)
Locomotion	1.5 (0.13)	1.3 (0.12)	1.4 (0.09)	1.7 (0.12)	1.8 (0.26)
§ Yodel	--	--	--	--	0.7 (0.33)
†Approach Female	0.1 (0.02)	--	0.1 (0.02)	0.4 (0.04)	0.3 (0.08)
†Attempted Copulation	0.5 (0.07)	0.5 (0.07)	0.5 (0.05)	0.9 (0.10)	0.5 (0.14)
†Copulation	0.8 (0.13)	0.9 (0.12)	0.8 (0.08)	1.3 (0.14)	0.9 (0.31)
†Non-Ag Flip	0.0 (0.00)	--	0.0 (0.00)	0.0 (0.00)	0.0 (0.01)
‡Female Aggression	0.1 (0.02)	0.7 (0.08)	0.4 (0.05)	--	--
‡Non-Contact	2.9 (0.27)	2.6 (0.18)	2.7 (0.13)	2.1 (0.16)	3.3 (0.37)
‡Contact	0.2 (0.04)	0.1 (0.06)	0.1 (0.02)	0.4 (0.06)	0.2 (0.10)
Reproductive	1.4 (0.19)	1.8 (0.27)	1.6 (0.16)	2.5 (0.20)	1.7 (0.45)
Aggressive	3.1 (0.21)	3.3 (0.17)	3.2 (0.14)	2.3 (0.17)	3.6 (0.40)
Non-Active	94.0 (0.33)	93.5 (0.39)	93.8 (0.25)	93.6 (0.36)	92.9 (0.73)
Active	6.0 (0.33)	6.5 (0.39)	6.2 (0.25)	6.4 (0.36)	7.1 (0.73)

**NR = North Rona Colony 1988 & 1989; SI = Sable Island 1990 (Twiss 1991).*
§ = *'Non-Active',* † = *'Reproductive'* , ‡ = *'Aggressive'*

3.3.4.2 Differences in activity budgets within Donna Nook: RAF vs PUB

Activity budgets for males were overall similar between the RAF and PUB sites, only differing in the amount of time spent in mating or male-female interactions (Table 3.2). In 2011, males at the PUB site spent a significantly greater percentage of time attempting copulations and in successful copulations than males at the RAF site (At Cop: t = -2.49, df = 55.75, P = 0.015; Cops: t = -1.86, df = 58.71, P = 0.07; Table 3.2). This pattern was reversed in 2012 but the difference was not significant. Similarly, in 2011, males at the PUB site spent a greater proportion of time in aggression with females than RAF males (Agg Fem: t = -2.04, df = 53.75, P = 0.04), while in 2012, males at the RAF site tended to spend more time in aggression with females (t = 1.74, df = 46.37, P = 0.09). In both years, males at the RAF site spent more time in male-male Non-Contact aggression than males at the PUB site, while PUB site males spent more time in Contact Aggression (Fights); however neither of these differences were statistically significant.

Table 3.2: Activity budgets at the RAF and PUB sites within Donna Nook (±SE). Activity Budgets were calculated with 5-min scan samples for males with >200 total scans.

	2011		**2012**	
	RAF (*n*=30)	PUB (*n* =31)	RAF (*n* =25)	PUB (*n* =31)
§Rest	86.8 (1.46)	86.2 (0.78)	84.3 (1.39)	86.7 (0.74)
§Alert	7.4 (0.76)	7.5 (0.50)	8.1 (0.88)	7.7 (0.50)
Locomotion	1.4 (0.18)	1.5 (0.20)	1.3 (0.15)	1.4 (0.18)
†Atcop	0.5 (0.13)	0.8 (0.12)	0.7 (0.14)	0.4 (0.05)
†Cop	0.6 (0.15)	1.0 (0.20)	1.1 (0.22)	0.8 (0.12)
‡Female Aggression	0.0 (0.10)	0.1 (0.11)	0.8 (0.16)	0.5 (0.06)
‡Non-Contact	2.6 (0.25)	2.0 (0.18)	2.5 (0.28)	2.1 (0.23)
‡Fight	0.2 (0.04)	0.2 (0.05)	0.5 (0.12)	0.3 (0.06)
Reproductive	1.1 (0.28)	1.7 (0.31)	2.5 (0.71)	1.3 (0.28)
Aggressive	3.4 (0.40)	2.8 (0.34)	3.8 (0.56)	2.9 (0.35)
Non-Active	94.2 (2.22)	93.9 (1.28)	92.4 (2.27)	94.4 (1.24)
Active	5.8 (0.85)	6.1 (0.85)	7.6 (1.41)	5.6 (0.76)

§ = *Behaviours included in 'Non-Active'*
† = *Behaviours included in 'Reproductive'*
‡ = *Behaviours included in 'Aggressive'*

3.3.4.3 Activity budgets for specific aggressive behaviours at DN

Activity budgets for the specific aggressive behaviours OMT and Chase (2.5.1) were not different across years, but males did spent significantly more time performing the Roll (2.5.1) behaviour in 2011 than in 2012 ($t = 4.67$, df = 101.32, $P < 0.001$). There was some variation by site, but no consistent trends. In 2011 males at the RAF site spent significantly more time using OMT than males at the PUB site ($t = 2.05$, df = 57.34, $P = 0.04$); this difference was not apparent in 2012. There were no differences in the amount of time males spent in Chase or Roll between sites for 2011; however in 2012 males at the RAF site were found to spend more time using the Roll behaviour than males at the PUB site ($t = 1.988$, df = 40.91, $P = 0.05$).

3.3.4.4 Diurnal patterns in activity budgets at DN

Activity budgets followed the general pattern of the highest levels of activity in the morning, followed by a reduction of activity levels during mid-day and afternoon. In 2011, males in the morning spent significantly less time resting than the remainder of the day ($F_{2,180} = 12.93$, $P < 0.0001$; morning to mid-day $P = 0.0002$; morning to afternoon $P = <0.0001$), more time alert ($F_{2,180} = 5.23$, $P = 0.006$; morning to mid-day $P = 0.04$; morning to afternoon $P = 0.006$), and more time in locomotion ($F_{2,180} = 19.48$, $P < 0.0001$; morning to afternoon $P < 0.0001$; morning to mid-day $P < 0.0001$; Figure 3.8). For Alert, Rest, and Locomotion behaviours, no difference was found between mid-day and afternoon activity budgets. In regards to aggression, males were found to spend the most time in aggression in the early morning and afternoon ($F_{2,180} = 3.63$, $P = 0.02$; morning to mid-day $P = 0.02$; Figure 3.8). No temporal pattern was found in regards to time spent in reproductive activities ($F_{2,180} = 1.60$, $P = 0.203$).

The 2012 breeding season followed a similar pattern to 2011. All three times of day were significantly different for percentage of time spent in Rest ($F_{2,166} = 27.74$, $P < 0.0001$)

and Alert ($F_{2,166} = 14.54$, $P < 0.0001$) with percentages in rest increasing throughout the day and time spent alert decreasing throughout the day (Figure 3.8). Locomotion shared a similar pattern of decreasing levels throughout the day in 2012 as it did in 2011 (Figure 3.8: $F_{2,166} = 6.01$, $P = 0.003$; morning to mid-day $P = 0.244$; morning to afternoon $P = 0.001$; mid-day to afternoon $P = 0.15$). Aggression in 2012 was again greatest in the morning but the percentage of time spent during mid-day and afternoon were not different (Figure 3.8; $F_{2,166} = 9.33$, $P = 0.0001$; morning to mid-day $P = 0.03$; morning to afternoon $P < 0.0001$; mid-day to afternoon $P = 0.17$). Finally, time spent in reproduction in 2012 was greater in the morning than the afternoon ($F_{2,166} = 6.87$, $P = 0.001$; morning to afternoon $P = 0.001$) but no significant differences were found between the other time periods (Figure 3.8).

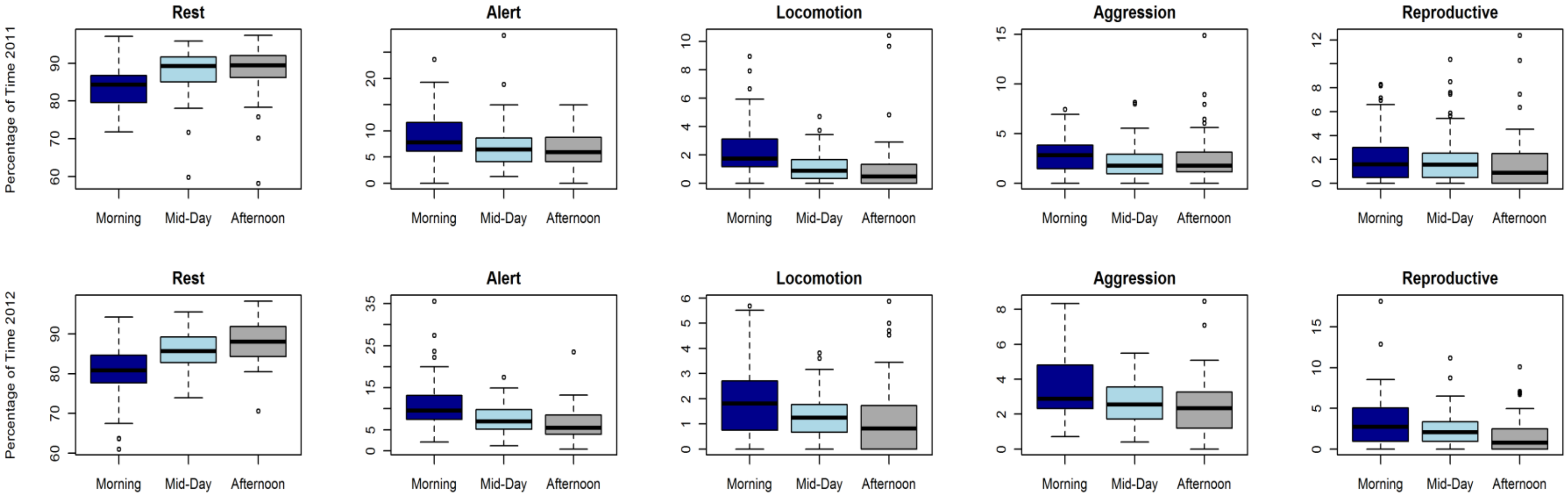


Figure 3.8: Diurnal patterns of activity budgets in 2011 (top) and 2012 (bottom) with time spent in each activity during the morning (0700-1000), mid-day (1001-1300) and afternoon (1301-1700).

3.3.5 Daily rates of aggression

3.3.5.1 Averages at Donna Nook and comparison to other colonies

Average daily rates of aggression (DAI) differed significantly by year at Donna Nook. When considering all males, the average DAI per male was significantly greater in 2013 than in 2011 (Table 3.30, $F_{2,512}$= 44.23, $P < 0.001$), but was not significantly greater than 2012 ($P = 0.66$). For Tenured males, 2013 again had the greatest average DAI per male (Table 3.3, $F_{2,277}$ = 273.33, $P < 0.001$), and DAI was also significantly greater in 2012 than 2011 ($P < 0.01$). The percentage of AIs which involved contact decreased from 2011 to 2012 and, further decreased from 2012 to 2013 (Table 3.3).

In comparison with other colonies, North Rona had the lowest rates of aggression of all three colonies, while Donna Nook and Sable Island both had greater rates of aggression (Table 3.3). Donna Nook on average had a greater rate of aggression compared to North Rona; however, in 2011 the rates of aggression were very similar (Table 3.3). Sable Island had greater rates of aggression and fewer interactions which escalated to contact than North Rona or Donna Nook (Table 3.3).

Table 3.3: Average number of aggressive interactions per male, per 8 hr (±SE), across years at Donna Nook and across colonies, DN, North Rona (NR) and Sable Island (SI).

	2011	2012	2013	DN	NR	SI
DAI (all)	4.3 (0.22)	11.2 (0.85)	10.4 (0.59)	8.7 (0.41)	3.8 (0.55)	15.1 (1.50)
n IDs (all)	183	140	192	399	68	66
DAI (tenured)	4.2 (0.24)	8.3 (0.61)	11.1 (0.82)	8.4 (0.48)	3.5 (0.63)	17.2 (1.70)
n IDs (tenured)	79	101	100	207	47	40
% escalated (tenured)	10.5%	6.5%	4.9%	7.3%	5.7%	3.5%

DAI = Daily Rate of Aggression (#AI per 8hrs)
Data for NR 1987 and SI 1990 from Twiss 1991; #AI per day of observation

3.3.5.2 Averages between sites within Donna Nook

Overall, aggression at the RAF site was significantly greater than the PUB site (t = 3.98, df = 145.54, P = 0.0001) but this appeared to largely be driven by the difference in aggression in 2012 and 2013 (2011**:** t = 0.37, df = 75.84, P = 0.71; 2012: t = 1.68, df = 83.19, P = 0.09; 2013: t = 5.08, df = 67.26, P < 0.0001; Table 4). For example, 2013, the mean DAI for males at the RAF site was almost double the average rate of those at the PUB site (Table 3.4). Finally, in 2011, the RAF site had a greater percentage of interactions containing physical contact than the PUB site, and the opposite was found for 2012 and 2013.

Table 3.4: Mean daily rate of aggression (DAI) per male per 8 hr across study sites within DN and across years; and % of all recorded Aggressive Interactions which contained physical contact at each site each year.

	*n**	2011	*n**	2012	*n**	2013
RAF DAI	40	4.3 (0.32)	56	9.1 (1.02)	51	14.5 (1.31)
PUB DAI	39	4.1 (0.36)	45	7.2 (0.55)	49	7.4 (0.46)
RAF % Contact	40	13.4%	56	6.4%	51	4.1%
PUB % Contact	39	12.1%	45	7.0%	49	5.7%

DAI = Daily Rate of Aggression (#AI per 8 hrs)

**Tenured males only (males with > 10 AIs and present for > 2d)*

3.3.5.3 Contest duration across years

Contest duration for interactions with clear winners and losers varied across years depending on the level of escalation. Non-Contact AIs with clear winners and losers were significantly longer in 2013 (146.4 s ± 12.7) than in 2012 (92.9 s ± 10.85; $F_{2,76}$ = 4.57, P = 0.013) and while the average for 2011 (105.2 s ± 11.62) was also longer than 2012 this difference was not significant (P = 0.31). There was no significant difference in duration across years for Contact AIs resulting in clear winners and losers ($F_{2,56}$ = 2.21, P = 0.12). When the interaction resulted in a draw, the duration of Non-Contact AIs did not differ across years ($F_{2,430}$ = 0.76, P = 0.46). The duration of Contact AIs ending in a draw was longest in

2011 (260.3s ± 33.08) in comparison to 2013 (175.9 s ± 15.80 $F_{2,48} = 3.67$, $P = 0.03$) but was not different compared to 2012 (243.5s ± 25.59; $F_{2,48} = 3.67$, $P = 0.06$).

3.3.6 Apparent polygyny and sex-ratios at Donna Nook and comparison colonies

3.3.6.1 Sex ratios and monopolization of observed copulations

Sex ratios at Donna Nook were on average 1.86 females to 1 male (2011-2013), but during peak season this shifts to approximately 3.6:1. Apparent polygyny at Donna Nook was similar to the observed values at North Rona and Sable Island. The top 10% of males monopolized 62.2-71.7% of the copulations at Donna Nook, 45-76% of observed copulations at North Rona (Twiss 1991: 1987-1989 data), and 80% of observed copulations at Sable Island (Twiss 1991: 1990 data). At Donna Nook, 66.2-79.6% of males gained no observed copulations while between 50-75% of the males gained no copulations at North Rona (Twiss 1991: 1987-1989 data) and >80% of males gained no observed copulations at Sable Island (Twiss 1991: 1990 data). A similar pattern was found when considering the standardized variance (I_s) of observed mating. Overall values for Donna Nook were greater than North Rona and similar to Sable Island (Table 3.5). Between years at Donna Nook, 2012 had lower values than the observed variation in 2011 and 2013 (Table 3.5).

Table 3.5: Values of standardized variance in mating success for Donna Nook (DN) between years and comparison of *RAF* and *PUB* sites separately by year. Values for North Rona (NR) and Sable Island (SI) added from Twiss 1991 for comparison.

Breeding colony or *Study Site*	I_s (Standard Variance)
DN 2011 (n = 182)	6.61
DN 2012 (n = 155)	4.64
DN 2013 (n = 192)	6.05
RAF 2011 (n = 97)	7.47
PUB 2011 (n = 85)	5.07
RAF 2012 (n = 90)	6.11
PUB 2012 (n = 65)	3.42
RAF 2013 (n = 102)	9.51
PUB 2013 (n = 90)	4.04
NR 1987 (n = 85)	2.15
NR 1988 (n = 117)	5.31
NR 1989 (n = 145)	5.26
SI 1991 (n = 80)	6.76

Results of the Kolmogorov Smirnoff 2-sample test testing the monopolization curve showed no significant differences between years or sites. In 2011, for Donna Nook as a whole, 79.6% of the males gained no successful observed copulations while approximately 10% of the males monopolized 71.7% of the observed copulations. The level of monopolization was lower than the Donna Nook average at the PUB site in 2011 and higher than the Donna Nook average at the RAF site. In 2012 there were slightly lower levels of polygyny overall with 10% of the males monopolizing approximately 62.2% of the copulations and 66.2% of the males were entirely unsuccessful at gaining observed copulations. Again the RAF site had higher apparent polygyny than the PUB site. In 2013, polygyny was high again with 74.1% of males achieving no copulations, and 10% of males monopolizing 67.6% of copulations. Polygyny again appeared to be higher at the RAF site in 2013 relative to the PUB site.

The values of the monopolization curve therefore suggest the perceived level of polygyny at DN is similar to the observed polygyny on North Rona and Sable Island (Twiss

1991). The standardized variance of observed mating success (or the potential for sexual selection to act on males) however, showed that overall values for Donna Nook were greater than North Rona and similar to Sable Island (Table 3.5). Between years at Donna Nook, 2012 had lower values than the observed variation in 2011 and 2013 (Table 3.5). In all years, the RAF site had higher values of variance than the PUB site; suggesting that not only were more males excluded at this site than the PUB site, the distribution of copulations amongst those males who did achieve mating success was also more disproportionate that at the PUB site.

3.3.7 Spatial characteristics at Donna Nook and comparison colonies

3.3.7.1 Male and female spacing and movement patterns

Comparing across colonies, proximity to neighbours was similar across Donna Nook and North Rona ($\Delta AIC_{Colony} = 6.76$, $\Delta AIC_{RandomEf} = 0$; Table 3.6). Similarly, the distances moved between hours at Donna Nook tended to be greater on average than the distances moved at North Rona, but the model without the variable of Colony and with only the random effects was retained within the selection criteria ($\Delta AIC_{Colony} = 0$, $\Delta AIC_{RandomEf} = 0.82$, Table 3.6).

Table 3.6: The daily averages (±SE) for spatial measures of: distance to nearest male (m), distance to nearest female (m) and hourly distance moved (m) across years at Donna Nook (2011-2013) and North Rona. Values were calculated for males present for >4 hr per day only for Donna Nook.

	Donna Nook 2011-2013 (n_{recs} = 2075, n_{ID}= 384)	**North Rona 2002-2003*** (n_{recs} = 1764, n_{ID} 184)
Nearest Male (DNM)	19.0 (0.15)	24.2 (0.29)
Nearest Female (DNF)	11.1 (0.34)	--
Hourly Distance Moved	13.0 (0.24)	10.0 (0.29)

**North Rona data from Twiss Unpublished*

Within Donna Nook, the mean DNM per male per day tended to be shorter at the RAF than the PUB site across all three years but there was no significant effect of SITE or YEAR on these two variables ($\Delta AIC_{RandomEf} = 0$). In contrast, the mean DNF per male per day tended to be farther away at the RAF site than the PUB site for all three years combined (ΔAIC_{Site} = 0, Table 3.7); the random effects only model was also retained in the criteria ($\Delta AIC_{RandomEf}$ = 2.11).

YEAR and SITE, and the interaction term were retained as significant predictors of average daily distance moved per hour ($\Delta AIC_{Year *Site}$ = 0, $\Delta AIC_{RandomEf}$ = 531.19; Table 7). Males moved farther per hour in 2012 than 2011 or 2013 ($P < 0.0001$; Table 3.7). Males at the PUB site had shorter mean distances moved per hour than males at the RAF site in 2011 ($P = 0.01$) and 2013 ($P = 0.0005$), but significantly greater distances moved in 2012 ($P = 0.024$) (Table 3.7). The distances moved between hours at Donna Nook in 2011 and 2013 were similar to the distances moved at North Rona (Table 3.7).

Table 3.7: The daily averages (SE) for spatial measures of: distance to nearest male (DNM), distance to nearest female (DNF) and hourly distance moved (HDM) across years and sites at Donna Nook. Values were calculated for males present for >4 hr per day only. There were no significant differences in DNM, but DNF was greatest in 2011.

	2011	**2012**	**2013**
n_{recs} (n_{ID})	*507 (183)*	*815(140)*	*797 (192)*
DNM	20.1 (0.31)	18.2 (0.19)	19.2 (0.22)
DNF	13.8 (0.70)	12.5 (0.53)	11.6 (0.58)
HDM	10.5 (0.48)	18.0 (0.19)	9.3 (0.34)
n_{recs} (n_{ID}) RAF *n_{recs} (n_{ID}) PUB*	*229 (100)* *278 (83)*	*383 (80)* *432 (60)*	*344 (102)* *453 (90)*
DNM RAF	20.2 (0.46)	18.0 (0.26)	19.0 (0.29)
DNM PUB	20.1 (0.42)	18.3 (0.28)	19.3 (0.32)
DNF RAF	14.0 (1.05)	14.6 (0.85)	13.7 (1.02)
DNF PUB	13.7 (0.92)	10.8 (0.64)	10.2 (0.68)
HDM RAF	11.2 (0.70)	17.6 (0.27)	12.0 (0.64)
HDM PUB	10.1 (0.66)	18.2 (0.28)	7.2 (0.31)

3.3.8 Individual behavioural consistencies

Males with >200 scans showed inter-year consistencies for percentage of time spent Alert, Resting and in Aggression, with Alert showing the greatest consistency (Table 3.8; Figure 3.9). When only considering males with >500 scans, only Alert and Aggression showed consistency between years and the consistencies were stronger than when considering all males with >200 scans (Table 3.8; Figure 3.10).

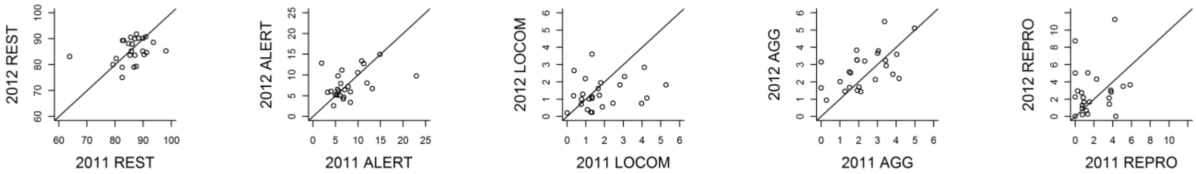


Figure 3.9: Activity budgets for Rest, Alert, Locomotion, Aggression and Reproductive behaviours in 2011 vs 2012. Males with >200 scans in both years are shown here as individual points. Line represents 1:1 relationship of pure consistency.

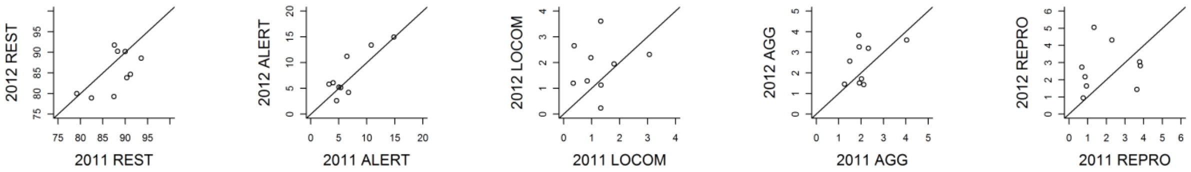


Figure 3.10: Activity Budgets for Rest, Alert, Locomotion, Aggression and Reproductive behaviours in 2011 vs 2012. Males with >500 scans in both years shown here as individual points. Line represents 1:1 relationship of pure consistency.

Table 3.8: Interclass correlation (ICC) for consistencies in male activity budgets between 2011 and 2012. Only males with >200 scans (n = 25) or >500 scans (n = 9) were used to compare across similarly Tenured males. Significant ICC relationships are where the 95% CI does not include 0; denoted by *.

		Rest	Alert	Locomotion	Aggression	Reproduction
>200 Scans	**ICC**	**0.40***	**0.52***	**0.19**	**0.47***	**0.15**
	UCI	0.68	0.75	0.53	0.72	0.50
	LCI	0.03	0.18	-0.20	0.12	-0.24
>500 Scans	**ICC**	**0.59**	**0.90***	**0.27**	**0.64***	**-0.27**
	UCI	0.89	0.98	0.77	0.91	0.43
	LCI	-0.02	0.65	-0.40	0.06	-0.76

3.4 Discussion

The results of this chapter provide a comprehensive update on the plasticity of male grey seal mating behaviours across the geographical distribution of the species, and demonstrate the selection factors potentially operating within the system. While Donna Nook has been monitored and managed by the Lincolnshire Wildlife Trust for over 30 years, the results of this study provide the first collection of behavioural data on males for this region of the grey seal distribution and for an expanding mainland breeding colony in the UK. My results suggest that the Donna Nook breeding colony lies in the middle of the known continuum of breeding colonies with regards to sex-ratios, variation in male mating success (I_s) and for both frequency and time spent in aggression by males (Figure 3.11). I will review how the observed similarities and differences between colonies highlight the strong selection pressures driving this species' behavioural patterns with regards to energetic trade-offs, human-wildlife interactions, and the behavioural flexibility of a species to adjust to natural and anthropogenic fluctuations in the environment.

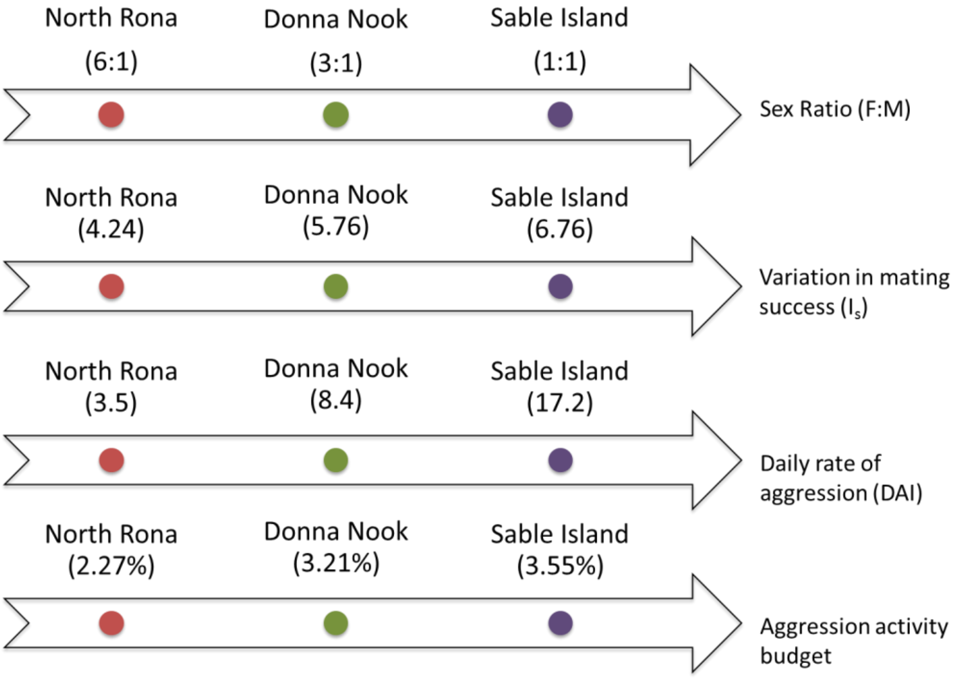


Figure 3.11: The continuum of behavioural variation across grey seal colonies, including the results of this study (Donna Nook). Data from North Rona and Sable Island are from Twiss 1991 and Twiss et al. 1998.

3.4.1 Cross-colony geographic variation in behaviours

3.4.1.1 Sex-ratios and aggression

An inverse link between rates of aggression and F:M sex-ratios has been suggested for polygynous, pinniped systems (Anderson and Harwood 1985, Twiss et al. 1998, Johanos et al. 2010). This trend is primarily thought to be driven by the inability of males to monopolize groups of females when fewer females per male are present (Emlen & Oring 1977, Reynolds 1996, Twiss et al. 1998); and that the greater relative number of males in a 1:1 sex-ratio leads to increased chance of interacting with other males (Tinker et al. 1995). Thus, a bell-shaped relationship between sex-ratios and aggression (instead of a strictly inverse one) has been supported across numerous taxa (Figure 3.12), suggesting that, as male-to-female ratios increase, aggression will subsequently increase but only to a threshold, after which aggression declines with decreasing benefits of fighting (Grant et al. 2000, Weir et al. 2010). The results of this study confirm this framework, and suggest that the colony with the greater female-to-male sex ratios (*e.g.*, North Rona) had the lowest aggression (Figure 3.11).

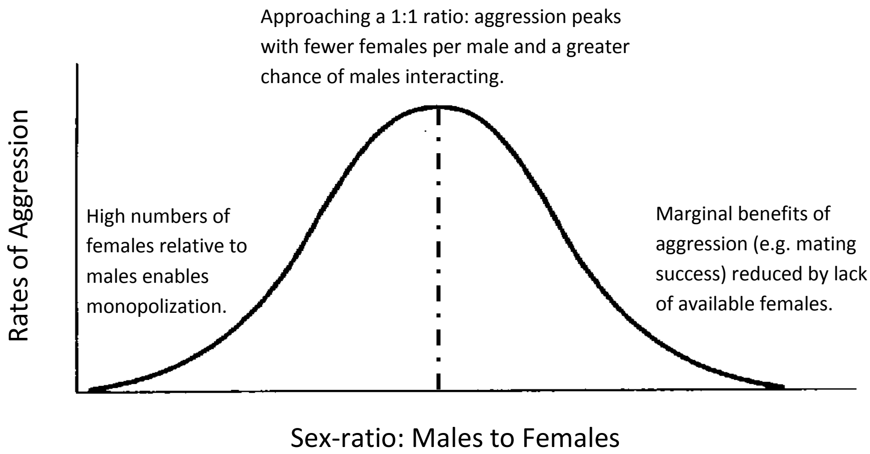


Figure 3.12: The relationship between aggression and sex-ratios is proposed to be a bell-shaped relationship with increasing aggression associated with an increase in male competitors, but then followed by a decrease in aggression as the marginal benefits are reduced (from: Grant et al. 2000, Wier et al. 2010). Grey seals mating patterns range to the left of the dashed line.

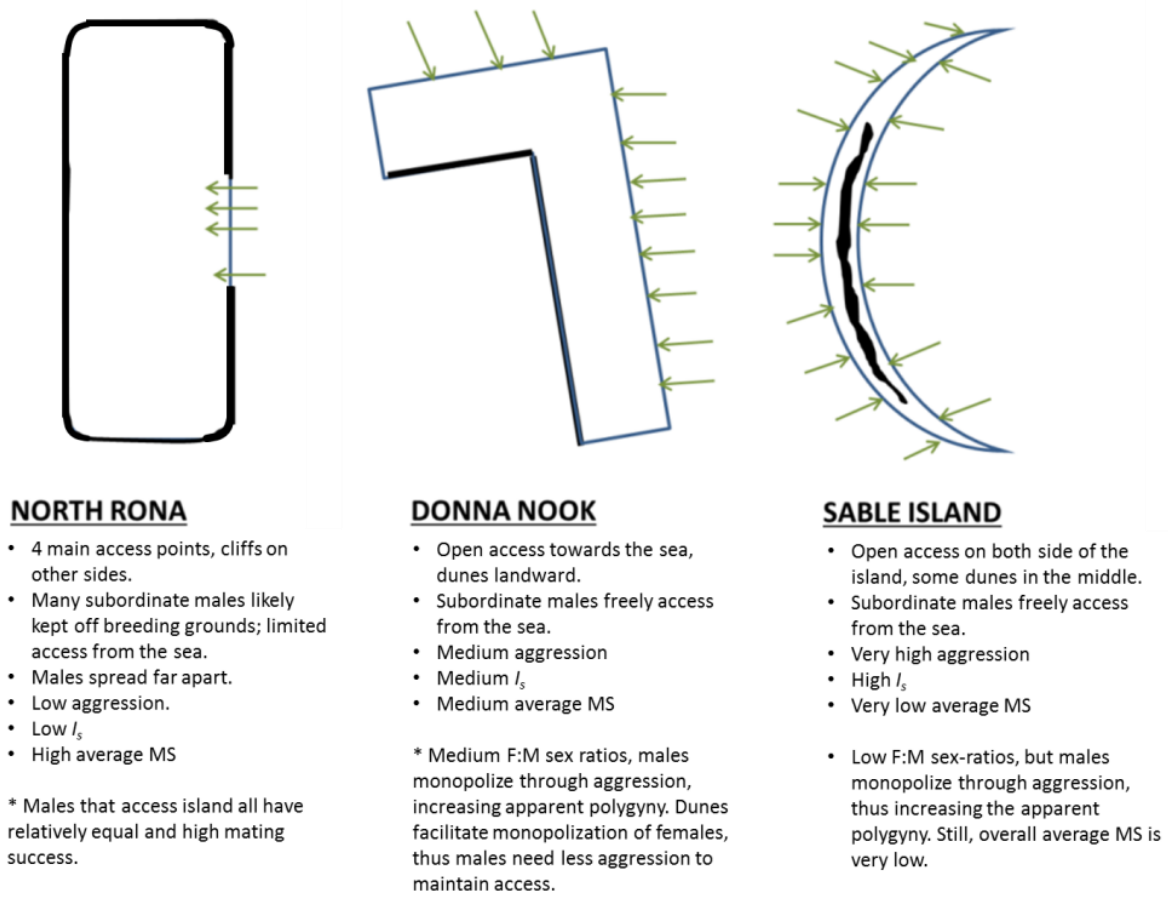
In addition to predicting the degree of male-male competition, many studies often use sex-ratios or operational sex-ratios (OSR), the ratio of reproductively active females to males, as a proxy for polygyny under the assumption that with relatively fewer females available, it is more difficult to monopolize access, and systems will revert to monogamy (Emlen & Oring 1977, Maynard-Smith et al. 1982, Reynolds 1996). Operational sex-ratios are very difficult to assess in breeding grey seal systems due to the spatial and temporal dispersal of satellite males, the short duration of time spent in oestrus, and the turnover of males and females throughout the breeding season (Twiss et al. 1998). However, since F:M sex-ratios appear to be relatively sufficient estimates of operational sex-ratios (Twiss et al. 1998), one would expect that the seal colonies with greater female-to-male ratios would have relatively greater OSRs and greater variation in mating success (Maynard-Smith 1982, Wier et al. 2010). The results of this chapter suggest the opposite (Figure 3.11).

3.4.1.2 Ease of access

The discrepancy between sex-ratio and the apparent degree of polygyny might be explained by the topography at each colony; particularly, how the ease of access from the sea and clustering of females shapes male demographics on the breeding colony (Emlen and Oring 1977). Anderson and Harwood (1985) first noted that topographic differences seemed to shape activity budgets across colonies. Stirling (1975) also suggested that topography could influence the level of apparent polygyny; however, the pattern he referred to only considered sex-ratios and not variability in mating success. At North Rona, males can only access the main breeding grounds from four main gullies. This likely restricts the number of subordinate males attempting or able to gain access to females, as they would have difficulty fighting their way onto the colony. With less subordinate males on the colony attempting to gain ‘sneaky copulations’ or any of the identified alternative mating strategies (Lidgard et al. 2001, Lidgard et al. 2004), the observed inter-male variability might be reduced as most males which achieve access gain similar numbers of copulations. This pattern would also explain the reduced aggression exhibited at North Rona as males who have gained access to the colony would not be exposed to ‘nagging’ from a large number of transient subordinates (Twiss et al. 1994, Boness et al. 1995). In contrast, the relatively open access at Sable Island and at Donna Nook would allow for a larger mix of males on the colony at any given time. The resulting lower female to male sex-ratios would reduce the expected average individual mating success as was observed in this study, but males might still maintain higher levels of inter-male mating variability through aggression and competition for spatially clustered groups of females.

The open topography at both Donna Nook and Sable Island also appears to promote the relatively greater rates of aggression; however, at Donna Nook, rates of aggression and time spent alert were both lower than for males at Sable Island. Sable Island is a wide sand-bar with access to the breeding areas from both sides in some places. The central area of Sable Island however, is bifurcated by high dunes, which limit the direction of access to the beach (Figure 3.13). The data for Sable Island presented in Twiss (1991) were collected at a location on the island amidst a collection of dunes, but the elevation and slope of these features were not perceived to present a ‘barrier’ to movement (pers. corr. SDT). Therefore, it is worth noting that in areas where the dunes did limit the direction of access to the beach, possible male behaviours might align more similarly to the patterns observed at Donna Nook (Figure 3.11). Also, there is some evidence to suggest female grey seals exhibit a gradient of mate choice in response to breeding site location and harassment from males (Pomeroy et al. 1994, Boness et al. 1995, Twiss et al. 2000, Lidgard et al. 2001, Lidgard et al. 2004, Twiss et al. 2012, Hardman 2014). As topography likely shapes the greater female to male ratios and greater inter-male spacing at North Rona, this could also allow females to move about the colony with less male harassment, more readily express mate-choice and, subsequently, reduce the amount of mating variability.

While spatial and temporal patterns of seals within a colony can drive patterns of mating success, aggression, and male strategies (Anderson and Harwood 1985, Twiss et al. 1998, Twiss et al. 2006), this study confirms that sex-ratio is not a perfect approximation of apparent polygyny, and that the feedback between colony topography, particularly ease of access, and the mating demographic can drive the observed variation in mating success (Figure 3.13).



NORTH RONA

- 4 main access points, cliffs on other sides.
- Many subordinate males likely kept off breeding grounds; limited access from the sea.
- Males spread far apart.
- Low aggression.
- Low I_s
- High average MS

* Males that access island all have relatively equal and high mating success.

DONNA NOOK

- Open access towards the sea, dunes landward.
- Subordinate males freely access from the sea.
- Medium aggression
- Medium I_s
- Medium average MS

* Medium F:M sex ratios, males monopolize through aggression, increasing apparent polygyny. Dunes facilitate monopolization of females, thus males need less aggression to maintain access.

SABLE ISLAND

- Open access on both side of the island, some dunes in the middle.
- Subordinate males freely access from the sea.
- Very high aggression
- High I_s
- Very low average MS

- Low F:M sex-ratios, but males monopolize through aggression, thus increasing the apparent polygyny. Still, overall average MS is very low.

Figure 3.13: Schematic of how access to the colony from the sea shapes male aggression, variability in mating success and average mating success at three different colonies. Blue borders = access to the sea. Black boarders = barriers to movement or access (cliffs or dunes). Green arrows = general ease of access or on North Rona, the number of access points. MS = observed mating success.

In contrast, the landward topography at Donna Nook, *e.g.*, the viewing fence in the public section or high dunes along the RAF portion of the beach, created an effective barrier to movement. The dunes limited the distribution of females and ensured that agonistic interactions at these locations could only come from the seaward side (Figure 3.13). Anderson and Harwood (1985) suggested rates of aggression and activity should decrease against such barriers, because the barriers would allow males to have their 'backs against the wall', thus restricting the area towards which they would have to be alert to intruders. These landward barriers were observed at the offshore, isolated, Monach Islands (Scotland; Anderson and Harwood 1985). However, the landward barriers at Donna Nook are the locations where seals also are at their highest exposure to anthropogenic activities, particularly on the weekends or during military training operations. It is possible that at Donna Nook seals have a differing perception of the barriers dependent on the presence of anthropogenic activities or context. Landscape of fear analysis, which spatially identifies perceived or actual predation risk based, has recently be used to assess the perception and use of the environment by individuals based on behaviours (Laundré *et al.* 2001, Willems and Hill 2009, Coleman and Hill 2014). Future studies can attempt to address this information gap by using landscape of fear theory and fine-scale mapping of behaviours associated with vigilance, such as the alert behaviour, to investigate the role of topography, perceptions of human activities, and potential for habituation on animal distributions.

3.4.1.3 Weather

Many studies mention topographic differences as drivers of geographic variability in behaviours, but how topography drives frequencies of agonistic interactions is likely also dependent on, or coupled with, temperature and rainfall variability. For example, thermal stress has been suggested as a driver for selecting against high levels of aggression in warm/arid environments (Ganem and Nevo 1996). The interactions between weather patterns and topography have been demonstrated for grey seals and other pinnipeds in the forms of: variation in apparent monopolization of mating success (Twiss et al. 2007), female breeding site choice (Redman et al. 2001, Stewart et al. 2014), and location of aggressive behaviours for California sea lions, *Zalophus californianus* (Bohórquez-Herrera et al. 2014). California sea lions' response to temperatures also appears to be dependent on the location of the colony and the 'typical' range of temperatures experienced (Bohórquez-Herrera et al. 2014). The activity budgets for many pinnipeds also follow a crepuscular pattern, in that the time of day with the greatest activity is the morning and late afternoon (Chrsitenson and LeBoeuf 1978, Twiss 1991, **3.3.4.4**). Presumably, this temporal pattern has been selected as a way to conserve energy, and minimize activity during the warmest periods of the day. Mean temperatures at Donna Nook during the 2011 breeding season were greater and mean rainfall was significantly lower than in 2012 and 2013. Furthermore, the mean temperature was greater than the average for the 10 year period. Male grey seals are dark in colour, relative to female and pups, which suggests they might be more prone to heat loading due to direct sunlight. If temperature and availability of water drive aggressive/active behaviours, this would suggest 2011 was perhaps an anomalous year relative to the other two years of the study. In 2011, there were fewer males ashore (**2.4**), males were more spread out (mean distance to nearest male/female), exhibited greater apparent polygyny than in 2012, engaged in agonistic interactions less frequently but spent the same percentage of time in aggressive behaviours (Bishop et al. 2015b). Additionally, anecdotal evidence suggests increased instances of digging and flinging sand by both sexes in the drier warmer years of 2011 and 2013 at Donna Nook, possibly as a mechanism to access cooler, wet sand below the surface. These results suggest that temperature and rainfall might not only drive spatial constraints on rates of aggression and polygyny between colonies, but that thermal limits might select for between-year variation in behaviours such as switching to fewer, but longer interactions under higher temperature conditions.

The role of temperature with regards to the geographic differences in behavioural activity can also be considered in regards to species' distributions. Donna Nook is nearing the southern limits of the species distribution in the Western Atlantic (NMFS 2009). For juvenile grey seals, hyperthermia only occurs at air temperatures greater than 30 °C (Boily and Lavigne 1996). Assuming this temperature also limits adults might be overly conservative as adults are larger and fatter and should therefore risk hyperthermia at lower temperatures. However, 30 °C is rarely if ever reached during the breeding season, thus suggesting that air temperatures might not be limiting the southern extent of breeding distributions. At present, the species distribution of grey seals does appear to be experiencing population growth at the southern margins, with breeding colonies along the south and eastern coasts of the UK in the Eastern Atlantic experiencing rapid pup production growth of 5-40% annually (Duck and Morris 2010). Similarly, in the Western Atlantic along the US northeast coast, there are three established southern breeding colonies at Muskeget Island, Massachusetts; Green Island, Maine, and Seal Island, Maine, with overall annual increases of 20.5% (not accounting for potential immigration; NEFSC report 2010). Changes in weather during the breeding season might be interesting to consider for the US/Canadian colonies, as breeding occurs later in the winter (Jan-Feb) with average temperatures of -0.2 °C (www.sable-island.climatetemps.com) compared to the average temperature of 7.42 °C at Donna. Future work investigating local and broad flexibility of individuals to adapt their behaviours to future changes in mean air temperature, or variation in temperature between years, can inform models of population growth dynamics, resource partitioning, stress-responses and population structure in regards to predicted climate change scenarios.

3.4.2 Effect of anthropogenic presence

My results indicate that there was no behavioural evidence of an impact of anthropogenic activities on breeding adult male grey seals, and males were not exhibiting increases in anti-predator, vigilance or movement behaviours in relation to the presence of human activities relative to isolated colonies. Male pinnipeds exhibit increased startle behaviours or displacement in response to human activities (Perry et al. 2002, Curtin et al. 2009, Pavez et al. 2011), but my evidence suggests that any acute responses observed at Donna Nook do not seem to scale-up to differences in activity budgets, relative to isolated colonies. This suggests the importance of conservation of energy for male grey seals, indicated by the similar amount of time spent in non-active behaviours between breeding colonies and years.

For male grey seals, the amount of time spent on the colony is strongly correlated to male observed mating success (Twiss 1991). As such, their behavioural activity budgets should reflect the trade-offs between maintaining access to females and losing energy through costly interactions and behaviours (Boness 1984, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1994). Active behaviours such as aggression, and reproduction can reflect these trade-offs and have been shown to vary across colonies in relation to factors such as topography (Anderson and Harwood 1985, Twiss 1991), sex-ratio (Twiss et al. 1998), or weather patterns (Twiss et al. 2007). The results of this study however, suggest strong selection pressures for overarching conservation of energy across the geographic range, across a variety of topographies, and in the presence or absence of human disturbance. The selection for this pattern is likely driven by the increased mating success of males who maintain their position amongst groups of females for the longest time; either through greater initial energy stores (mass) or by reduced energy spent on active behaviours (Twiss 1991, Lidgard et al. 2001, Lidgard et al. 2004).

Although limited research has focused on the potential impacts of aircraft activities on pinnipeds (Perry et al. 2002), there appears to be a lack of consensus on whether or not tourism activities, whether by land or by vessels, negatively impacts pinniped behaviours (Engelhard et al. 2002, Curtin et al. 2009, Pavez et al. 2011, Hoover-Miller et al. 2013, Granquist and Sigurjonsdottir 2014). Studies which do cite negative effects, found that these manifested in increased rates of alert or variation in spatial distribution in relation to the source (Curtin et al. 2009, Pavez et al. 2011, Granquist and Sigurjonsdottir 2014). My results demonstrated that not only was the time spent in Non-Active behaviours conserved across colonies, but males at Donna Nook were found to spend the least amount of time Alert, which is the opposite of the prediction based on the hypothesis that human activities elicit anti-predator, vigilance responses. Furthermore, I found that although the intensity of human activities differed between years for both wildlife tourism and military actions, there were no corresponding between-year differences in activity budgets for Alert or Non-Active behaviours at Donna Nook. These results match the findings of Perry et al. (2002) who also found no behavioural or displacement effects of sonic booms on breeding, adult grey seals. The same study simultaneously examined harbour seals and found increases in vigilance and heart rate following sonic booms (Perry et al. 2002). Harbour seals have also exhibited correlations between increases in alert behaviours and the number of humans present as wildlife viewers (Granquist and Sigurjonsdottir 2014). This suggests that specific selection pressures and ecological constraints should be considered if attempting to infer management strategies, even across closely related species.

While the findings of this chapter suggest strong selection pressures driving their activity budgets during the breeding season, this study was not able to discern the mechanism driving this pattern. The apparent lack of effect of human activities on Non-active or Alert behaviours in other studies has been attributed to: (1) individuals not exhibiting any anti-predator response in respects to human activities (Cobley and Shears 1999), (2) differences in tolerance thresholds resulting in intolerant individuals being displaced (Bejder et al. 2009), or (3) individual males exhibiting initial acute responses to anthropogenic presence but subsequently habituating (Bright et al. 2003). None of these are mutually exclusive, and I will consider each scenario in terms of the behavioural ecology and potential management implications.

Many of the species which exhibited increases in vigilance are social species under considerable selection for anti-predator behaviours (Roberts 1996, Lusseau 2003, Duchesne et al. 2000). However, the last terrestrial predator of grey seals in the UK, the wolf *Canis lupus,* was extirpated around 1770 (Nilsen et al. 2007). Additionally, since the Conservation of Seals Act of 1970, human culling of grey seals in England has been banned, further reducing any potential for males to experience perceived risks while hauled out. Donna Nook formed in the 1980s and did not begin to rapidly expand until 1992 (Duck and Morris 2010, RLS). Furthermore, while tourist visitation numbers gradually increased through 2006, direct access to the colony was limited by a fence since 1997 and further limited by a second fence layer in 2000 (RLS). Therefore, it is possible male seals at Donna Nook have not had any referential learning which would have led individuals to perceive human activities as a threat. Gentoo penguin (*Pygoscelis papua*) colonies in Antarctica also have little to no history of land predators, and are an example of a species which does not exhibit behavioural changes in response to human activities (Cobley and Shears 1999). However, from personal observations, and other studies at Donna Nook (James 2013), males and females did respond acutely to anthropogenic stimuli with alert behaviours; suggesting that it is more likely the lack of within- or cross-colony responses found in this chapter are driven by selection for conservation of energy and/or that responses are reduced through habituation (discussed later). This demonstrates that neither acute, nor cross-colony comparison methods, are ideal in isolation, and that studies will benefit from utilising a combination of methods. Furthermore, focusing on the potential evolutionary selection pressures and life-histories could assist managers and conservationists to determine which species might be good candidates for future wildlife viewing opportunities, and simultaneously suggest avoiding species which have been selected for greater anti-predator responses.

Secondly, a wide range of animals have demonstrated inter-individual differences but behavioural consistency in their responses to stimuli (Bell et al. 2009). For example, male grey seals have demonstrated individual behavioural consistencies in the amount of time they spend alert (Twiss and Franklin 2010, **3.3.8**). Twiss et al. (2012) also demonstrated that female grey seals vary in their response to disturbance and either display proactive or reactive behavioural types. This behavioural consistency suggests that colonies could be selecting for individuals with specific behavioural types such as high tolerance to disturbance and displacement of individuals with lower thresholds (Bejder et al. 2009, Higham and Shelton 2011). If individuals with lower tolerance thresholds are temporally or spatially displaced, this suggests the potential for masking population level effects dependent on the spatial or temporal scale of the sample. The male seals at Donna Nook are at present not space-limited and large portions of the beach are still available for breeding seals (pers. obs). This suggests that if males differed in their tolerance, displacement might not result in being driven off the colony altogether, as it might at colonies with more limited available breeding substrate. Displacement within Donna Nook might be occurring; however it is unlikely to have influenced our results as the males sampled for this study ranged in distances of 10 m-350 m from the viewing fence and all seals were exposed to the military training exercises. In regards to temporal displacement, unlike hauling-out behaviours which can be temporally and spatially displaced due to wildlife viewing (Granquist and Sigurjonsdottir 2014), breeding seasons are temporally linked to female pupping and oestrus (Pomeroy et al. 2000), thus restricting the plasticity males can demonstrate in their responses. Subsequently, it is possible that as capital breeders, during the breeding season the selection pressures for maintaining access to females and for conservation of energy override any between-individual differences in tolerance resulting in no differences in alert and non-active behaviours across colonies during this time period. Future work attempting to discern the individual tolerance levels at different times of the year or at different life-history stages could inform management in regards to issues such as population structure, tolerance thresholds, potential effects of space-limitation, and genetic diversity.

Finally, the current similarity in alert responses across colonies could be the result of males initially demonstrating behavioural responses to human activities at Donna Nook, but subsequently habituating to their presence. Since ‘not losing’ aggressive interactions or positions on the breeding colony is strongly correlated with individual male mating success for grey seals (Anderson and Fedak 1985), alert behaviours during the breeding season are likely a mechanism for monitoring threats from competitor males and potential intrusions (Twiss 1991, Lawson 1993). Donna Nook has been exposed to anthropogenic presence since the formation of the colony and initially, visitors were able to access the colony without restriction. During this time, if humans were perceived as potential intrusions into male grey seals’ loose spatial territories, it is possible males increased the frequency of alert behaviours. However, visitor presence has increased over the years simultaneously with the number of seals, potentially leading to gradual habituation. Species such as the dabchick, *Poliocephalus rufopectus*, initially exhibited behavioural changes in response to human presence, but after protracted exposure to a human stimulus the behaviours returned to pre-exposure levels (Bright et al. 2003). While I cannot comment on cause and effect at Donna Nook, it is possible the long-term exposure to humans, combined with the initiation of stricter regulations limiting human-wildlife contact could have led to a loss of behavioural responses and habituation of males to human presence. Additionally, in this study, only adult, tenured males were included in our selection criteria as these males experience the highest rates of mating success (Twiss 1991, Lidgard et al. 2001, Lidgard et al. 2005). As Donna Nook is an expanding colony (Duck and Morris 2010), it is possible population growth is a product of both internal growth as well as immigration. If this is occurring, some males sampled could potentially be un-habituated, or if these newcomer males are younger, or males exhibiting the alternative, transient mating strategy (Boness and James 1979, Lidgard et al. 2001) they might have been excluded based on our sample criteria. Future studies would thus benefit from looking in more detail at these peripheral or newcomer individuals to determine the potential for non-habituated responses to human activities or to monitor the potential occurrence of habituation over time.

Habituation in response to human activities has been criticized as a negative effect, as it could potentially reduce the overall fitness of a population by reducing the natural fight-or-flight response, or by promoting further human-wildlife conflict (Bejder et al 2009). Others however have argued that in terms of scientific research, habituation to observers by primates or small mammals is considered acceptable (Higham and Shelton 2011). The present study cannot ascertain if males have habituated at Donna Nook, but the current management of the colony restricts any direct human-seal contact and the continual population growth at Donna Nook and other mainland colonies in the region suggests that at present, there appears to be no adverse effects for individual fitness on population levels.

3.4.2.1 Management implications

Ecotourism is often argued to be beneficial to wildlife through public education and establishments of wildlife reserves, but it is also criticized as an economy which can result in reduced fitness for populations of animals (Shackley 1996). Likewise, military training grounds can often provide refuge or habitat for animals (Warren and Büttner 2008) but with potential costs of increased wildlife disturbance (DeRuitter et al. 2013). It is unlikely that either side of the argument is universal and applicable to all species. This study provides evidence that although breeding periods can be indivudally energy limited and considered critical times (Hoover-Miller et al. 2013), strong selection pressures during this discrete time can potentially mitigate the pressures to change behaviours across a gradient of anthropogenic exposure. I recognize the specific conditions of the study (*e.g.*, I only considered breeding males and not females, pups or subordinate males) but provide evidence suggesting that understanding the selection pressures, spatial and temporal constraints, and life-history of a particular species in question, or sex within a species, is important for effective management. This study is an initial, behavioural assessment for impacts of human activities, but future work in the field of human-wildlife interactions and management will benefit from studies which; (1) are targeted to specific sexes and life history stages to examine potential differences in how selection pressures and responses vary, (2) are spatially explicit across a wide range of exposure levels within and between colonies to examine within and between species differences in responses to disturbance, and (3) which incorporate both behavioural and physiological metrics such as heart rate (Lydersen and Kovacs 1995) or release of stress hormones to examine for ‘hidden’ effects and individual variation in responses. Finally, while I cannot ascertain the causal effect of particular management practices at Donna Nook, I note that in this case study, the management of the breeding colony has been adaptive in response to the seal population expansion by restricting the potential for direct human-wildlife contact through physical barriers and by appealing for voluntary mitigation; both of which have been shown to be instrumental in mitigating disturbance in other studies (Curtin et al. 2009, Strong and Morris 2010, Hoover-Miller et al. 2013).

3.4.3 Conclusions

In summary, this study has reviewed the previous findings on geographic variability in male breeding behaviours and contributed the first broad male behavioural assay for a mainland breeding grey seal colony. I have added to the present knowledge of how individuals appear to be flexible in their behaviours, and responsive to local topography, ease of male access to a breeding colony, and environmental factors such as weather. Lastly, I demonstrated that at present there appear to be no behavioural indications of human disturbance at Donna Nook, relative to two isolated colonies. This study has demonstrated that inclusion of traditional behavioural assays can provide valuable ecological information for regions within a species distribution which have been overlooked or in terms of behavioural ecology and wildlife management.

Chapter 4

Good vibrations by the beach boys

Investigating the use of, and information contained in, the geographically isolated aggressive Body Slapping behaviour

Published Manuscripts from this Chapter:

Bishop AB, Lidstone-Scott R, Pomeroy P, Twiss SD (2014) Body Slap: An innovative aggressive display by breeding male grey seals (Halichoerus grypus). Marine Mammal Science 30:579-593.

Bishop AB, Denton PD, Pomeroy PP, Twiss SD (2015) Good Vibrations by the Beach Boys: Magnitude of substrate vibrations is reliable indicator of male grey seal size. Animal Behaviour 100:74-82.

4.1 Introduction

4.1.1 Use of signalling in animal contests

Incredible diversity exists in the form and function of animal communication, particularly during animal contests (Miller 1991, Lawson 1993, Arnott and Elwood 2009). Signalling, here defined as the transfer of information between a signaller and receiver, is often selected for as a mechanism during agonistic interactions to convey information regarding correlates of RHP, such as size, mass, or ornamentation (Maynard-Smith 1979, Sneddon et al. 1997, Carlini et al. 2006, Vannoni and McElligott 2008, Insley and Holt 2011). Opponents can then use the information in assessment to avoid costly escalations (Parker 1974, Clutton-Brock et al. 1979, Maynard-Smith 1979, Miller 1991, Arnott and Elwood 2009). Signals can convey information via air-borne acoustic, mechanical, optical or chemical pathways (Arnott and Elwood 2009), and are particularly common in polygynous systems with intense male-male competition; for example: roaring in male red deer (Clutton-Brock and Albon 1979) or vocalizations by northern elephant seal bulls (Sanvito et al. 2007b). In some cases, the information about RHP will be honest, meaning the receiver is obtaining accurate information about the signaller's RHP, intentions or needs (Wilson and Angilletta Jr. 2014); but 'dishonest' signalling also occurs where individuals exaggerate their RHP (Backwell et al. 2000, Wilson and Angilletta Jr. 2014). It was originally thought that this form of signalling would be selected out of a population, but recent investigations have determined that as long as a signal is honest 'on average', then dishonest signalling can be a successful strategy for individuals able to manipulate their signal (Wilson and Angilletta Jr. 2014).

4.1.2 Substrate vibrations as a signalling modality

While the literature investigating air-borne acoustic and visual displays as indicators of male or female RHP is extensive (Clutton-Brock and Albon 1979, Sanvito et al. 2007b, Vannoni and McElligott 2008, Arnott and Elwood 2009), only a few studies have extended these questions to signals that generate substrate-borne vibrations (Rivero et al. 2000, Elias et al. 2008). The lack of studies is particularly evident in mammalian systems. Interest in mammalian use of substrate vibrations as a mode of communication has risen in recent years (O'Connell-Rodwell 2007, Hill 2009), but has generally focused on the use of vibrations to convey information about the presence of conspecifics (Brownell and Farley 1979, Shipley et al. 1992, Randall and Matocq 1997), group cohesion and spacing (O'Connell-Rodwell 2007) or predator avoidance (Randall 2001). Some studies have postulated links (Shipley et al. 1992), but few have explicitly investigated the use of the characteristics of substrate-borne vibrations as advertisement of male RHP in mammalian systems.

Substrate vibrations generated by animal signalling are extensively documented across numerous animal taxa and conservative estimates suggest that in the order Insecta alone, a total of 195,000 species use this mode of communication (Hill 2009). In comparison, the number of mammalian species known to use this form of communication is estimated at 32 species across 11 families (Hill 2009). These signals can be generated via direct contact: stridulation (Gordon and Uetz 2011), tremulation (Caldwell et al. 2010) or percussive drumming (Randall and Matocq 1997, Elias et al. 2008); or through vocalizations strong enough to excite substrate-borne vibrations (Shipley et al. 1992, O'Connell-Rodwell 2007, Hill 2009). Previous work has identified that the substrate-vibration components of signals can be used in various forms of communication; stridulations and tremulations can advertise quality during conflict and mate choice, while foot drumming and substrate coupled vocalizations have been linked with conspecific avoidance and group cohesion (Elias et al. 2008, Hill 2009).

4.1.3 Aggressive behavioural repertoires of the pinnipeds

The evolution and diversity of specialized threat displays have been examined systematically for many of the terrestrially breeding pinnipeds (Sandegren 1976, Campagna and Le Boeuf 1988, Thomas et al. 1988, Miller 1991, Caldwell et al. 2010) but additions or alterations to known repertoires are rare. For example, the social system of the grey seal has been investigated extensively over the past 50 yr with considerable attention given to male aggression (Cameron 1967, Boness and James 1979, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998, Lidgard et al. 2006). It is well understood that male access to females is maintained through aggressive interactions between males throughout the breeding season as male positions shift and new males arrive (Boness and James 1979, Twiss 1991, Twiss et al. 1994). This inter-male aggression is typically characterized by low-cost, Non-Contact displays, but some interactions escalate to fights (Boness 1984, Twiss 1991). The known correlates for RHP for grey seals and other closely related pinnipeds are length and mass (Anderson and Fedak 1985, Carlini et al. 2006); however, some studies have suggested that for grey seals, intermediate values of these traits are the best correlate of RHP (Lidgard et al. 2005). Prior to contact interactions, males often use a suite of non-vocal behaviours such as the Open-Mouth Threat (OMT, **2.6.1**), where slight alterations to positioning, gape, and height of the head convey differing signals (Miller and Boness 1979, Twiss 1991, Lawson 1993, Twiss et al. 1998). In general, grey seal threat behaviours are considered to be more inconspicuous than behaviours used in similar contexts in closely related species (Boness and James 1979, Miller and Boness 1979). For example, the cephalic threat displays in male hooded seals (*Cystophora cristata*) involve hood distension and inflation of the nasal septum, which creates a large, red, ‘balloon-like’ protrusion (King 1966, Tyack and Miller 2002).

Elephant seals are well known for their use of vocalizations in threat behaviour (Sandegren 1976, Thomas et al. 1988, Sanvito et al. 2008, Insley and Holt 2011) but also use a variety of striking non-vocal signals such as chest plate size, proboscis positioning, Rearing and Neck-up positions to convey information in prefight encounters (Sandegren 1976, Sanvito et al. 2007a).

4.1.4 An undocumented behaviour: the Body Slap

While extensive ethological research has been done in the past, no new variants to the grey seal repertoire have been noted in over 20 y (Lawson 1993). In the autumn of 2011, I began research on a breeding colony of grey seals at Donna Nook along the North Lincolnshire coast, UK and immediately noticed a type of male display that was strikingly common at Donna Nook but absent at other colonies. The Body Slap (BS) has been present in populations along the East Coast of England since at least 1993 and has since been observed at the north Norfolk colonies of Blakeney Point and Horsey approximately 50 mi south of Donna Nook (*personal correspondence*: E. Stubbings, R. Jarvis, Bishop et al. 2014). To my best knowledge it has not been seen at any other UK colonies (*personal correspondence*: P. Pomeroy, S. Twiss) or at Sable Island in the western Atlantic (*personal correspondence* D.L; Bishop et al. 2014). The Body Slap has been ignored in the literature for over 15 yr, highlighting a need for documentation and meticulous defining of such behaviours.

4.1.5 Potential signalling modalities of the Body Slap

In the performance of the Body Slap, males lie prone, push their ventral surface off the ground with their flippers and then let their chest and stomach fall back to the substrate (Bishop et al. 2014 Supplemental Video 1). A Body Slap event typically consists of 2 to 3 repetitions of this general motor pattern in immediate sequence (Bishop et al. 2014 Supplemental Video 1). The display generates a distinct slapping noise as contact is made with the ground (Bishop et al. 2014 Supplemental Video 1); the arching of the back potentially serves to display lateral area; and vibrations can be felt through the substrate by observers (AB, ST pers. obs.) suggesting that the display likely serves as a multi-modal form of non-vocal communication (Miller 1991).

Investigations into multi-modal signals have shown that when substrate-borne vibrations are present, they often serve as a mechanism for complementing acoustic or visual displays (Stratton and Uetz 1983, Shipley et al. 1992, Hebets and Uetz 1999, Elias et al. 2005). For northern elephant seals, playback experiments demonstrated that males responded more strongly to stimuli with substrate-borne vibrations and air-borne acoustic components than air-borne alone (Shipley et. al 1992). Similar findings were demonstrated in insect systems (Stratton and Uetz 1983, Hebets and Uetz 1999, Elias et al. 2005). There are also cases where acoustic, visual or chemical modes were thought to be the primary component of a communication signal, but upon further inspection the substrate-borne vibration component was found to be the most important (Torr et al. 2004, Gibson and Uetz 2008, Hebets et al. 2013). While the Body Slap does have an air-borne acoustic component, grey seals generally do not have stereotypical vocal displays, with the exception of a ‘yodel call’ on Sable Island (Boness and James 1979) and the slight hiss associated with the OMT (**2.6.1**). Their other agonistic behaviours have been described as visual displays (Miller and Boness 1979, Twiss 1991, Lawson 1993). While little work has been done on night-time activity budgets for breeding pinnipeds (Anderson 1978, Culloch et al. 2015), elephant seal behaviours that generate substrate-borne vibrations were found to persist through the night (Shipley et al. 1992), lending support to the hypothesis that the visual component of these displays may not be the primary mode of communication.

4.1.6 Aims and objectives: part 1

Baseline descriptions of the Body Slap behaviour

As the Body Slap had not previously been documented or described, the first aim of this study was to: 1) describe and interpret the communication significance of the Body Slap, 2) test for intraspecific behavioural correlates, 3) test if Body Slaps are used at greater rates in areas within the study site characterized by packed wet sand than grassy dune locations as wet substrate is likely to maximize signal conveyance and, finally, 4) test if the Body Slap signals dominance or submission.

4.1.7 Aims and objectives: part 2

Characteristics of substrate vibrations as reliable indicators of RHP

Once the baseline behavioural assessment of the Body Slap was established, I then chose to investigate the substrate-borne vibrations of the Body Slap and ask: are the characteristics of the substrate-borne vibrations of a Body Slap an indicator of male RHP, and do the characteristics of individuals' displays vary across environmental conditions? To test this, I compared both the maximum magnitude of the substrate-borne vibrations a male produced while Body Slapping and the mean magnitude across all his Body Slap events, with his length, mass and dominance in order to determine which of the two measures of the substrate vibrations was more reliable in predicting known correlates to RHP (Anderson and Fedak 1985, Lidgard et al. 2005, Carlini et al. 2006). As any air-borne acoustic components of the Body Slap could be influenced by wind direction, air temperature, and substrate dampness (Hill 2009), I also examined the effects of these environmental variabiles on the reliability of the substrate-borne vibrations by testing to see if individuals' signals varied with substrate saturation due to tidal fluctuations or rain on the beach breeding site.

4.2 Methods

4.2.1 Baseline descriptions of the Body Slap behaviour

4.2.1.1 Field seasons and general data collection considerations

Data from the 2011 breeding season were used to address the aim of defining and providing a baseline of data for the Body Slap behaviour at Donna Nook. It was decided to only use one field season of observations as this would provide baseline information for the follow-up studies investigating specific characteristics of the behaviour.

4.2.1.2 Additional definitions of terms

Some of the behaviours focused on for this study are defined in **2.6.1** (Approach, AP, and Open-Mouth Threat, OMT), while others are defined here:

> **Reinitiating (RI):** A male resumes physical contact following a brief respite during a Contact AI. During a Contact AI, males exchange physical blows in the forms of Aggressive flippering, Bites, Chest pushes, and Lunges ("Fight", Twiss 1991). During these exchanges, males will often pause and exchange OMT. Often this pause is followed by a male departing (DPA or RAW: Lawson 1993) or being chased away by the victor (Chase, Twiss 1991; RAW or CHA: Lawson 1993). In other cases, the males resume physical contact. The act of Reinitiating can be done through any agonistic contact behaviour described by Twiss (1991) or Lawson (1993).
>
> **Body Slap:** A threat consisting of a prone, stationary male arching his back or pushing his torso off the ground with his fore-flippers then letting his ventral surface fall to the ground, emitting a distinct slapping sound (Figure 4.1).

OMT was chosen as a behaviour of interest as it is the predominant male threat display seen at other sites in the UK (Twiss 1991). AP and RI behaviours were chosen because they indicate motivation to begin or resume interacting, and in the case of AP, the baseline motor pattern is very similar to a Body Slap motion.

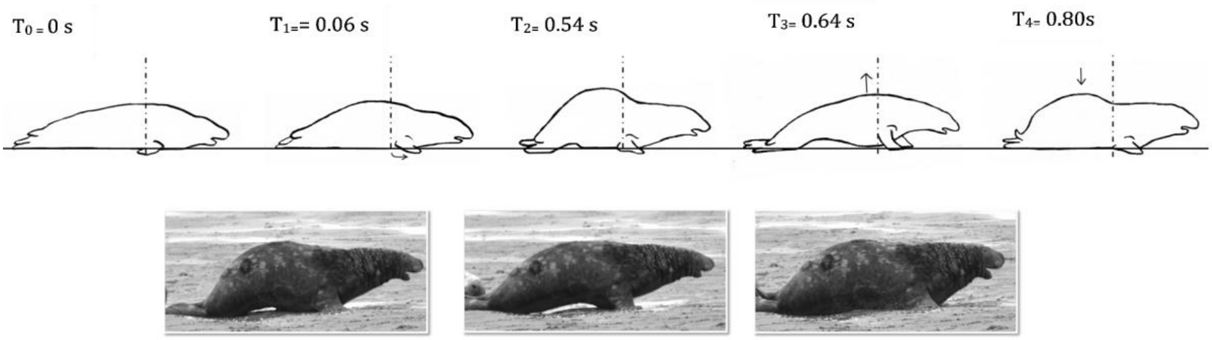


Figure 4.1: Visualization of the motor pattern of the Body Slap. Dashed vertical lines represent static reference points and the stationary nature of the Body Slap. Photo sequence provides example of simultaneous display of OMT with Body Slap. See supplemental videos in Bishop et al. 2014, or Bishop et al. 2015a for examples of this display in male-male context.

4.2.1 3 Behavioural data collection

Due to their attention-grabbing and relatively rare occurrences, all instances of Contact AIs were recorded while *ad lib*. recording was conducted for Non-Contact AIs (Altmann 1974) in 2011 and 2013. For each AI, identity of interactants, presence or absence of physical contact, start and end times, outcome classification, and observational notes were recorded *in situ*. In 2011, from the 908 observed AIs, all Contact AIs (*n* = 67), and 212 Non-Contact AIs were recorded using a Canon DC40, 35 mm digital camcorder. Each video is a discrete AI. Combined, the videos total 13.4 h of recordings. Of the 170 males in the catalogue, 159 were represented in the video recordings.

All analyses were conducted on data from the video footage of AIs. Data were extracted using a bespoke Microsoft Excel VBA data recording programme and Microsoft Windows Media Player for viewing. For each AI video, frequency of aggressive behaviours (**2.6.1**), their sequence of performance and the identity of clear winners and losers were recorded and combined with data collected in the field. For each male which performed Body Slaps within an AI, I noted the frequency of Body Slap displays performed, the frequency of repetitions per display (a display of Body Slapping could consist of multiple repetitions of the slapping behaviour), the inter-seal distance (using estimated seal body lengths), and I calculated the average rate of displays (Body Slaps per sec).

4.2.1.4 Dominance score

To determine whether the Body Slaps signal dominance or submission, males' rates of display were compared with their respective dominance score. Dominance scores were defined according to the proportion/frequency of AIs won. A weekly David's Score (DS) was calculated for each Tenured male (David 1987; Gammell et al. 2003; de Vries et al. 2006) using SocProg 2.4 social network analysis software (Whitehead 2009). Photo-ID records indicated no interchange of Tenured males between the PUB and RAF sites, so weekly dominance scores and hierarchies were calculated for individuals at the RAF and PUB sites separately. David's Score is recognized as the best static dominance measure for small systems where not all males interact with each other, and generates a whole season average dominance score (Gammell et al. 2003). Since a small sample of AIs for a male could potentially skew an individual's calculated dominance score, I chose to follow the protocol in Twiss (1991): only males which partook in a minimum of 10 AIs and were present for ≥ 2 d were included in dominance score calculations. To compare relative rankings between the sites, DSs were standardized: NormDS = (DS + |minimum DS|) / (Range of DS), which resulted in values of 0 to 1 (low to high dominance). Finally, due to *ad. lib* recording of Non-Contact AIs, it is possible a few interactions were overlooked and not included in our DS calculations.

Calculation of DS requires proportions of wins and losses; however, for male grey seals, not losing (*e.g.*, a Draw or Win) is positively associated with mating success (Anderson and Fedak 1985, Twiss et al. 1998). I therefore selected to treat any interaction in which the outcome was a Draw as a win for each interactant to prevent unnecessary exclusion of records. However, as the David's Score calculation matrix requires a winner and a loser, this meant that each interaction which resulted in a draw was entered as two samples (*e.g.,* AB and BA). This approach of classifying draws as a win and a loss for each male potentially introduced issues of pseudoreplication. In subsequent calculations of dominance, I used an alternative method, Elo rating, which more explicitly allowed for inclusion of draws without pseudoreplication (**4.2.2.4, A6.2**). The hierarchies generated by using the AB-BA draw scheme for David's Score were comparable to those generated by explicitly accounting for draws in the Elo ranking method (**A6.2**); however, the David's Score approach tended to under-estimate ranks, particularly for mid-ranked males. Therefore, for the present study only, instead of using continuous variables of DS, males were categorized weekly as high (DS > 0.8), mid-high (0.6 < DS < 0.8), mid-low (0.4 < DS < 0.6) or low dominance (DS < 0.4).

4.2.1.5 Statistical analysis

The initial assessment of the prevalence of Body Slaps in interactions and across males was conducted across all video AIs. The primary aims were to investigate what influences the frequency and rate of usage when the Body Slap is present, and how the usage of the Body Slap relates to other intraspecific behaviours. Therefore, all further analyses were conducted only using video AIs containing at least one Body Slap or using individual males' rates of display when at least one Body Slap was performed. To examine factors contributing to variation in individual rate of display, I used (generalized) linear mixed models ((G) LMMs) with male ID as a random effect to account for unequal sampling across males and pseudo-replication (Fossette et al. 2008, Bolker et al. 2009). Final model selection followed Richards' (2008) guidelines for AIC selection. For retained fixed effects, I present Markov

Chain Monte Carlo (MCMC) estimated P-values with an alpha of 0.05. All statistical analyses were conducted using R package version 2.13.1 (R Development Core Team 2011) and the R packages lme4 (Bates et al. 2011) and languageR (Baayen, 2008).

The first LMM tested whether male rate of display varied across broad topographic categories by using the fixed effect of Site: RAF vs. PUB (*n* Records = 247 across *n* ID = 91) and the second compared the rate of display across dominance categories (*n* Records = 113 across *n* ID Tenure = 41). Body Slap rates were logarithmically transformed to meet normality assumptions when necessary and values are given as means ±SE. A generalized mixed effects model (GLMMs) with binomial error and logit-link was used to test how the relative proportion of the total combined Body Slap displays in an AI that an individual male performed was correlated to the relative proportion of the total RI and/or proportion of total AP he performed. Since the RI behaviour requires contact to have occurred between males, only Contact AIs with Body Slaps present were used for this analysis. Also, since proportional data in dyadic records are not independent across males (e.g., if Male A = 40% of total combined Body Slaps, then Male B = 60%), only one male per AI was selected at random to meet independence assumptions (*n* Records = 42, *n* IDs = 30).

To further examine whether Body Slaps were associated with dominance or submission I used paired t-tests to compare the difference in rates of display between eventual winners and losers (Jennings et al. 2002). I also used chi-squared tests to see if AIs in which the winner displayed at a greater frequency than the loser, and AIs with the first and last Body Slaps performed by the AI's eventual winner, were more frequent than expected at random.

4.2.2 Characteristics of substrate vibrations as reliable indicators of RHP

4.2.2.1 Seismometer deployment and behavioural data collection

Field observations were conducted across the autumn breeding season in 2013 (27 October – 12 December) during all daylight hours for an average of 8 h 48 min daily. I deployed 2 Guralp 6TD seismometers (Guralp Systems Ltd) from 30 October to 23 November 2013. The seismometers were both buried at 53.47491 N, 0.15503 E, at a depth of 1 m. Continuous seismic data were recorded over 24 h for 25 consecutive days, encompassing a frequency bandwidth of 0.03 Hz-500 Hz (Brisbourne 2012). Velocity was measured in 3 axes (X, Y, and Z); however, for the purpose of this study I chose to follow the methods of previous work on northern elephant seals (Shipley et al. 1992) and focus on the vertical movement axis only. During daylight hours, field observers recorded Body Slap events, noting ID of male and time of event to the second (h:m:s). An event was defined as a bout of displaying, usually comprising two repetitions of the motor pattern, but the range varied from 1 - 6 repetitions (Bishop et al. 2014). Events were labelled as being performed on ‘wet’ or ‘dry’ sand. As only during spring tides would the water reach the dunes, wet sand was any sand exposed to tidal inundation within the past 12 h or with visibly pooled water. Locations of events were mapped onto aerial photographs of the study area using a Nikon laser 550 rangefinder (6x21), with accuracy of 0.5 m up to 100m and ±1 m at >100 m distance, along with horizon reference points. Maps were digitized and distance (km) of each Body Slap event to the seismometer was calculated using ArcMap 10 (ESRI 2011).

4.2.2.2 Post-processing seismic data

Post deployment, I matched the time of an observed event to the seismic record of vertical velocity traces using *Scream!* v 4.5 (Guralp Systems Ltd). The unfiltered peak to peak amplitudes (nm/s) of the signals were extracted. To minimize potential false positive matches, only signals that were at least double in amplitude relative to the background were considered positive matches (Shipley et al. 1992). As males performed Body Slaps at different distances from the seismometer, in order to compare their relative magnitudes the signals had to be distance corrected. The seismometer measures amplitudes as velocity in nm/s (*v*); however, the distance correction formula required this measure to first be converted into vertical displacement in nm (*A*) using the formula:

$$A = \left(\frac{[v]}{f * 2\pi}\right) \tag{4.1}$$

where *v* is the vertical velocity in nm/s of an event, and *f* is the frequency in Hz of the signal. Frequency analysis of the signals indicated that the bulk of the energy contained in these signals lay within the 20 Hz band. To ensure that all calculations were carried out using the same formula, I used this frequency to convert peak-peak velocity amplitudes to displacement.

Magnitude values, which could be compared relative to each other, were then calculated using Booth’s (2007) distance correction equation generated specifically for seismic activity in the UK (Booth 2007)

$$Magnitude = \left(1 * LOG10(A)\right) + \left(1.11 * LOG10(D)\right) + (0.00189 * D) - 2.09 \tag{4.2}$$

where *A* was the displacement amplitude of the signal in nm and *D* was the distance in km an event was from the seismometer (see: Booth 2007 for derivation of constants). The maximum magnitude generated per male, mean magnitude per male (for males with 4 or more events), and the variation in magnitude (standard error around the mean for males with 4 or more events) were calculated and used in further analyses.

4.2.2.3 Photogrammetric measures of morphological features

Photogrammetric methods followed those previously outlined in **2.7**. I selected to use standard length (cm) and lateral area (proxy for mass) as my morphological measures of male RHP. For male grey seals, the links between male mass and RHP suggests that mid-sized males have highest mating success, likely due to trade-offs between mass and manoeuvrability (Twiss 1991, Lidgard et al. 2005). Lidgard et al. (2005) also found a positive relationship between standard length and length of stay, the latter of which is a known positive correlate of mating success for males adopting the primary strategy of 'residency' (Twiss 1991). Finally, Anderson and Fedak (1985) found that larger males lost fewer male-male encounters than smaller males by mass, again suggesting that size is positively associated with RHP. The final dataset of photogrammetric measurements for 2013 included estimates for 70 of 105 males.

4.2.2.4 Dominance and local density

In addition to morphometric measures, I calculated a daily dominance score for each male to compare to the values generated in the seismic record. Dominance has also been positively linked to mating success (Twiss 1991, Twiss et al. 1998) and individual dominance scores can vary throughout the season in response to turnover of males and females. In contrast to the first part of this study which used David's Scores for dominance, I selected to use the dominance calculation of Elo scores (Neumann et al. 2011) as this method allows for calculation of dominance scores sequentially through time. Only males who were present on the colony for at least 2 days and were involved in a minimum of 10 aggressive interactions were included for this analysis (Twiss et al. 1998, Bishop et al. 2014). For each male, the mean Elo score on the day of a Body Slap event (Elo) was calculated using records of his wins, losses and draws up to that date in the season (see Neumann et al. 2011 and **6.2.1** for further details of calculation). The mean Elo score across the entire study period was also calculated per male; this value is directly comparable to the male's David's Score used in the previous part of this study (Neumann et al. 2011). Lastly, to account for unequal density of males within the study site, I mapped male positions on the colony hourly and calculated the average nearest neighbour distance (DNM) per day for each male using ArcMap 10 (ESRI 2011).

4.2.2.5 Statistical analysis

My objective was to determine if maximum Body Slap magnitude or an average magnitude was the most reliable indicator of male RHP. To do this, I used generalized linear models test if male's maximum standard length (MSL), maximum lateral area (MLA), Elo on the day of maximum magnitude, mean distance to nearest neighbour (DNM) on the day of maximum magnitude, and/or the substrate type on which the maximum was performed (1 = wet sand; 0 = dry sand) explained the variation in the maximum magnitude a male generated (*n* = 26 males). Because lateral area as a proxy for mass would be expected to decrease through time due to fasting (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005) there was a potential temporal disconnect between the date of maximum seismic magnitude and the date of the photogrammetric MLA. Twiss (1991) found individual variation in mass loss was not correlated with dominance, age, arrival weight or other metrics; therefore, to account for mass loss over time I included a variable of the difference between the date of the maximum magnitude generated by a male and the date when the photograph of his MLA was taken (DayDIFF), which ranged from 0 – 23 d. MSL would not be expected to change substantially throughout the course of a breeding season, so no temporal measure was included for this variable. Similar models were run with the response variable set as either the mean magnitude per male (*n* = 22 males) or standard error of the mean magnitude per male (*n* = 22 males). In the models examining mean magnitude and standard error, the predictor variables of mean dominance and mean nearest neighbour distance were calculated across the whole season, and the mean substrate type across all displays per male was used instead of a single value. To account for temporal disconnects in these models, the number of days over which the mean was calculated (DayMEAN) and the difference in days between the first Body Slap event and the date of MLA were included in the models (DayDIFF). Models for all analyses were run in R 2.13.2 (R Development Core Team 2011). Final model selection followed AIC minimization criteria (Richards 2008; **3.2.6**).

While the last two models account for mean substrate type, this was modelled across males and not within individual IDs. To test if substrate dampness enhances or degrades the magnitude of an individual's signal, for males that I observed displaying on both wet and dry sand I also tested for differences in mean and maximum magnitude of a display by substrate. Due to the small sample size (*n* = 11 males), I used small-sample randomization tests designed for two-repeated measures on small group or single-case blocks (Todman and Dugard 2001).

4.3 Results

4.3.1 Baseline descriptions of the Body Slap behaviour

4.3.1.1 Description of the Body Slap

In 2011, I observed a total of 850 Body Slap displays across 91 individual males, and Body Slaps were present in 66.3% of all videoed AIs. In many cases, a display comprised multiple, successive repetitions of the Body Slap; the average repetitions per display was 1.8 ±0.03 (range: 1-6; *n* = 850; Bishop et al. 2014 Supplemental Video). The average inter-seal distance during a Body Slap was 2.9 seal body lengths ±0.07 (*n* = 850), or approximately 6-7 m. Duration of AIs with Body Slaps ranged from 10 to 1,671 s (0.17 - 27.8 min) and individual males varied in the number of AIs in which they engaged, in their frequency per AI, and rates per AI (Figure 4.2). In all field observations and video records, the Body Slap was performed exclusively by males. While predominantly used in the context of male-male AIs, occasionally the display was seen performed by solitary males or in male-female social interactions. Further estimates of the frequency of Body Slaps used in male-female contexts are unavailable.

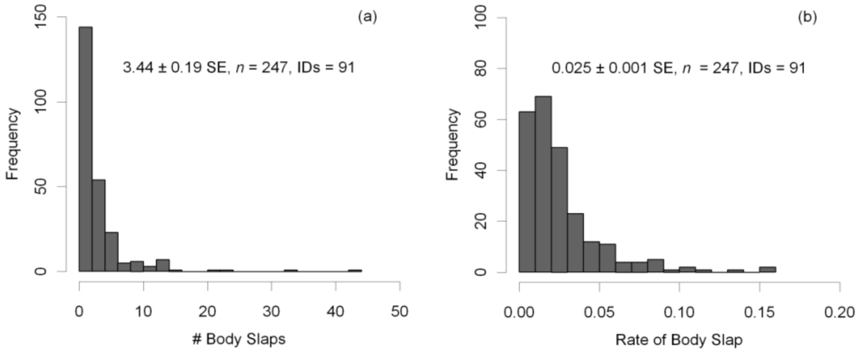


Figure 4.2 Frequency of Body Slap displays by a male in an interaction (a); and rate of Body Slap displays (Body Slap s^{-1}) by each male in an interaction (b). Only records where males used the Body Slap are displayed.

4.3.1.2 Influence of topographic variation within Donna Nook

Site was retained as an explanatory variable for the rate of display of Body Slaps ($GLMM_{site}$ ΔAIC = 0, t = 2.64, P = 0.009), indicating that the average rate of display for males at the RAF site (0.03 ±0.003, *n* Records = 126, *n* IDs = 48) was significantly greater than the average rate for males at the PUB site (0.02 ± 0.002, *n* Records = 121, *n* IDs = 43).

4.3.1.3 Intraspecific behavioural correlates to Body Slaps

Of the 850 Body Slaps recorded, 681 were performed with a simultaneous OMT (i.e. the mouth was gaped while slapping and an exaggerated exhalation was produced as the ventral surface hit the ground) (Figure 4.1, Bishop et al. 2014 Supplemental Video). Individual males varied in their association of the display with OMT. More than half of the males who were observed performing Body Slaps always performed their Body Slap with an Open-Mouth Threat (*n* = 51 of 91), and only five were never observed combining the two behaviours. Body Slapping also shared a positive association with Approach and Reinitiating behaviours. The model with both AP and RI as fixed effects and the model with only AP both had ΔAIC<6 but under Richard's (2008) criteria, the AP only model was selected as the final model (Table 4.2). This model indicated a significant positive relationship between the relative proportion of the total Approaches during an interaction performed by a male and the proportion of Body Slaps he did (Table 4.2, Figure 4.3).

Table 4.2 Results of GLMMs fit with binomial (logit-link) distributions with ID as random effect (n Records = 42, *n* ID = 30). M3 was selected as best model with the lowest ΔAIC (bold); it indicates a positive association between the proportion of total combined Body Slaps in an AI and the proportion of total combined Approach behaviours performed by an individual male.

Model	df	AICc	ΔAIC	Intercept Estimate (*P*-value)	Prop RI[a] Estimate (*P*-value)	Prop AP[b] Estimate (*P*- value)
M1: Prop RI and Prop AP	3	44.1	2.0	-1.6 (0.04)	0.2 (0.86)	2.8 (0.016)
M2: Prop RI only	2	49.1	7.0	-1.1 (0.11)	1.6 (0.08)	--
M3: Prop AP only	**2**	**42.1**	**0**	**-1.5 (0.01)**	**--**	**2.9 (0.004)**
M4: Null model	1	50.2	8.1	-0.1 (0.86)	--	--

a) Prop RI = Proportion of Total Reinitiating in an AI
b) Prop AP = Proportion of Total Approaches in an AI
*Terms Defined in Methods

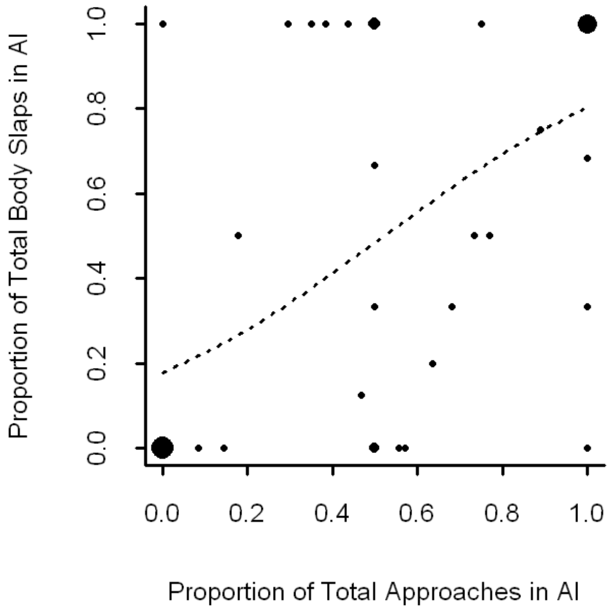


Figure 4.3 The model retaining proportion of total Approaches as a fixed effect was selected as the best model. Points represent one randomly selected male from each Contact AI pairing (*n* = 42) with larger marker sizes representing multiple, overlapping data points. The line represents the best fit from the binomial GLMM (Table 2) and indicates the proportion of the total Body Slaps during an AI that a male performs is positively related to the proportion of the total Approaches in the AI he performs.

4.3.1.4 Does the Body Slap signal dominance or submission?

Of the AIs with clear winners and losers, 85 also had Body Slaps present. Winners performed on average 68% ±4% of the total Body Slaps in each interaction, and winners were significantly more likely to perform more Body Slaps than losers (χ^2 = 8.57, df = 1, P = 0.003). The average rate of display for winners (0.02 ±0.003) was significantly greater than the average rate for losers (0.01 ±0.002; Paired T-test: t = 2.79, df = 184, P = 0.006). Winners also exhibited a greater likelihood for performing the first and last Body Slap in an AI (χ^2 = 12.81, df = 1, P < 0.001). Tenured males with dominant and mid-high dominance ranks had elevated rates of display (relative to mid-low and subordinate) but there was no significant difference between dominance groups and the model with no fixed effects was retained ($\text{GLMM}_{\text{RandomID}}$ ΔAIC = 0; F = 1.22, P = 0.30).

4.3.2 Characteristics of substrate vibrations as reliable indicators of RHP

4.3.2.1 Seismic signature of the Body Slap

The Body Slap generated a stereotyped seismic trace with raw amplitudes ranging from 10,752 nm/s to 475,136 nm/s, and after distance corrections, magnitudes ranged from – 1.62 to -0.14 (Figure 4.4a). Frequency was broadband and ranged from 10-80 Hz (Figure 4.4a). Other male behavioural events were observed *ad lib* and matched to the seismic record for comparison, including male locomotion (Figure 4.4b). Body Slap signals were measurable up to 126.3 m from the source; of the observed Body Slap events in the field, 94.3% were positively matched in the seismic record up to 70 m distance, but proportion matched dropped to 71.7% from 80-100 m and to 37% on average beyond 100 m (Figure 4.5). I recorded events for 39 individual males (within-male sample sizes ranging from 1-255 events; median for males with >4 events = 22.5) for a total of 470 observed events comprised of 990 individual slaps matched in the seismic trace. Similar to findings in the previous section (**4.3.1.1**, Bishop et al. 2014), 9.45% of events consisted of a single slap, 61.5%

consisted of 2 slaps, and 28.9% consisted of >3 repetitions. Inter-repetition intervals were typically 1s apart and separately distinguishable (Figure 4.4a).

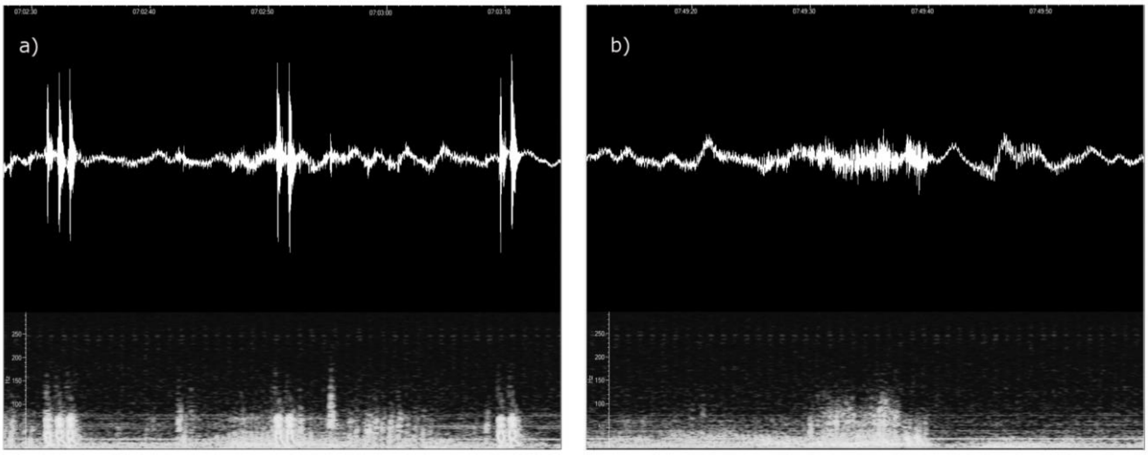


Figure 4.4: Oscillogram displaying a 45s trace (top) and spectrogram displaying 0-300 Hz (bottom) recorded at 0.03-500 Hz. a) 3 BS events (3 repetitions at 7:02:31; 2 repetitions at 7:02:50; 2 repetitions at 7:03:09). Distance from source = 50 m. All three events presented between 20-80 Hz with highest energy at 20-40 Hz.; b) Male locomotion at 7:49:30. Distance from source = 40 m.

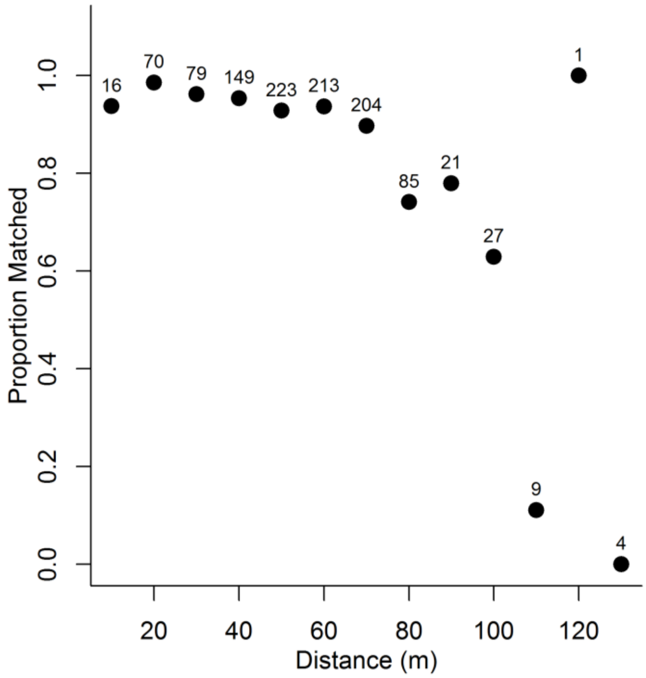


Figure 4.5: Proportion of Body Slap events positively matched in the seismic record to the number observed in the field across distance (10 m bins). Labels represent number of events observed in field. Detectability dropped off after 80 m from source and maximum distance detected was 126.3 m.

4.3.2.2 Body Slap contains information on male size

MSL and DayDIFF were retained in the best model (ΔAIC = 0) for predicting maximum magnitude; however, the model with only MSL had a ΔAIC of 0.21 suggesting this variable on its own is a strong predictor of maximum magnitude (Table 4.3). In both models, MSL shared a significantly positive relationship with maximum magnitude a male produced (Figure 4.6a; Table 4.3). The best model predicting mean magnitude retained MSL and DNM as predictive parameters. MLA and Elo were each retained in two models but both with greater ΔAIC values and small effect sizes (Table 4.3). The relationship between MSL and mean magnitude was weaker than that seen between MSL and maximum magnitude (Figure 4.6b; Table 4.3). DNM shared a statistically significant negative relationship with mean magnitude, suggesting mean magnitude decreases as competitor density decreases (Figure 4.6c; Table 4.3). A total of 7 models were retained by the selection criteria for predicting mean magnitude with varying parameters (Table 4.3). DNM was retained in the top 4 models, and was retained in more models than any other parameter (Table 4.3). I fitted a further three models to test if the relationship between mean magnitude and DNM was the result of larger/more dominant males occupying areas of greater conspecific density (Table 4.4), but found no evidence of MSL, MLA or Elo correlating with DNM (Table 4.4). Finally, variability in magnitude per male was best predicted by only the null model, suggesting that none of the variables were good predictors of variability in magnitude.

Table 4.3: GLM model outputs of signal information analyses. Displayed models include all retained models within **6** ΔAIC, ignoring more complicated versions of nested models that had higher ΔAIC (Richards 2008). Values for predictor variables represent coefficient estimates; significant variables are in bold.

Seismic Component	AICc	ΔAICc	n	Intercept	MSL	MLA	Elo	DNM	SUB	DayDIFF	DayMEAN
**Maximum Magnitude*											
Model 1	0.8	0	26	**-3.32**	**0.013**					-0.009	
Model 2	1.0	0.21	26	**-3.43**	**0.013**						
†Mean Magnitude											
Model 1	-21.11	0	22	**-1.50**	**0.005**			**-0.020**			
Model 2	-19.84	1.27	22	**-1.34**			0.0007	**-0.018**			
Model 3	-19.34	1.77	22	**-0.85**		0.00004		**-0.019**			
Model 4	-19.15	1.97	22	**-0.50**				**-0.023**			
Model 5	-17.72	3.39	22	**-1.97**			**0.0010**				
Model 6	-17.30	3.81	22	**-2.03**	**0.005**						
Model 7	-17.21	3.90	22	**-1.33**		**0.00005**					
†SE Magnitude											
Model 1	-125.0	0	22	**0.032**							

** MSL = maximum standard length (cm); MLA = maximum lateral area (cm^2); Elo=mean dominance score up to and including the day of maximum magnitude; DNM = mean distance to nearest neighbour on day of maximum magnitude; SUB = substrate (1=wet; 0=dry); DayDIFF = difference in dates between maximum magnitude and maximum LA measure. n = number of individual males.*

† MSL, MLA (same as above). Elo= mean dominance score for whole season; DNM = mean distance to nearest neighbour for whole season, SUB = mean substrate across all BS events; DayDIFF = difference in dates between first BS event and maximum LA measure; DayMEAN = number of days mean seismic magnitude was calculated across.

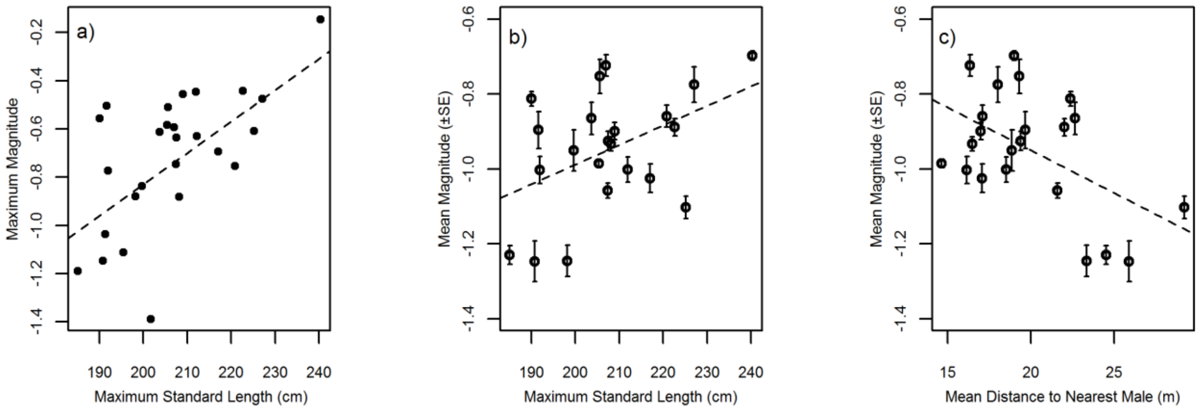


Figure 4.6: Results of best GLM models. Correlations for maximum (a) and mean magnitude ±SE (b) indicated a positive relationship with maximum standard length. Mean magnitude ±SE also shared a negative relationship with mean nearest neighbour distance (c). See Table 1 for coefficient estimates.

Table 4.4: Generalized linear model (GLM) testing for relationship between: 1) MSL and DNM, 2) MLA and DNM, and 3) Elo and DNM. The Null models were the best for all three response variables (bold; Richards 2008).

Model (*n* = 22)	AICc	ΔAICc
1) MSL ~ DNM	184.0	2.24
MSL ~ 1	**181.7**	**0**
2) MLA ~ DNM	380.8	0.78
MLS ~ 1	**380.0**	**0**
3) Elo ~ DNM	257.4	0.81
Elo ~ 1	**256.6**	**0**

** MSL = maximum standard length (cm); MLA = maximum lateral area (cm^2); Elo = mean dominance score for whole season; DNM = mean distance to nearest neighbour for whole season.*

4.3.2.3 Body Slap signals on wet and dry sand

The maximum magnitude of displays for males who had events recorded on both wet and dry substrates was not different across substrate type (2-tailed: t = 0.069, 1000 permutations, P = 0.432). Similarly, no difference was found comparing the mean magnitude of displays for males who had events recorded on both wet and dry substrates (2-tailed: t = 0.008, 1000 permutations, P = 0.919).

4.4 Discussion

4.4.1 Updating the grey seal behavioural repertoire

This study has defined a behavioural variant performed by male grey seals that is limited in its geographic extent. The results indicate that Body Slaps are pervasive in two-thirds of aggressive interactions at Donna Nook and were used by over half of the observed males. When attempting to place new agonistic behaviours within a known repertoire, basic questions need to be addressed, the simplest of which would be whether or not the behaviour is a display of dominance or submission. There was no significant correlation between dominance score category and rate of display, but subsequent winners did display more frequently and at higher rates than losers, and winners also performed the last displays proportionally more than losers. Additionally, a positive association between the use of the Body Slap and the Approach behaviour was identified, which suggests that the Body Slap likely signals motivation state or behavioural willingness to interact. These findings support the hypothesis that Body Slaps do not signal for submission and likely communicate a threat or information to be used in assessment.

Unlike other phocids, male grey seals do not have a distinct vocal threat repertoire, but have instead evolved a suite of non-vocal, communication behaviours that are used in social, agonistic and sexual interactions (Miller 1991, Boness and James 1979, Twiss 1991, Lawson 1993). While the Body Slap is an apparently new addition to this repertoire, the use of slapping, against the body or environment, is a common mode of non-vocal communication in marine mammals e.g., “Belly Clapping” in Steller sea lions, *Eumetopias jubatus*, (Sandegren 1970); “Flipper Slap” in harbour seals (Sullivan 1982); and “Pectoral Slap” in humpback whales, *Megaptera novaeangliae* (Tyack and Whitehead 1983, Deakos 2002). In grey seals, Lawson (1993) described a suite of Flipper Slap behaviours at North Rona (Scotland) which appear to share a similar auditory component to the Body Slap.

However, their use was more varied and was observed primarily outside of male-male aggression in contexts such as female-pup affiliation and female-female social behaviours. Also in these examples, the behaviour is performed with an appendage and the emphasis of the signal conveyance is likely on the air-borne acoustic or visual component. Since the Body Slap is performed using the entire ventral surface and the motion is against the substrate, the air-borne acoustic component is unlikely to be the only information pathway.

4.4.2 Comparison across species of similar behaviours to the Body Slap

Arguably the most similar pinniped display to the Body Slap is the ‘Body Slam’ (SLM), performed by northern elephant seals. This involves males in prefight sequences rearing up and slapping their forequarters down on the substrate (Bartholomew and Collias 1962, Sandegren 1976, Shipley et al. 1992). Due to the size of male elephant seals, the information conveyed by the Body Slam has been suggested to be transmitted through auditory and substrate-vibration pathways (Sandegren 1976, Shipley et al. 1992, Holt et al. 2010). Shipley et al. (1992) explicitly tested the seismic conveyance of various elephant seal behaviours. They found that the Body Slam generated significant, measurable vibrations in the substrate and confirmed that elephant seals are able to sense seismic waves, but did not explicitly examine the information conveyed through the signal (Shipley et al. 1992). The vibrations caused by the grey seal Body Slap were perceptible to observers (RLS, ST) but the initial, 2011 study was not able to address quantitative measurements of acoustic or seismic signals in the Body Slap. It did however demonstrate that although the number of males who used Body Slaps was similar between the RAF and PUB sites, males at the RAF had elevated average rates of Body Slaps compared to the PUB site. The flat, sandy substrate dominating the RAF site is similar to conditions at elephant seal colonies where surface waves were recorded as the predominant seismic signals (Shipley et al. 1992). Alternatively the PUB site is characterized by mixed vegetation and dry soft sand which is perhaps less suitable for seismic signal transmission. The 2011 analysis only examined rates of display greater than zero, but this does inform us that when males use the Body Slap, they are doing so at greater rates at the RAF site than the PUB site. This difference in display rate could be similar to patterns seen in other social systems where males adjust their behaviours to suit local conditions (Rushbrook et al. 2010).

While there are similarities between the elephant seal Body Slam and grey seal Body Slap, this study has also identified a number of differences. Body Slaps were found to be used in 66% of interactions at Donna Nook, while Body Slams were only present in 8% of interactions when examining five males of various dominance ranks (Sandegren 1976). The lower presentation of Body Slams is likely due to the importance of other displays in male elephant seal repertoires. Elephant seals rely on numerous acoustic, and visual cues such as chest shield size, rostrum position, and neck rugosity to convey information regarding dominance or condition (Bartholomew and Collias 1962, Sandegren 1976, Insley and Holt 2011). In this manner, the rearing motion of the Body Slam has been suggested to be an optical display of body size (Shipley et al. 1992). Grey seal neck rugosity has been noted as a possible analogue to chest size in elephant seals (Boness and James 1979) but during the Body Slap display the chest is typically kept parallel to the substrate (Figure 4.1, Supplementary Video in Bishop et al. 2014, Bishop et al. 2015a). Sandegren (1976) alternatively noted that the rearing and display of the chest during the Body Slam motion was similar to blow delivery during fights and was likely a ritualized form of this element indicating a willingness to charge. In contrast, the Body Slap motion was most similar to the undulatory motor-pattern of Locomotion (Lawson 1993). Furthermore, the positive association between Body Slaps and Approaches suggests the Body Slap might be a ritualized or exaggerated form of Locomotion. In this way, Body Slaps and Body Slams both likely convey probabilistic information regarding willingness to charge or fight; however, each distinct behaviour appears to have arisen from a different basal motor pattern.

4.4.3 The Body Slap as an apparently geographically isolated behaviour

From personal correspondence with numerous grey seal colony managers and researchers, the Body Slap appears to be isolated to colonies along the Eastern coast of England at present. The occurrence of geographic variations in behaviours has been demonstrated across numerous taxa (Luyten and Liley 1985, Burnell 1998, Podos and Warren 2007). For grey seals, threat behaviours such as Open-Mouth Threats, Rolls, and Vocalizations like the ‘yodel call’ at Sable Island have previously been shown to vary between colonies (Hewer 1957, Boness and James 1979, Lawson 1993). In some cases, the observed variation has changed over time. For example, colony specific differences in the use of the “Roll” were noted by Hewer (1957), however, by 1993, Lawson found no difference in the frequency of this display between his three study colonies which spanned the East and West Atlantic populations. Studies in other phocid seals such as the Weddell seal, *Leptonychotes weddellii*, harp seal, *Pagophilus groenlandicus*, bearded seal, *Erignathus barbatus* and harbour seal have also shown geographic variations in vocalizations used during the breeding season (Thomas et al. 1988, Perry and Terhune 1999, Van Parijs et al. 2000, Risch et al. 2007). This trend, along with the documented ability of pinnipeds to use vocal or display learning (Ralls et al. 1985, Sanvito et al. 2006), provides a baseline for interpretation of any future spread or transmission of the Body Slap, or other non-vocal communicative behaviours, in this species from cultural or learned perspectives.

4.4.4 Substrate vibrations of the Body Slap as a reliable indicator of RHP

The results of the 2013 follow-up study confirmed that male grey seals generate substrate-borne vibrations associated with a specific, stereotyped display. Furthermore, while the frequency of the percussive display was broadband, the maximum generated magnitudes of this display were reliable indicators of male size. The results of this study also indicate that, while the breeding colonies at which the Body Slap has been observed are all open-access beach sites with variable surface water pooling due to tidal and rain fluctuations, individuals' maximum and mean magnitudes were not significantly different across wet or dry sand conditions.

In a polygynous mating system, selection should favour signals of male RHP to maximize information transfer and minimize the costs of agonistic interactions (Maynard-Smith 1979, Arnott and Elwood 2009). Since percussive, vibratory signal energy depends on both mass and available muscular power (Markl 1983), one would expect maximum magnitudes to correlate with size (*e.g.,* mass) and strength (*e.g.*, height a male can achieve in 'push-up'). The results of this chapter support this relationship but I found that of my predictor variables, only standard male length significantly correlated with the magnitude of the seismic signal in the best model. The proxy for mass, MLA, and dominance score were retained in models for mean magnitude, but these models did not perform as well and the effects were expressed by very low coefficients. In male grey seal agonistic encounters, wrestling is the primary form of physical contact (Boness and James 1979). Considering my results, along with those of previous studies of determinates of mating success in male grey seals, it is possible length and mass are selected for in two separate processes: length provides manoeuvrability for fighting agility, while mass provides ability to fast for longer periods and maximize mating success through length of stay (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005). In this system, it seems likely stabilizing selection has favoured males with intermediate masses and males of longer standard lengths to maximize the trade-offs between manoeuvrability and prolonged residency (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005). In the closely related northern elephant seals, length was also positively correlated with dominance (Carlini et al. 2006). Other examples of mass not being the best predictor of RHP have been found in species that rely on manoeuvrability, and often these cases are found in aquatic habitats. Standard length in male sword-tails (*Xiphophorus cortezi*) was the strongest predictor of RHP (Moretz 2003) and while mass was a good predictor of RHP for large male maritime earwigs (*Anisolabis maritima*), smaller males benefited from weapon asymmetry as a possible enhancement of manoeuvrability (Munoz and Zink 2012). I found that both maximum and mean vibration magnitudes were correlated to standard length; males might therefore benefit from attending to their opponent's magnitude if it could be used to determine manoeuvrability and/or strength. However, there was still some unexplained variation which may provide information on other characteristics of the performer. For example, inter-individual variation in musculature, possibly associated with length or mass, could subsequently produce greater magnitudes. Alternatively, winners on average performed the Body Slap at greater rates than losers (**4.3.1.4,** Bishop et al., 2014) and rate of percussive displays has been shown to signal stamina in other animal systems (Briffa, and Elwood 2004). Therefore, it might be interesting in future work to consider the potential trade-offs between the physical constraints of generating substrate vibrations (manoeuvrability and musculature) and the physiological constraints (available energy for repeat displays) to determine what other potential information might be available in the Body Slap display.

4.4.5 Reliability of substrate vibrations across variable environments

Compared to other vibratory signals, communication via percussive behaviours which generate broadband substrate vibrations has been considered highly adaptive to conditions requiring communication over long distances, sensory-limited environments (e.g. caves, subterranean), or for home-ranges that span a variety of environmental conditions (Randall and Matocq 1997, O'Connell-Rodwell et al. 2001, Hebets et al. 2008, Hill 2009). In regards to vibrations in sand, early research has demonstrated that even soft, desert sand substrate can carry vibrations such as those used by the predatory desert scorpion (*Paruroctonus mesaensis*) to orient to and determine the distance to prey (Brownell, 1977, Brownell and Farley 1979). Aicher & Tautz (1990) tested for difference in signals across dry and wet beach sand, and found that dry sand appeared to reduce the velocity of vibrations simulated from fiddler crab (*Uca pugilator*) percussive behaviours, but this was for signals in the frequency range of 340-370Hz. In the present study, I found that individuals' maximum and mean magnitudes did not vary across surface saturation of the substrate. This might be explained by the environment at the site for this study, Donna Nook, and at similar sites where the Body Slap behaviour has been observed. The site is characterized by expansive, uniform tidal flats of packed sand that experience a high variability in the levels of surface water; however, the underlying substrate likely remains fairly well saturated throughout the tidal cycle. Seals were not observed performing in the soft, dune sand. Therefore, while the variation in surface substrate dampness and visible pooling of water would arguably alter the airborne acoustic characteristics, there is no evidence that surface dampness has an effect on the magnitude of the substrate vibrations across the substrates occupied by seals. Another potential component of the Body Slap display which might act as a signal, the visual component, would also be limited by the visual range of grey seals on land, which is particularly attenuated in low-light conditions (Schusterman 1981), and the grey seals' low line of sight being obscured by other seals. Furthermore, there was evidence of Body Slap traces in the seismic record during the night-time; although, observational confirmation of these was not possible. If the visual component is used at all, it is likely to be most effective at very short range and only during daylight (Culloch et al. 2015). These findings suggest the possible adaptive significance of using the substrate-borne vibration component of the percussive Body Slap display as a way to transmit information in a variable environment.

4.4.6 Density dependent plasticity of behaviour

According to operational sex-ratio theory, the intensity and/or frequency of aggressive behaviours are predicted to increase relative to number of competitors or male density (Weir et al. 2011, deJong et al. 2013) and this has been demonstrated in numerous studies, mainly in controlled conditions (Quinn et al. 1996, Smith 2007). As the grey seal breeding season progresses, sex-ratios shift from male-biased to female-biased and local densities of both sexes increase (Boness and James 1979, Twiss et al. 1998). In this study, mean magnitude of the Body Slap signal increased with relative male density, but maximum magnitude did not. This could suggest that longer males occupy areas of greater densities, but I found no evidence of male length, lateral area or dominance correlating to mean neighbour distances. Alternatively, local competitor density might influence the amount of effort put into a display. Males that can maintain position in high density female areas have been shown to have greater mating success (Twiss et al. 1994); therefore, males in patches of higher female, and subsequently higher male, densities might consistently display closer to their maximum because the costs of losing access to females outweighs the energetic costs of displaying at their physical limits. This corresponds with previous work that suggests, for male grey seals, not losing a position on the breeding grounds was more important than physically besting an opponent (Anderson and Fedak 1985, Twiss 1991). Similar mechanisms for maximizing mating opportunities while minimizing costs can be seen in the Natterjack Toad (*Bufo calamita*) mating system, where males escalate the intensity of their signalling as female densities increase by switching from stationary calling to active movement and clasping (Arak 1983). Agonistic displays by male mosquitofish (*Gambusia affinis*) to other males increased as competitor density increased, and were greatest when male and female density were high (Smith 2007). My study provides some evidence that characteristics of the substrate-borne vibrations of the Body Slap might be tailored to local competitor densities, but further examination is needed to determine how flexibility of male displays are in regards to matching local conditions.

4.4.7 Future work: determining the receiver use of the Body Slap vibrations

Male northern elephant seals vocalize during contests and multiple components of this signal contain information regarding male RHP (Sandegren 1976, Shipley et al. 1981, Thomas et al. 1988, Sanvito et al. 2007a, Sanvito et al. 2007b, Insley and Holt 2011). Similarly, in intra-sexual interactions in sexually dimorphic species, vocalization components such as formant frequencies have been found to correlate with male size (Vannoni and McElligott 2008). Determining if components contain information associated with RHP is the first step to understanding the potential usage of a behavioural display by a receiver. My results have demonstrated a positive relationship between the magnitude of the Body Slap's substrate-borne vibrations and proxies for RHP, but how the receiver responds to the information in the Body Slap still requires further examination and is likely context dependent. For example, a recent playback study indicated that while calls of male elephant seals contain information regarding RHP, recipients did not appear to respond to information regarding size from the signal (Casey et al. 2012, Casey et al. 2013). Instead, researchers found that males recognize the individual pattern associated with a dominant or subordinate male (Casey et al. 2012, Casey et al. 2013). As the proportion of males returning between years in the elephant seal system is relatively high (~50%, LeBoeuf 1974), there might be selection for 'remembering' individual signals and the dominance rank of the sender within and between years. While grey seals are closely related to elephant seals, in the grey seal system, male return is lower in comparison (31.4% Donna Nook) and the Body Slap is highly stereotyped, suggesting that it is unlikely a similar recognition mechanism is in effect. Still, further work utilizing playback manipulations (*e.g.*, observations of receivers' response when presented with a range of substrate-borne vibration magnitudes) could be done to investigate the honesty of the information in the Body Slap display and if active or passive receivers are deriving the information regarding size from the Body Slap's substrate vibrations and basing decisions on that information or if information is not being conveyed (Lawson 1993).

4.4.8 Conclusions

These two closely linked studies have defined a long overlooked aspect of the European grey seal behavioural repertoire and placed it within the framework of non-vocal pinniped communication (Miller 1991). They also have demonstrated that the substrate-borne vibrations of a male-male agonistic behaviour in a polygynous mammal contain information about the performer's RHP, and that this component is reliable in a variable environment.

Descriptions and baseline analyses are essential for improving the knowledge of an individual species' repertoire, but also contribute to the known diversity of evolution and adoption of non-vocal communication across taxa. The Body Slap is not the first unique or geographically divergent behaviour observed for this species or taxonomic grouping, but it does reflect a widespread pattern for male-male agonistic behaviours to exhibit geographic variation (Wilkins et al. 2013). Furthermore, the Body Slap is a behaviour that has only been noted within the past 30 years and is at present geographically isolated. At present, grey seals breed on a variety of substrates; however, the Body Slap display has only been observed at colonies with flat sandy beaches (Bishop et al. 2014). Other colonies across their range exhibit similar substrate types and conditions but observers have not reported usage of this behaviour. Furthermore, the usage of this behaviour appears to have evolved in a reasonably short period of time. An exciting aspect of these findings therefore is that while it is likely the Body Slap originated as an extension of the locomotor pattern, it is possible the substrate and local environmental conditions at Donna Nook and nearby colonies promoted the use of this behaviour.

Chapter 5

Investigating the assessment strategies in male grey seal contests

5.1 Introduction

5.1.1 Contest assessment theory

Aggressive interactions arise as a means of resolving access to resources such as food, habitat or mates, but these interactions are often costly in time, energy, or physical damage (Maynard-Smith and Price 1973, Parker 1974, Arnott and Elwood 2008, 2009). Due to the trade-offs between the benefits of gaining access to limited resources and the associated costs of aggression, selection should favour 'limited wars' (that is aggression without fatal injuries; Maynard-Smith and Price 1973) along with accurate information gathering and decision making at the level of the individual (Parker 1974, Arnott and Elwood 2008, 2009). As such, the evolution of decision-making processes in animal contests has had considerable theoretical and empirical attention across a range of taxonomic groups (Maynard-Smith and Price 1973, Parker 1974, Taylor and Elwood 2003, Prenter et al. 2006, Arnott and Elwood 2008, 2009, Reichert 2014).

Recently, there has been considerable effort to simplify models of decision-making in animal contests and to discern how the resource holding potential (RHP) of competitors drives behaviours (reviewed in Arnott and Elwood 2008, 2009). From this, a number of frameworks were proposed on the assumption that an individual's ability to win an interaction (RHP) will influence how a contest is settled. Arnott and Elwood (2009) group these frameworks, also referred to as individual 'assessment strategies', into three categories: (1) pure self-assessment, (2) cumulative assessment (CAM), and (3) mutual assessment (Table 5.1, Figure 5.1). These models differs in when and how the decision to give up is made (Taylor and Elwood 2003, Prenter et al. 2006, Arnott and Elwood 2009). In self-assessment and CAM, individuals base their decision of when to give up based on their own RHP alone and thus will incur some costs until their threshold is met (Taylor and Elwood 2003, Morrell et al. 2005, Prenter et al. 2006, Briffa 2008). For mutual assessment, each individual evaluates his or her opponent's RHP relative to their own in a similar fashion to a statistical sampling process and gives up when some probability of losing is met (Enquist et al. 1990, Taylor and Elwood 2003, Leiser et al. 2004, Arnott and Elwood 2009). While physical costs to an individual might be reduced by avoiding escalation under mutual assessment, costs associated with assessing an opponent's RHP (time, energy) will still be incurred and there is also potential for incorrect or imprecise information to be gathered under this strategy.

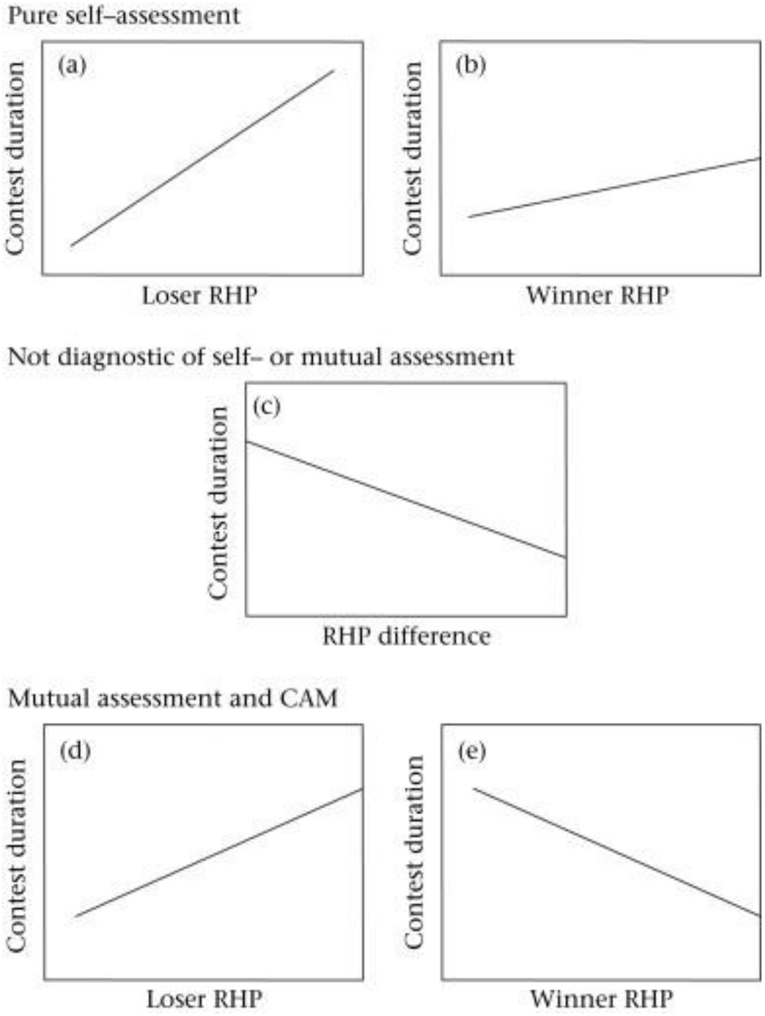


Figure 5.1: Relationship between resource-holding potential (RHP) and contest duration across the assessment models of self-, mutual- and CAM assessment (Arnott and Elwood 2009)**.**

Table 5.1: Characteristics used to discern assessment strategies (adapted from Arnott and Elwood 2009).

	Self-assessment	**CAM**	**Mutual Assessment**
Information gained	No information on opponent; opponent's actions do not inflict costs but both accrue costs from own actions. Loser stops when threshold reached.	No information on opponent; opponent's actions inflict costs. Loser stops when threshold reached.	Information on opponent's RHP relative to own is gained. Loser stop sooner if more likely to lose (e.g., winner RHP increases), but will persist longer if own RHP increases.
<u>Linear relationships:</u>			
Prior Knowledge:	Duration does not change	Duration does not change	Duration is shorter

An easily-applied method for determining assessment strategies across taxa was developed based on game theory predictions using information on both contestants' RHP and contest duration (Taylor and Elwood 2003, Arnott and Elwood 2009, Hardy and Briffa 2013, Figure 5.1). These methods have been used to assess the selection pressures driving information gathering across various taxonomic groups, and they have led to empirical evidence of all three types of assessment strategies (Jennings et al. 2004, 2005, Morrell et al. 2005, Kelly 2006, Hsu et al. 2008, Jennings et al. 2012). Following this initial taxonomic-driven research into assessment strategies, the expansion of the basic models to incorporate additional contexts and parameters revealed that in many systems, animals are not necessarily expressing a single strategy, and that some will switch their assessment strategies from mutual assessment during pre-escalation threat phase to self- or CAM assessment during the escalated phase of a contest (Morrell et al. 2005, Hsu et al. 2008).

Due to ease of experimental contest staging and opponent manipulation these methods have been commonly applied to small invertebrates such as crustaceans (Briffa 2008) or arachnids (Hsu et al. 2008). Jennings et al. (2012) investigated assessment strategies in wild fallow deer (*Dama dama*), but examples from other large, free-ranging mammals are still rare. Additionally, these previous studies only use aggressive interactions which are resolved with clear winners and losers, and to my knowledge none have considered what information gathering and decision making processes are used during contests which have ambiguous outcomes: draws. A large number of studies do not mention draws at all when discussing contest outcomes (Table 5.2), and those that do typically attribute the lack of inclusion of draws to: a lack of draws in some systems (Colléter and Brown 2011), laboratory contest methods requiring a winner and loser as part of the criteria (Barki et al. 1991), or explicit exclusion of these cases (Bierbach et al. 2013). Still, draws are prevalent as a contest outcome in many systems (Table 5.2, Anderson and Fedak 1985, Riechert and Hedrick 1993, Whiting 1999, Jennings et al. 2005, Whiting et al. 2006), and this represents a relatively understudied facet of animal decision making, information gathering, and cost-benefit trade-offs.

Table 5.2: A survey of 100 studies was conducted by E. Hobkirk to determine if draws were mentioned as a part of the aggressive system, and if they were included in calculations of dominance scores. Search words included: *dominance hierarchies, linear hierarchical ranking, dominance contest outcomes*. Some examples are presented here.

	Authors of study	**Species**
Draws were included (n = 7) including:	Jennings et al. 2005	*Dama dama*
	Greenberg et al. 1984	*Anolis carolinensis*
	Puppe et al. 2008	*Sus scrofa domesticus*
	Copp 1986	*Procambarus clarkii*
	Amsalem et al. 2013	*Bombus terrestris*
	Craig et al. 1965	*Gallus gallus domesticus*
Draws were mentioned but excluded from analysis (n=14) including:		
	Sheppard et al. 2013	*Gymnogyps californianus*
	Hamalainen et al. 2012	*Tetrao tetrix*
	McDonald and Shizuka 2012	*NA*
Specifically stated no Draws occurred (either through methodology or lack of unclear outcome; n=6)		
	Bradypodion pumilum	Stuart-Fox et al. 2006
	Colléter and Brown 2011	*Melanotaenia duboulayi*
	Garland et al. 1990	*Sceloporus occidentalis*
	O'Donnell 1998	*Mischocyttarus mastigophorus*
	Forkman and Haskell 2004	*Gallus gallus domesticus*
	Cordoni 2009	*Canis lupus*
Draws were not mentioned (n= 76) including:	Lemel and Wallin 1993	*Parus major*
	Holekamp et al. 1996	*Crocuta crocuta*
	Markham et al. 2012	*Pan troglodytes*
	Bauer and Smuts 2007	*Canis lupus*
	Bergstrom and Fedigan 2013	*Cebus capucinus*
	Bang et al. 2010	*Ropalidia marginata*
	Lu et al. 2013	*Semnopithecus entellus*
	Issa et al. 1999	*Procambarus clarkii*
	Herberholz et al. 2007	*Procambarus clarkii*
	Stamps 1984	*Anolis aenus*
	Haley et al. 1994	*Mirounga angustiroris*
	Jennings et al. 2012	*Dama dama*

5.1.2 Rationale and objectives

The grey seal breeding system is ideal for addressing this information gap as 40-60% of the male-male aggressive interactions which occur while attempting to maintain access to breeding females result in a draw (Twiss 1991, Bishop et al. 2014). Also, for male grey seals, mating success is determined by length of stay, not dominance score, a measure of ‘winning-ness’(Twiss 1991), and while larger males had greater mating success and were less likely to lose, winning did not correlate with absolute size. These findings suggest that ‘not losing’, be it a specific aggressive interaction or a position on the colony in general, is as important, or more important, than ‘winning’ for this species (Anderson and Fedak, Twiss 1991).

Therefore, the objective of this chapter is to investigate the assessment strategies used by wild, male breeding grey seals, and to determine if male assessment strategies vary across contest phase (threat vs. escalated physical contact) and/or across contest outcome (win-loss vs. draws). It can be hypothesized that self-assessment or CAM will be the primary strategy as these would result in males with the greatest energetic thresholds experiencing the greatest contest success. Self-assessment or CAM could also be the selected strategy if it reduced the potential for incorrect assessment of an opponent’s RHP, and subsequently retreating from a position near a female. Alternatively, it is known that grey seal aggression follows a sequential escalation pattern from low-cost threat phases to escalated contact fights (Boness and James 1975, Boness 1984, Anderson and Fedak 1985, Twiss 1991). Within these initial threat phases, males perform repeatable signals which contain honest information on RHP (Twiss 1991, Lawson 1993, Bishop et al. 2014, Bishop et al. 2015a, **Chapter 4**). Males also exhibit site fidelity within and between seasons (31.4% return inter-annually at Donna Nook), allowing for potential long-term associations between individuals (Twiss et al. 1994). Based on these factors, it could also be hypothesized that mutual assessment, through the use of cues and behavioural signals, might be selected for in this system as a way to minimize energetic costs by terminating or not escalating an interaction unless a particular RHP asymmetry was present. This hypothesis would in turn fit within the 'not losing' paradigm (Anderson and Fedak 1985).

In order to test these hypotheses and determine which assessment strategy is used by male grey seals, I first determined what measures were associated with male RHP by comparing the probability of an individual winning an AI based on his morphometric features (MSL and MLA; **Chapter 4**) and his length of stay on the island as these have previously been linked to RHP in this species (Twiss 1991, Lidgard et al. 2005, Bishop et al. 2014, **Chapter 7**). This information was then used to determine assessment strategies when there were clear winners and losers and (1) the contest was resolved only with threats, or (2) the contest is resolved after an escalated phase. To do this, winner and loser RHP is compared to contest duration to determine the drivers of time to retreating (Taylor and Elwood 2003, Figure 5.1, Table 5.1). Finally, this method was replicated for contests where the outcome was a draw to determine if strategies in unresolved contests differ or are conserved.

5.2 Methods

5.2.1 Contest duration

Of the aggressive interactions (AIs) recorded *in situ* a subset were video recorded (definitions and methods: **2.6.2**). Each video represented a discrete AI and was further classified based on the presence (Contact AI) or absence of physical contact (Non-Contact AI; Twiss 1991, Bishop et al. 2014). Interactions were also classified by outcome as either "Win-Loss" or "Draw", where a male was determined to have won an encounter if his opponent moved or was chased away and lost his position amongst a group of females; otherwise the AI outcome was defined as a draw (**2.6.2**; Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998, Bishop et al. 2014). When there was a clear winner and loser, the AI duration (DURTOT) was defined as the interval between the onset of the first aggressive behaviour and the end of the final aggressive behaviour. In draws, there is not always a discrete ending from which to calculate duration (DURDRAW), so I followed the criteria for determining the end of ambiguous AIs described in **2.6.2** from Boness et al. (1982) and Bishop et al. (2014). Finally, for interactions with a Contact phase (in both draw and win-loss outcomes), the duration of the escalated phase was calculated as the interval between the first point of contact and the final point of contact (DURCT).

5.2.2 Statistical analysis

5.2.2.1 Logistic analysis for predicting measures of RHP

Only video recorded AIs in which there was a clear winner and loser and both males were known were used for RHP predictions. Generalized mixed-effects models (GLMMs) with binomial distribution were used to determine the probability of winning based on my candidate RHP values of: (1) the male's photogrammetric estimates of MSL and MLA (**2.7**, Bishop et al. 2015), (2) rate of displaying of the Body Slap (**4.2.1.2**) and (3) cumulative length of stay on the colony in days, DOC (Twiss 1991, Lidgard et al. 2001). Lidgard et al. (2005) found that intermediate sized males had the highest probability of mating success. As this suggests RHP might not be linear in respects to absolute MSL or MLA, I also included 'centred' versions of MSL and MLA which described how different a male's size was relative to an intermediate value. I centred MSL and MLA at the median and at three divisions of the upper IQR as males are expected to gain some advantages from length or mass but also face a trade-off between strength and manoeuvrability (Twiss 1991, Lidgard et al. 2005). MSL was centred by taking the absolute value of a male’s MSL - 200 (median), -205, -210, or -215 cm, and MLA was centred as the absolute value of a male’s MLA - 5500 (median), -6000, -6500, or -7000 cm^2. Year and male ID were included as random effects to account for unequal sampling across males (pseudo-replication) and across-year variance (Fossette et al. 2008, Bolker et al. 2009). Models were fitted for all aggressive interactions (*n* = 260), Contact interactions (*n* = 124), and Non-Contact interactions (*n* = 136) to see if RHP predictors differed across aggressive contexts. Models for all analyses were run in R 2.13.2 (R Development Core Team 2011) with the lme4 package (Bates et al. 2011). Model selection for all analyses was conducted by following AIC selection criteria (Richards 2008).

5.2.2.2 Assessment strategy

Using the results of the RHP predictor analysis, assessment strategies used during contests were investigated via the methods outlined by Arnott and Elwood (2009) and summarized in Briffa et al. (2013). To determine the mode of assessment across phases of aggression (Hsu et al. 2008), I tested the relationship between RHP of winners (WRHP) and losers (LRHP) and DURTOT for Non-Contact (*n* = 79) and Contact AIs (*n* = 59) separately. This was done using GLMMs (Poisson distribution, Log-Link). I also fitted a third model using DURCT in Contact AIs only to see if assessment strategies in just the contact phase differed from the entire interaction (*n* = 59). In addition to the variables of RHP and asymmetry in RHP (difference in RHP between combatants), I included Prior Knowledge (PK), defined as 0 if the two males were not observed in an AI prior to the focal video or 1 if they had previously been observed in an AI. This was included as an interactive term in the model to account for any social effects on aggression (**Chapter 6**). Additionally, for Non-Contact AIs only, I included a categorical measure noting if Body Slaps were present or not, as previous studies have suggested these behaviours play a role in male assessment and therefore could contribute to variation in contest duration (Bishop et al. 2014, Bishop et al. 2015a). Because some males were recorded in more than one interaction as either winner or loser, and due to overall changes in intensity and rate of aggression across a breeding season (Twiss 1991), both winner and loser ID, by day of season (DOS, starting on Oct 27), were included as random effects to account for pseudoreplication of males within and across days (Fossette et al. 2008, Bolker et al. 2009, Jennings et al. 2012).

Finally, I examined what type of assessment strategy was used in interactions with draw outcomes. This posed a difficulty as there was no ‘winner’ or ‘loser’ for these interactions, and at present, all the assessment strategy models are based on the assumption that the duration of a contest reflects the decision to give up by the loser (Arnott and Elwood 2009, Briffa et al. 2013). This theory is based on the assumption that winners are typically the males with the larger absolute RHP value relative to the loser; therefore, it might be suitable instead to fit the response variables as the RHP of the male with the larger RHP of the two opponents (“Bigger RHP”: $WRHP_0$) and the RHP of the male with the smaller RHP of the two opponents (“Smaller RHP”, $LRHP_0$) instead of winner and loser RHP when dealing with interactions which have draw outcomes (Briffa et al. 2013). With this method, the predictions and interpretation of each model would only differ slightly for the context of a draw relative to win-loss contests. For example, for self-assessment, instead of the contest ending when the male with the smaller RHP reaches his limit first and retreats, in a draw, self-assessment might reflect both males reaching their threshold at the same time. Therefore, one would still expect the traditional relationship of self-assessment to be expressed (Table 5.1), in which duration increases in response to increases in both the larger and smaller male’s RHP. Under the model of mutual assessment, the contest typically is assumed to end when the loser decides that his opponent's RHP is too great to risk the costs of escalation. Instead, in a draw it might be interpreted that the greater RHP male will take longer to decide if the costs of chasing away a neighbour outweigh the benefits as the smaller male's RHP increases (positive relationship between Duration and $LRHP_0$). Simultaneously, the smaller male will decide more quickly not to push the interaction into escalation or to an outcome as his opponent's RHP increases (negative relationship between Duration and $WRHP_0$). While I acknowledge that this modelling requires some assumptions which were not part of the original framework (Taylor and Elwood 2003), this method and proposed interpretation of the model allows for an initial investigation of the process of assessment in draws, and should provide some insights into the decision making occurring in these contexts. Specifically, to do this, three separate models were fitted comparing individual RHP values to DURDRAW. The parameters included were identical to those included in the previous models of Win-Loss contests and were fitted to predict the duration of Contact AIs (n = 51), Contact phase (n = 51), or Non-Contact AIs (n = 433) separately. Models for all analyses were run in R 2.13.2 (R Development Core Team 2011) with the lme4 package (Bates et al. 2011). Model selection for all analyses was conducted by following AIC selection criteria (Richards 2008).

5.3 Results

5.3.1 Correlates of RHP

Across all interactions combined, and Contact AIs and Non-Contact AIs separately, the model with the lowest ΔAIC retained the parameter of MSL centred at 205 cm (difference = 0) suggesting males with lengths closest to this value have the highest probability of winning an interaction (Table 5.3, Figure 5.2). While MSL centred at 205 cm was retained in all three contexts, there was some uncertainty in the evidence for predicting the probability of winning. When considering Contact AIs and Non-Contact AIs separately, the model selection process also suggested alternative parameters increased the likelihood of winning (Table 5.3). For example, under the Contact only AIs context, there were 15 models retained under the selection criteria, and DOC shared a negative relationship with probability of winning in two of the top models (Table 5.3). In contrast, for Non-Contact AIs only MSL centred at 205 cm was retained in the best model (Table 5.3). Acknowledging these measures of uncertainty, the models with MSL centred at 205 cm consistently performed well and support previous findings of mid-sized males having increased mating success (Lidgard et al. 2005); thus, this value was determined to be a suitable measure for RHP and was used in the subsequent analysis for determining assessment strategy.

After determining MSL centred at 205 cm was the best predictor of RHP, I re-ran the model with the addition of an interaction term to determine if the relationship with the probability of winning differed depending on whether the male was greater than or less than 205 cm. This would provide information on whether or not it was better to be bigger than optimum or smaller than optimum when in combat. While there appeared to be a trend that males greater than 205 cm had a steeper negative relationship with probability of winning than males smaller than 205 cm (e.g., Contact AIs: slope estimate (±SE) for Greater-than 205 = -0.09 (0.04), Less-than 205 = -0.06 (0.03); Figure 5.3), the interactive parameter did not improve the AIC of any of the models (e.g., Contact AIs: $AIC_{without}$ = 155.2, AIC_{with} = 156.7) and was thus not further considered.

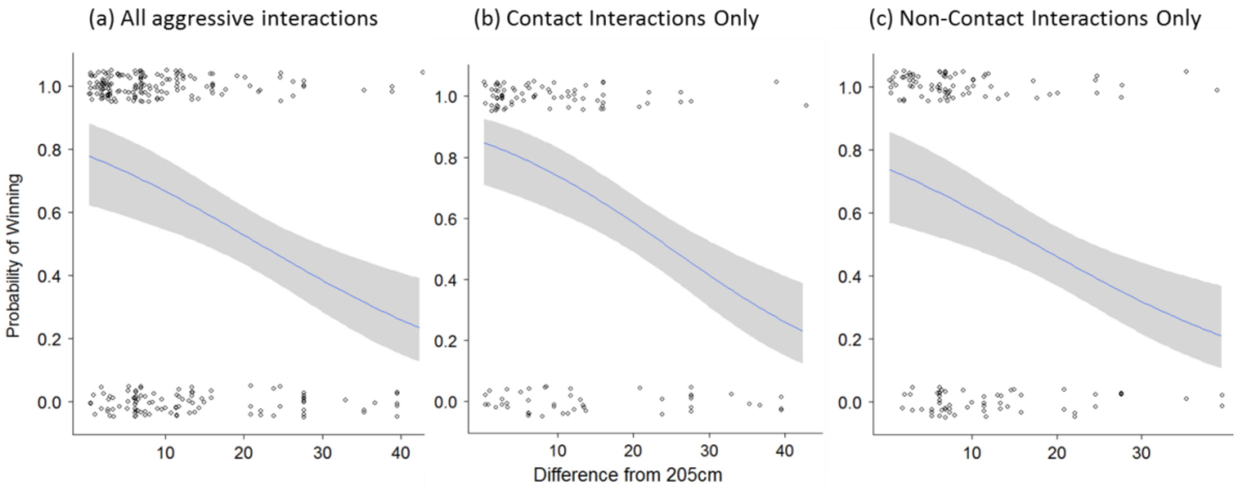


Figure 5.2: Predicted probability of winning from simplest model as a function of the magnitude difference between a male's MSL and 205 cm. All AIs (a), Contact AIs only (b) and Non-Contact AIs only (c). Shaded areas are 95% CI. Points represent jittered raw data.

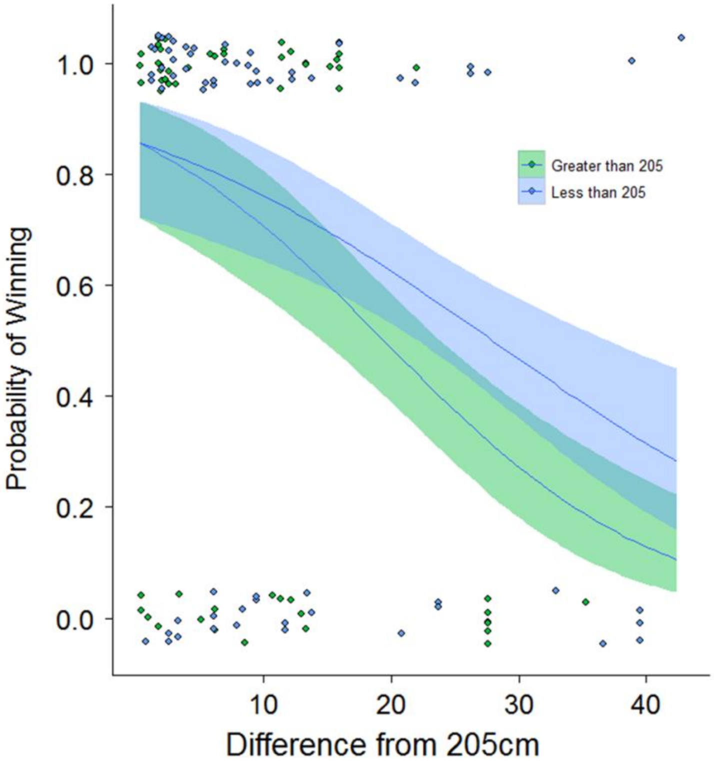


Figure 5.3: The effect of centred MSL at 205 cm on probability of winning a Contact interaction depending on if male was greater (G) or less than (L) 205 cm. The interactive term was not retained in any model. Points represent jittered raw data. Shaded areas are 95% CI.

Table 5.3: GLMM models for predicting the probability of a male winning a contest. The retained models are displayed for each of the three AI context models (Richards 2008). In all three conditions, males closest to 205 cm in standard length (MSL) were most likely to win an interaction.

Model	n_{records}	*Ran Ef.* n_{IDs}	AIC_c	ΔAIC
GLMM with binomial error distribution (YEAR, ID Random)				
Probability of Winning: All Interactions				
CSL @ 205 cm	260	109	327.9	0
CSL @ 210 cm	260	109	329.4	1.5
CSL @ 215 cm + MSL	260	109	330.9	3.1
CSL @ 215cm	260	109	331.6	3.8
Probability of Winning: Contact Only				
CSL @ 205 cm + DOC	124	68	155.1	0
CSL @ 200cm + DOC	124	68	155.2	0.2
CSL @ 205cm	124	68	155.5	0.5
CSL @ 200cm	124	68	155.9	0.8
CSL @ 210cm + DOC	124	68	156.4	1.3
CSL @ 215cm + MSL + MLA	124	68	156.5	1.5
CSL @ 215cm + MSL + DOC	124	68	156.9	1.8
CSL @ 215cm + MSL	124	68	156.9	1.9
CSL @ 210cm + MSL +MLA	124	68	157.0	1.9
CLA @ 7000 cm^2 + DOC	124	68	157.1	2.0
CSL @ 210cm	124	68	157.1	2.1
CLA @ 6500 cm^2 + MSL + MLA	124	68	157.3	2.3
DOC	124	68	157.5	2.4
CLA @ 6000 cm^2 + MSL + MLA	124	68	158.0	2.9
CLA @ 7000 cm^2 + MSL	124	68	158.2	3.2
Probability of Winning: Non-Contact Only				
CSL @ 205cm	136	73	184.4	0
CSL @ 210cm	136	73	185.1	0.7
CSL @ 200cm	136	73	188.5	4.1
Random Effects Only	136	73	188.7	4.3

†MSL, MLA, DOC and RBS represent Standard Length (cm), Lateral Area (cm^2), Cumulative Days on Colony, and Rate of Body Slapping behaviour (per second) respectively. CSL, CLA are centred values for standard length and lateral area. Ran Ef N_{ID} = number of individual IDs included in the model; Year (2011-13) was also a random effect.

5.3.2 Determining assessment strategy when winners and losers are clear

Using MSL centred at 205 cm (CSL 205) as the measure of RHP, the results of the models for determining assessment strategy for interactions with clear winners and losers varied depending on the intensity of escalation. The average CSL asymmetry between opponents for win-loss Contact AIs was 11.4 cm (± 1.21 SE) and 9.4 cm (± 1.07 SE) for Non-Contact AIs; this variable was not retained in any models. For Contact AIs when the combatants had not previously been observed interacting, as both WRHP and LRHP increased (values drew closer to zero difference from 205 cm MSL) duration of the contact phase, and duration of the whole contest increased, which supports the self-assessment model (Figure 5.4a-c; Table 5.4). When opponents had previously been observed interacting, increasing WRHP lead to a decrease in contact phase and whole contest duration (Figure 5.4a-b, Table 5.4) which suggests either CAM or mutual-assessment is used (Figure 5.1). Furthermore, if opponents had previously interacted, contact phase and whole contest durations were both lower on average (Table 5.4) which fits the mutual-assessment strategy (Table 5.1) and rules out CAM as an assessment model. There was no clear support for any assessment models for Non-Contact AIs with clear winners and losers. No measures of RHP were retained, but the duration of the whole contest was significantly longer if Body Slap behaviours were present or vice-versa (Table 5.4).

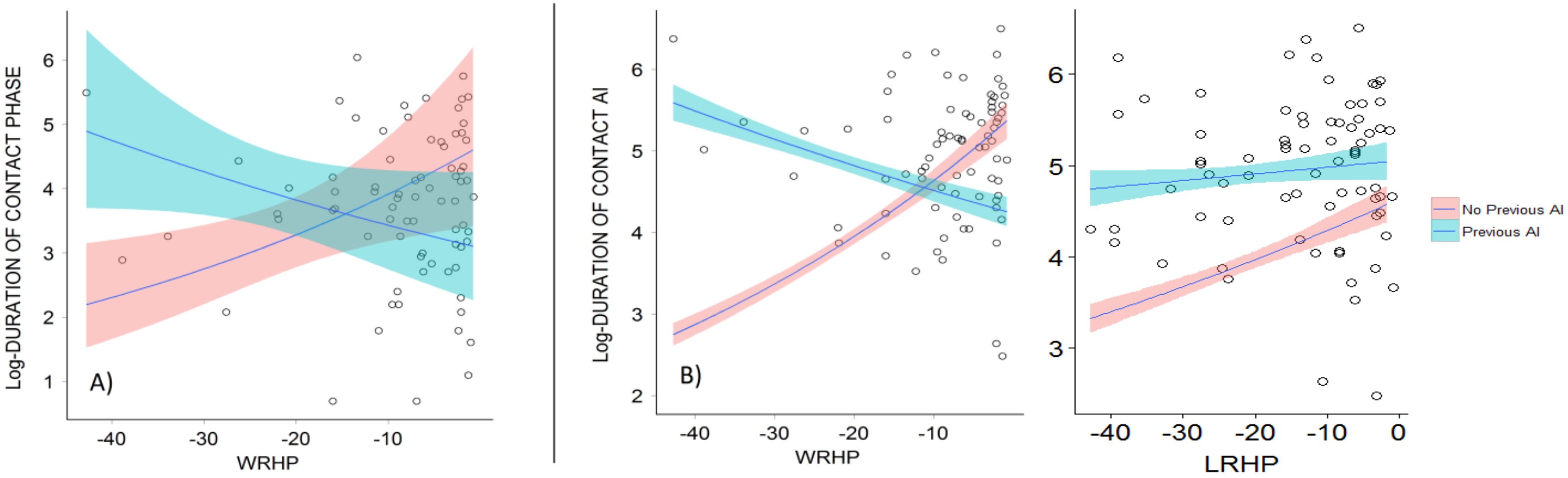


Figure 5.4: For duration of a contact phase, DURCT, (A) only Winner RHP was retained and the effect differed depending on whether the males had interacted previously. For total duration of an AI with contact, DURTOT, (B-C) both Winner (B) and Loser RHP (C) were retained. The effect differed depending on whether the opponents had previously been observed interacting. Due to RHP being measured as a difference from 205 cm and smaller values representing greater RHP, I multiplied WRHP and LRHP by -1 to correct the directionality of these relationships. Thus, the scale ranged from low RHP of -50 to high RHP of 0. Models suggest self-assessment if opponents have not been observed previously interacting or mutual-assessment if they had been observed interacting previously. Shaded areas are 95% CI.

TABLE 5.4: Retained GLMMs predicting the effect of RHP on Duration of Contact AIs (DURTOT), the Contact phase (DURCT), and on Non-Contact AI (DURTOT) when there were clear winners and losers (selection criteria: Richards 2008). Values given for predictor variables are the effect size and direction. Due to RHP being measured as a difference from 205 cm and smaller values representing greater RHP, I multiplied WRHP and LRHP by -1 to correct the directionality of these relationships. Thus, the scale ranged from low RHP of -50 to high RHP of 0.

Model	Asym	WRHP: PK$_0$	LRHP: PK$_0$	PK$_1$	WRHP: PK$_1$	LRHP: PK$_1$	BSP	n	*Ran Ef.* $n_{ID1:}$	*Ran Ef.* n_{ID2}	AIC$_c$	ΔAIC
Duration Contact Phase												
WRHP + PK + WHRP:PK	---	0.057	---	-1.5	-0.04	---	NA	59	56	49	312.15	0
LRHP + PK + LRHP:PK	---	---	0.014	-1.4	---	-0.006	NA	59	56	49	314.58	2.43
PK	---	---	---	-1.2	---	----	NA	59	56	49	315.54	3.39
Duration Contact AI												
WRHP + LRHP + PK + WRHP:PK + LRHP:PK	----	0.062	0.03	-1.6	-0.032	0.007	NA	59	56	49	343.67	0
Duration Non-Contact AI												
BSP	---	----	---	---	---	---	0.75	79	70	67	441.54	0

†Asym = absolute value of the difference in winner and loser RHP; WRHP = the absolute difference the winner's MSL was from 205cm; LRHP = the absolute difference the loser's MSL was from 205 cm; PK= previously observed interacting =1 or no prior observations of interacting = 0; BSP = if Body Slap behaviour is present = 1 or absent= 0. Ran Ef. = random effect (number of IDs for winners (ID1) and losers (ID2) within Day of Season).

5.3.3 Determining assessment strategy when outcome is a Draw

There was not a significant difference in RHP for interactions resulting in a Draw (mean asymmetry = 8.6 ± 0.36 SE) or contests with clear winners and losers (10.3 ± 0.87 SE; *t* = -1.66, df = 174.3, *P* = 0.097). There was no clear evidence for any assessment strategy for Contact AIs which resulted in a draw; models did not retain any of the chosen measures of RHP_0 and were best fit by the random effects of individual ID (Table 5.5). For Non-Contact AIs resulting in a draw, as $WRHP_0$ increased (values drew closer to zero difference to 205 cm MSL) duration decreased, and the opposite was found for $LRHP_0$, suggesting mutual or CAM assessment strategies (Figure 5.5, Table 5.5). This relationship changed in effect size depending on whether the opponents had previously been seen interacting; but the directionality did not change (Figure 5.5, Table 5.5). In Non-Contact AIs, duration was longer on average when the opponents had previously interacted or when Body Slap behaviours were present (Table 5.5).

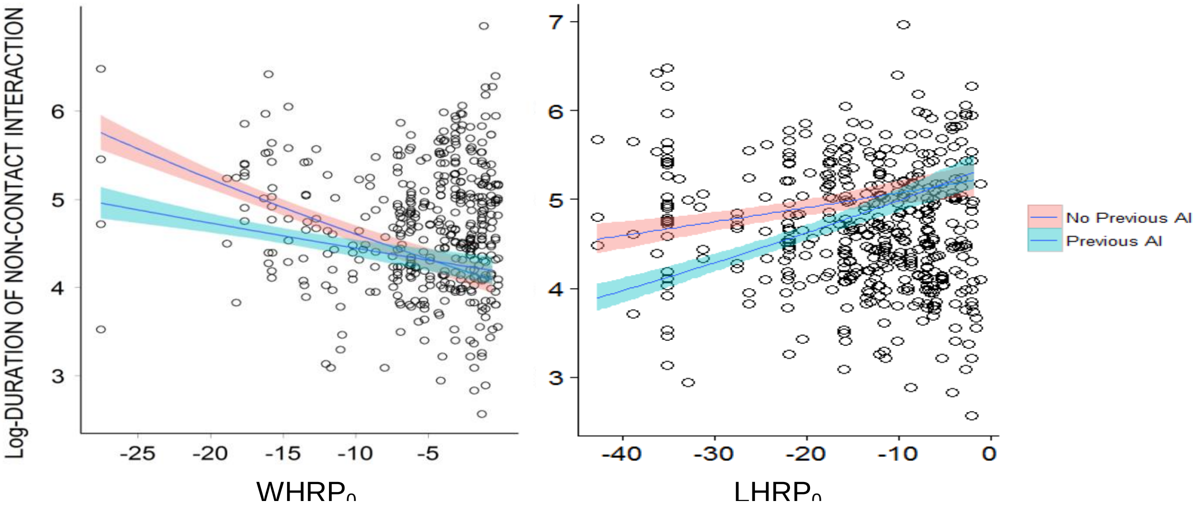


Figure 5.5: For Non-Contact interactions which resulted in a draw: $WHRP_0$ and $LRHP_0$ were both retained with opposite effects; the effect size differed depending on if the opponent was previously seen interacting. *As there are no winners or losers in draws: $WRHP_0$ and $LRHP_0$ correspond to the RHP of the male with the centred MSL value closer to 205 cm and farthest from 205 cm, respectively. Conditions suggest mutual or CAM assessment is used in this context. Shaded areas are 95% CI.

Table 5.5: Retained GLMMs predicting the effect of absolute RHP on Duration of Contact AIs, the Contact phase, and on Non-Contact AI when the outcome was a draw (selection criteria: Richards 2008). Values given for predictor variables are the effect size and direction. As there are no winners or losers in draws: WRHP$_0$ and LRHP$_0$ correspond to the RHP of the male with the centred MSL value closer to 205 cm and farthest from 205 cm, respectively. For RHP centred at 205 cm, lower values represent greater probability of winning, so effect direction is opposite to the estimate sign.

Model	Asym	WHRP$_0$: PK$_0$	LRHP$_0$: PK$_0$	PK$_1$	WRHP$_0$: PK$_1$	LRHP$_0$: PK$_1$	BSP	BSP: PK$_1$	*n*	*Ran Ef.* $n_{ID1:}$	*Ran Ef.* n_{ID2}	AIC$_c$	ΔAIC
Duration Contact Phase													
Random Effect Only	---	---	---	---	---	---	NA	NA	51	49	48	268.67	0
Duration Contact AI													
Random Effect Only	---	---	---	---	---	---	NA	NA	51	49	48	271.84	0
Duration Non-Contact AI													
BSP + WRHP + LRHP + PK + WHRP:PK + LRHP:PK + BSP:PK	---	-0.062	0.016	1.03	-0.028	0.034	1.45	0.53	433	273	266	8840.9	0

†Asym = absolute value of the difference in RHP between combatants; WRHP$_0$ = the absolute difference the male with the MSL closest to 205cm was from 205cm; LRHP$_0$ = the absolute difference the male with the MSL farthest from 205cm, was from 205cm; PK= previously observed interacting =1 or not previously seen interacting = 0; BSP = if Body Slap behaviour is present = 1 or absent= 0). Ran Ef. = random effect (number of IDs for bigger (ID1) and smaller males (ID2) within Day of Season).

5.4 Discussion

The results have confirmed previous findings that for male grey seals, having mid-sized length resulted in the greatest probability of success in aggressive interactions. This information was used to consider what assessment strategy, if any, was used for decision-making in contests. It was found that assessment strategy varied across contest escalation stage and contest outcome. RHP predicted duration of contests resulting in clear winners and losers when the contest included a contact phase, and suggested under this condition males used self-assessment if they had not been observed interacting with their opponent previously. However, when opponents had been observed interacting prior to a contact interaction, evidence suggested either no assessment or mutual assessment was used. For interactions resulting in a draw, none of the assessment models were supported for contact interactions, but there was strong evidence of mutual-assessment in Non-Contact interactions. This study provides the first investigation into assessment strategies for pinnipeds, and for interactions resulting in draws; as such, it adds to our understanding of the diversity of assessment strategies within and between species.

5.4.1 Male size and contest outcome

In a polygynous mating system, male RHP is often associated with large mass or size (Maynard-Smith 1979, Arnott and Elwood 2009); however the evidence of the present study suggests that for male grey seals, being of median length is associated with higher probabilities of winning an interaction. The proxy for mass, lateral area, was generally not a good predictor of success. In the closely-related northern elephant seal, length was also positively correlated with dominance (Haley 1994, Carlini et al. 2006). Other studies have found that mass was not the best predictor of RHP, particularly in species that rely on manoeuvrability, and often these cases are found in aquatic habitats (Moretz 2003, Munoz and Zink 2012). In male grey seal agonistic encounters, wrestling is the primary form of physical contact (Boness and James 1979), and there was some limited evidence that while males with lengths more different from 205 cm had lower probabilities of winning, the males with lengths greater than 205 cm had even more strongly reduced probabilities of winning in contact interactions. Considering these results, along with those of previous studies of determinants of mating success in male grey seals (Lidgard et al. 2005), it is possible length and mass are selected for in two separate processes leading to the optimal SL not being the absolute largest size, but an intermediate length. For example, an intermediate length could provide manoeuvrability for fighting agility and the ability to inflict damage quicker. Conversely, while increased mass likely provides ability to fast for longer periods (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005), the energetics required to move a larger body, by both mass and length, might limit fighting prowress. This pattern would explain why in Non-Contact interactions, which presumably have low energetic costs, there was not a clear of indication of as optimal body length, as there was in the contact scenario. It is also possible that males might adopt different strategies. Some males might rely on intermediate length and reduced mass to increase their fighting success. Others, such as those that can maintain a position amongst a stable neighbourhood thus reducing their probability of engaging in contact interactions (**Chapter 6**), might opt instead for a strategy of increased mass to prolong tenure, even at the potential cost of reduction of fighting ability. Ultimately, in this system, it seems likely that stabilizing selection has favoured males with intermediate standard lengths, likely as a way to maximize the trade-offs between manoeuvrability and prolonged residency, both of which factor into male fitness (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005). Identifying these correlates of RHP and the marginal benefits of increases in a particular characteristic for male grey seals was essential for examining the decision-making processes used by male grey seals in contests.

5.4.2 Assessment strategies: Draws

Draws often occur in cases where males are equally matched, or are familiar neighbours (Whiting 1999, Jennings et al. 2005). However, the literature concerning assessment strategies has exclusively utilized contests with clear winners and losers (Arnott and Elwood 2009, Briffa et al. 2013). I sought to examine assessment strategies in contests resulting in a draw, and the evidence suggests mutual assessment or CAM is the primary form of decision making during Non-Contact contests resulting in a draw. In Non-Contact phases, there is limited potential for the focal male to incur costs from the actions of his opponent (Taylor and Elwood 2003), suggesting that CAM is not the likely assessment strategy. Also, while on average, interactions between males who had previously been observed interacting had longer durations, over much of the range of RHP values interactions between males who had previously interacted had reduced durations for draws, which is in agreement with the mutual assessment model (Arnott and Elwood 2009). Therefore, the evidence suggests that males in Non-Contact interactions which have inconclusive outcomes are mutually assessing each other.

As mentioned previously (**5.2.2.2**) this finding suggests that the interpretation of mutual assessment needs to be reconsidered in regards to decision making of males when the result is not to retreat. At present, in win-loss contests, mutual assessment is characterized by both males assessing their opponent relative to their own RHP and the loser making withdrawal decisions more quickly when his as his opponent’s RHP increases (Taylor and Elwood 2003, Arnott and Elwood 2009, Briffa et al. 2013, Figure 5.1). In a draw, the male with the smaller RHP is likely still assessing his potential for success against his opponent’s RHP, but instead of deciding when to retreat, it might be interpreted that he decides not to escalate more quickly as opponent’s RHP increases (Figure 5.1e). Simultaneously, the male with the larger RHP would be assessing his opponent’s RHP in order to decide whether or not to risk pushing the interaction into a decisive outcome (*e.g.,* chasing the opponent away). This decision might take longer as his opponent's RHP increased (Figure 5.1d), producing the positive association between $LRHP_0$ and contest duration that was observed in this study. These decision processes under the mutual assessment model, as well as the outcome of a draw itself, are likely driven by the benefits/costs of social stability and 'not losing' (**Chapter 6**, Anderson and Fedak 1985), information reliability (**4.4.4-5**), and prior relationships.

5.4.2.1 Body Slapping

The evidence for mutual assessment during Non-Contact interactions suggests that males are gathering information on each other during threat phases of contests; this finding potentially clarifies some uncertainty regarding if the honest information of RHP contained in the Body Slap might be actively used in assessment (Bishop et al. 2015a-**Chapter 4**). Arnott and Elwood (2009) urged caution in assuming that when cues containing information regarding RHP are present the opponents are gaining information from the behaviour. For example, some spiders use visual and vibratory cues (Taylor et al. 2001) but there is no supporting evidence of mutual assessment based on visual cues in that system. However, the finding that male grey seals mutually assess in pre-contact phases with draw outcomes, and the presence of behaviours during these phases which contain reliable information regarding RHP (**Chapter 4**), give some support to the hypothesis that male grey seals might be using the information contained in the Body Slap's seismic magnitude to assess opponents. When at least one male performed a Body Slap, the duration increased, possibly due to information gathering and processing times; but furthermore, the duration was lower when at least one male used a Body Slap *and* the males had previously interacted. This might suggest information is retained from prior bouts of threats. Ultimately, while these results provide additional evidence, as mentioned in **Chapter 4** (Bishop et al. 2015a), determining if the information in the seismic modality of the behaviour is being used by the receiver, and that males are not only relying on visual or air-borne acoustic components of the Body Slap or other behaviours, would still require experimental manipulations in the form of playback studies (Casey et al. 2013).

5.4.2.2 Prior knowledge

A second characteristic of mutual assessment is that due to the information gathering nature of the assessment, contest durations are typically reduced when opponents have prior knowledge about their opponent's RHP (Arnott and Elwood 2009). As mentioned, for much of the range of RHP values, the duration of draws were shorter when males had been observed interacting previously; however, the models showed that on average, durations were longer when males had prior knowledge. While contradictory, this does suggest that other variables might be contributing to the decision-making process aside from absolute RHP values after an initial interaction between two males. One such variable might be the local spatial stability of males and neighbour identity. As capital breeders, selection has strongly favoured behaviours which conserve energy for male grey seals (Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1994, Bishop et al. 2015b, **Chapter 3**). Anderson and Fedak (1985) proposed that for male grey seals, 'not losing' was as important, or more important, than 'winning' outright (Twiss 1991) and hypothesised that this differentiation was potentially driving the relatively large proportion of draws observed for this species. Further discussed in **Chapter 6**, the importance of social stability was examined in relation to fine-scale conflict reduction, and it was found that males who maintained local social stability (that is, they neither chased off opponents, nor lost their own positions) benefited in reduced costs through reduction of aggression frequency. Similar patterns are also apparent in other species (Whiting 1999). For male northern elephant seals, after opponents have been previously observed interacting, RHP indicators such as vocalizations were less important than the identities of the combatants, and the previously-established dominance relationship was key in determining the response of each male (Casey et al. 2013). In angelfish (*Centropyge bicolor*) hierarchies, it has been suggested that there is a greater requirement for chronic mild aggression from dominants to subordinates after initial contact otherwise the dominance hierarchy becomes destabilized (Ang and Manica 2010). Therefore, threat contests resulting in a draw might serve as a both a means of mutual assessment initially, and then subsequently provide a way of reinforcing previously-determined relationships. Under this hypothesis, prolonged interactions that use less risky behaviours and outcomes could reflect the selection for social stability amongst neighbours and 'not losing' paradigm (Anderson and Fedak 1985). To fully test this hypothesis, the current model of contest assessment might not be appropriate for draw contests amongst males who have previously interacted. Further development of models which address decision making where opponents seek to gather information and/or reinforce relationships will be needed to elucidate the specific strategies within draws.

Table 5.6: Simplification of costs (behavioural = physical injuries and energy; outcome = loss of position amongst females (loser) or loss of stable neighbour (winner)) associated with different types of contests and the results for assessment strategies. Low costs were arbitrarily given a value of 0 and high costs a value of 1. Assessment strategies were strongly supported for the lowest cost interactions and the highest cost interactions (bold).

	Non-Contact Draw	Non-Contact Win-loss	Contact Draw	Contact Win-loss
Behavioural Costs	Low (0)	Low (0)	High (1)	High (1)
Outcome costs	Low (0)	High (1)	Low (0)	High (1)
Costs Score	0	1	1	2
Assessment Type	**Mutual/CAM**	**Unclear?**	**Unclear?**	**Self/Mutual**

5.4.3 Assessment strategies across contexts

While there was clear evidence for mutual assessment under Non-Contact draw contexts, the only other context with clear evidence for an assessment strategy was Contact AIs resulting in a clear win-loss (Table 5.6). A similar pattern of context dependent assessment strategies has been found previously (Hsu et al. 2008), and other work has also suggested that the three generalized models for assessment actually exist as parts of a continuum (Prenter et al. 2006, Mesterton-Gibbons and Heap 2014). Due to the high costs of physical contact in escalated interactions, selection should favour mutual assessment in pre-contact or Non-Contact interactions to decide whether or not to escalate; however, once males have entered into a ‘fight’, males should switch their decision making process away from their opponent’s relative RHP and withdraw when a personal threshold has been reached either through an accumulation of costs (CAM) or by depletion of energy (Hsu et al. 2008). Considering the results across contest outcomes, there was some evidence of this apparent shift from mutual assessment during Non-Contact interactions where the outcome was a draw (low-cost behaviours and low-cost outcome) to self-assessment during contact phases of AIs when the outcome was a clear win or loss and opponents had not been previously observed interacting (high-cost behaviours and high-cost outcome). Due to the low costs of interactions resulting in a draw, this could also allow for some unreliability of signals or assessment while minimizing the energetic costs of continuing until a threshold is met under the CAM or Self-assessment models (Arnott and Elwood 2009). Conversely in the context of escalated contests resulting in a win-loss, males would benefit from fighting until their personal threshold was met without regard for opponent’s RHP, as the costs of losing a position would result in a probable loss of mating success (Twiss 1991, Lidgard et al. 2001).

The contexts with intermediate ‘costs’ had unclear results (Table 5.6) which could reflect the ‘continuum’ of assessment strategies proposed by Prenter et al. (2006). The lack of support for any assessment models under the two intermediate conditions could alternatively be due to the relatively small sample sizes of interactions which fit these contexts (Non-Contact *n* = 79, Contact n = 51 draw). In the grey seal mating system, there is considerable variability in the 'fighting styles' and behaviours in aggressive interactions. For example, in the high cost scenario, interactions might take on one of many stereotyped endings such as: ending when one male reaches his opponent's hind-flippers (Twiss 1991), or ending with a protracted sequence of approaches and lunges from the winner towards the loser (pers. obs). These stereotyped sequences are not consistently presented when contact aggression results in a draw, and this could lead to difficulties discerning 'exit-strategies' for the smaller males in these contexts. A similar lack of stereotyped sequences can be observed in the other context with intermediate costs; Non-Contact AIs that have clear winners and losers. In these interactions, the winning male might chase the losing opponent away, but at other times the losing male will retreat without pursuit. In addition to this behavioural variability, the models were also not able to account for some of the natural variability in environmental factors across the breeding seasons, such as weather or stochastic disturbance events, which have been shown to contribute to changes in other aggressive behaviours (**Chapter 6**). Future work characterizing these types of interactions into similar sub-groups based on sequences or presences of behaviour, and incorporating environmental variability across the season might better reveal decision-making processes in the intermediate cost scenarios and clarify how assessment strategies are selected for in these contexts.

In escalated contests, there was evidence of a shift to self-assessment when there was a win-loss outcome, but only when the opponents had not been observed interacting previously. The evidence of self-assessment with a novel opponent supports the hypothesis that when no prior information on an opponent is available, in a costly interaction, it is better to rely on one's own thresholds than to sequentially assess relative RHP (Hsu et al. 2008, Briffa 2008). However, this appears to change when there is prior knowledge; when there was prior combat between the two opponents, the winner's RHP shared a negative relationship with duration. This pattern does not differentiate between mutual assessment and CAM, but as average contest duration decreased when opponents had previously interacted, the evidence supports the conclusion that some factor of mutual assessment information gathering was occurring (Table 5.1). Mutual assessment could be favoured in an escalated contest if prior knowledge allowed males to retreat early ("run away to fight another day"), even after incurring some costs associated with physical contact. This strategy would likely only be beneficial when there is ample access to females, and costs of surrendering positions are low (*e.g.*, early season before oestrus or late in the season). However, recent studies have suggested in addition to the three assessment model characterizations from Taylor and Elwood (2003), there is also the possibility of 'no-assessment' or 'competitor-only' assessment models (Rillich et al. 2007, Prenter et al. 2008, Reichert and Gerhardt 2011, Jennings et al. 2012). For example, for male swordtails (*Xiphophorus helleri*), as the sword size of the winning male increased, contest duration decreased; this appeared to be independent of the size of the loser's own sword (Prenter et al. 2008). This pattern is described as 'competitor-only' assessment. In the present study, the retention of the winners' RHP, and the negative relationship it has with contest duration when opponents had been observed previously interacting, shares some similarities with the mutual assessment and CAM models, but it also matches the description of 'competitor-only assessment'. Sample sizes for Contact contests with clear winners and losers were relatively small, and individuals were subject to large environmental and social variability across years. It is tempting to speculate that the males shift from self-assessment to 'competitor-only' strategy in contact interactions when they have prior knowledge. Regardless of the unclear pattern of assessment for contact interactions when opponents had previously interacted, these preliminary findings clearly demonstrate plasticity across contexts for assessment and suggest avenues for further research to discern how flexible male assessment strategies are in wild populations in relation to inter-individual relationships and across varying temporal scales.

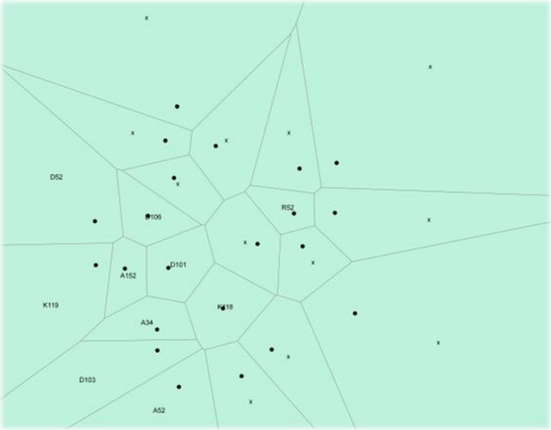
5.4.4 Conclusions

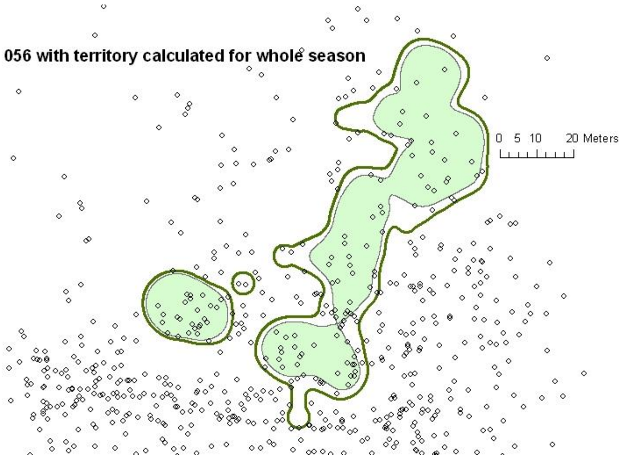
In summary, this chapter provides the first examination of decision-making processes for animal-contests which result in a draw and through this, has provided evidence that as the behavioural and outcome costs of interactions increase, there is a shift from mutual assessment via cues (**Chapter 4**) to self-assessment. For grey seals, prior knowledge appears to impact the decision-making process through reduced durations and shifts in assessment strategies. This likely reflects the strong selection for local-social stability underpinning the cost-benefit assessment process (**Chapter 6**).

Chapter 6

Variability in individual rates of aggression in wild grey seals

Fine-scale analysis reveals the importance of social and spatial stability.





Manuscripts from this Chapter:

Bishop AB, Pomeroy P, Twiss SD (in review). Variability in individual rates of aggression in wild grey seals: Fine-scale analysis reveals importance of social and spatial stability. Behavioral Ecology and Sociobiology.

6.1 Introduction

6.1.1 Conflict reduction

Animals face conflict within social groups as members compete for limited resources (Maynard-Smith and Price 1973, Maynard-Smith 1974). Aggressive interactions arise as a means of resolving access to contested resources such as food, habitat or mates, but can be costly in time, energy, or physical damage (Briffa and Elwood 2004). Due to the trade-offs between the benefits of gaining access to limited resources and the associated costs of aggression, there is considerable variation in the rates and intensity of aggression observed across species, and across individuals within populations (Maynard-Smith and Price 1973). Some of this variation is driven by intrinsic characteristics of individuals such as size, age or experience (Briffa and Elwood 2004), but additionally, various factors have been found to contribute to the variation in individual rates of aggression such as dominance hierarchies, winner/loser effects, honest signals of resource holding potential (RHP), and social relationships (Arnott and Elwood 2009, Kokko 2013). Furthermore, the relative variation in individual rates and intensity of aggression, can be context-dependent in relation to broader ecological processes such as resource availability (Leiser 2003), physiological constraints (Bohórquez-Herrera et al. 2014), and the underlying social system within a population or species (Ang and Manica 2010).

For social animals, the formation of a linear, transitive dominance hierarchy based on RHP asymmetries between individuals can result in minimized interaction costs for individuals. In stable groups, hierarchies can provide decision-making information to individuals about relative costs and benefits of escalated aggression (Drews 1993). The presence of dominance hierarchies, and the unequal access to resources, has direct fitness consequences for individuals including increased opportunity for mating and mating success for dominant individuals (Drews

1993, Anderson and Fedak 1985, Haley et al. 1994, Herberholz et al. 2007, Gerber et al. 2010), but studies have shown the presence of hierarchies can also lead to individual variation in the rate or the probability of escalation of fighting (Rosenthal et al. 1992, Drews 1993, Goessmann et al. 2000, Ang and Manica 2010). In some breeding systems, high rank is associated with a greater intensity or increased frequency of aggression associated with defending a territory or mates (Francis 1988, Rosenthal et al. 1992, Goessmann et al. 2000, Ang and Manica 2010). However, other studies have demonstrated that dominant individuals have relatively reduced costs, and experience lower rates of directed aggression or lower intensity of aggression in comparison to subordinates (Twiss 1991, Heitor et al. 2006, Ostner et al. 2008).

Such apparent contradictions might be generated by the available methodologies for calculating an individuals' dominance score or rank, as these are generally only applicable to data spanning relatively long temporal scales (Boyd and Silk 1983, David 1987; Gammell et al. 2003; de Vries et al. 2006). Recent additions to the dominance score calculation toolbox such as Elo ranking (Neumann et al. 2011) now allow for calculations of dominance in sequence (*e.g.*, for an individual male, his dominance score is updated after each interaction) and at a finer temporal scale (see **A6.1** for further information on the calculation of Elo). Adopting this method might provide insights into conflicting results regarding the role of dominance in individual conflict reduction. Furthermore, while there is support for considering dominance rank as a potential driver of conflict reduction, theoretical work modelling conflict reduction has also suggested that individual qualities such as dominance rank might not be as important in explaining differences in individual rates of aggression as the overarching environment, and the spatial clustering of combatants and resources in which hierarchies are formed (Hemelrijk 2000).

6.1.2 Previous work on grey seal conflict reduction

Investigations into the variation in aggression between individuals have often been examined using the polygynous breeding pinnipeds as model systems (Anderson and Fedak 1985, Haley et al. 1994, Twiss et al. 1998, Lidgard et al. 2005, Carlini et al. 2006, Bohórquez-Herrera et al. 2014). The grey seal is a colonial, capital breeder where there is high skew in male mating and reproductive success (Twiss et al. 2006, Twiss et al. 2007), where male energy is limited during the approximately eight week annual breeding season (Twiss 1991), and where there is considerable variability between years, colonies and individuals in the frequency of male-male agonistic interactions (Boness 1984, Twiss 1991, Lawson 1993, Twiss et al. 1998). Inter-male aggression during the grey seal breeding season occurs as males strive to maintain access to shifting groups of females, and males form a non-linear dominance hierarchy, where apart from a few clearly dominant and subordinate individuals, most males have very similar dominance scores (Anderson et al. 1975, Twiss 1991, Twiss et al. 1994, Twiss et al. 1998, Twiss et al. 2007). Apparent polygyny varies on multiple temporal and spatial scales (**3.3.6**), but in general, dominant males experience the greatest levels of mating success by remaining among groups of females for as long as possible (Boness and James 1979, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998, Lidgard et al. 2004, Twiss et al. 2006, Twiss et al. 2007, Worthington-Wilmer et al. 2000). Based on these characteristics, there should be strong selection for individual conflict reduction; however, studies of the intrinsic and extrinsic factors underpinning the variability in rates of aggression between individuals have been constrained to comparisons of individuals at the scale of a seasonal average. For example, dominant males have been shown to experience relatively reduced average intensity and average rates of aggression across a breeding season (Twiss 1991), but Twiss's study did not consider the daily fluctuations in aggression in relation to sex-ratios, distributions of competitors and distributions of females, all of which shift throughout a season (Twiss et al. 1994, Pomeroy et al. 1994). Furthermore, grey seal males and females exhibit site fidelity between seasons (Twiss et al. 1994, Pomeroy et al. 1994), and for females, breeding site location does not fully explain inter-annual associations (Pomeroy et al. 2001, 2005). This potential for inter-year male associations and within-year spatial social stability have been discussed as possible drivers of conflict reduction in grey seals (Anderson et al. 1975, Twiss 1991), but the relative importance of such factors in explaining the fine-scale variation in individuals' rates of aggression has not been examined previously.

6.1.3 Aims and objectives

Hemelrijk (2000) advocated studying animal behaviour not in isolation, but through the feedbacks of spatially explicit individual and social behaviours. When determining the factors associated with rates of aggression, most studies utilize paired-contestant tests in controlled experimental arenas. This can simplify analysis by controlling variables such as sex-ratios and competitor densities, both of which have been shown to directly impact the degree of polygyny and subsequently the rates of aggression (Emlen and Oring 1977, Anderson and Harwood 1985, Tinker et al. 1995, Reynolds 1996, Twiss et al.1998, Grant et al. 2000, Weir et al. 2011). While controlled, experimental studies have provided essential knowledge about factors which contribute to variation in aggression between individuals, these methods are not suitable for investigating the conflict and conflict reduction among large, free-ranging vertebrates in their natural environment where manipulations are not feasible.

Therefore, the aim of this study was to use the wild grey seal breeding system to investigate at a fine temporal and spatial scale which intrinsic and extrinsic factors best explain the variability in individual males' rates of aggression and probability of an interaction escalating in intensity. I hypothesize that at the daily scale, based on the previous findings of Twiss (1991), individuals' dominance scores will be correlated to rates of aggression, with males of higher rank having lower aggression. In addition to dominance, I have included two density related spatial factors that vary at a fine temporal scale within a breeding season (Twiss et al. 1994) but have not been included in previous models of aggression for this system: proximity to competitors as a measure of competitor intensity and, proximity to females as a measure of ease of access to the contested 'resource'. These variables were chosen because although male grey seals do not form distinct territories, male attendance shifts within a breeding season changing the social structure at a fine temporal scale (Twiss et al. 1994). Additionally, social stability has been shown to play a role in determining female grey seal breeding behaviours (Pomeroy et al. 2005), and recent evidence demonstrated a reduction in aggression between weaned grey seal pups which had previously been penned together, relative to pups which were 'strangers' (Robinson et al. 2015). Therefore, I also included a measure of the stability of a male's local 'neighbourhood' as a social factor, and predict that males with high local social stability will have lower rates and intensities of aggression (Anderson and Fedak 1985, Twiss 1991, Booksmythe et al. 2010, Cross et al. 2013). These factors were modelled within three successive breeding seasons, which further allowed for examining how stochastic environmental events and broad environmental variability across seasons might change how these factors are associated with individual rates and intensity of aggression.

6.2 Methods

6.2.1 Measures of dominance

Thus far I have used two methods to calculate dominance, David's Score and Elo (**4.2.2.4**). Due to sample-size requirements, many dominance score calculations, such as the David's Score (David 1987; Gammell et al. 2003; de Vries et al. 2006), are only capable of generating one score per male for a user-defined time period (*e.g.,* a month, a year, a breeding season) using the results of all of the male's interactions in relation to other males in the specified sample. This limitation obscures temporal variation within individual male's scores and ignores the variability in timing or presence on the colony among males (Neumann et al. 2011). If David's Score is used, in a system such as that of the grey seal, a male who was only present for the final week of the breeding season but won every interaction could have a higher score than a male who was present all season and lost a handful of interactions. Additionally, males may be expressing or asserting dominance at different points of the season as a mating strategy, but this trajectory of dominance would be lost or masked in a dominance metric that relies on seasonal averages, such as David's Score. This temporal disconnect has rarely been considered in dominance literature due to lack of appropriate methodology; however, a recent addition to the dominance-score calculation methodologies, Elo ranking, has been advocated for ecological systems when sequential information about aggressive interacitons is available (Neumann et al. 2011). Used traditionally for chess tournament rankings, this calculation generates rank vaules that are temporally fixed in sequence, and can account for draws and incomplete interaction matrices, all limiting factors of David's Score (Neumann et al. 2011). Seasonal mean Elo is comparable to David's Score (Neumann et al. 2011), so broad assessments and comparisons can still be made (for further comparisons of these two methods see **Appendix Chapter 6**).

For this study, I selected to use Elo scores to examine conflict at the daily scale as opposed to a whole-season average. To calculate Elo scores for males at Donna Nook, I first restricted the sample pool to males who were present for a minimum of two days and 10 agonistic interactions for consistency with previous work (Twiss 1991, Bishop et al. 2014). The parameters of the Elo calculations were set with an initial value of 1,000 for every male and a *k* of 200, where *k* is the amount a male's score will shift with a win or loss, weighted by the score of his opponent (Neumann et al. 2011). I selected a starting score of 1,000 as this was similar to the method used by Pörschmann et al. (2010) for calculating dominance of male Galápagos sea lions (*Zalophus wollebaeki*). Pörschmann et al. set *k* at 50, but I selected to use the higher, default value, of 200 to account for the heavy costs associated with losing in this system (Anderson and Fedak 1985, Twiss 1991). Elo scores were calculated across all three years (Elo_3Y); this approach uses a male's last Elo score from the previous year as the starting value in the subsequent year, allowing for previous dominance to predict starting male values. The rationale for this was that males exhibit moderate site fidelity for pinnipeds (**4.4.7**), are long-lived, and evidence has suggested that males do not shift dominance ranks substantially between years (Twiss 1991, Twiss et al. 1994, Twiss et al. *unpublished data*). Therefore, for each male, a daily Elo score (DayElo) was calculated as the average of all his scores for that day using only the Elo_3Y values. As the range of possible Elo scores can vary depending on the individuals and aggressive events within a given day, year, or site (Neumann et al. 2011), DayElo values for individuals were normalized to allow for comparisons: $\text{DayEloN} = (\text{DayElo}_{\text{ID}} - \min(\text{DayElo}_{\text{day}}) / (\text{Range of DayElo}_{\text{day}})$, which resulted in a range of individuals' average scores per day of 0-1, from low to high dominance.

6.2.2 Stability of neighbour identity

Hierarchy stability is one approach to track changes in inter-individual relationships for large social groups (Neumann et al. 2011). It is suitable for tracking broad changes in the hierarchy composition across the season or between seasons, but this approach does not take into account how localized spatial differences in individual identities change over time. Therefore, I selected to calculate a measure of the local social stability, which could be extracted on an individual and daily scale.

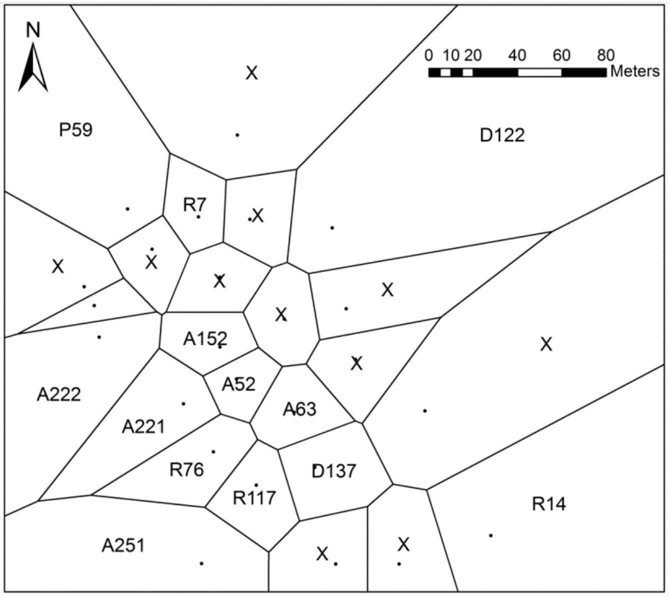


Figure 6.1: An example of Theissen polygons generated around male positions on Day of year 325 at the RAF site in 2012. Black points represent mapped locations of males for the given hour (known = Alphanumeric code; unknown = x). The lines are drawn at the midpoints between adjacent points, creating polygons. Males were considered 'neighbours' if their polygons shared an edge for the given hour.

For colonially breeding pinnipeds, social stability has been previously estimated for females using the consistency of individuals' and their neighbours' spatial locations instead of pair-wise associations (Ruddell et al. 2007). Ruddell et al. (2007) suggested that neighbour affiliations could be defined as any females within 10 m of each other; however, since male grey seals do not form discrete territories and are typically more dispersed than females this method was not deemed suitable (Twiss et al. 1994). Instead, associations were calculated by deriving Theissen polygons, around each individual male using ArcMap 10.1 (ESRI; Figure 6.1). Theissen Polygons are generated by creating lines at the midpoint between two adjacent points for each hourly map (Figure 6.1). From this, any male whose polygon was adjoined to the focal male's polygon was classified as a neighbour for that hour. Ruddell et al. (2007) found that Jaccard's Similarity index (JSI) was the best metric for quantifying local social stability in colonial pinnipeds; so I calculated a neighbour JSI for each focal male to measure how many of his neighbours were similar between two consecutive 1 hour periods (Eq. 6.1).

$$\text{NJSI} = \#\text{Same} / (\#\text{Same} + \#\text{New} + \#\text{Lost}) \tag{6.1}$$

Due to a number of transient, non-identified males on the colony at any given time, I selected to amend the JSI calculation to account for un-identified neighbours as part of the total neighbour pool (Eq 6.2):

$$\text{NJSI} = \#\text{Same} / (\#\text{Same} + \#\text{New} + \#\text{Lost} + \text{Unknown}_{\text{Hour } n} + \text{Unknown}_{\text{Hour } n\text{-}1}) \tag{6.2}$$

This assumed that any unknown males from the previous hour were not the same individuals as the unknowns from the present hour. This likely over-estimates neighbour turnover rates, but males within the study area that were present for more than 1 hour were photographed for identification, reducing the number likely to be double-counted. Also, under this assumption, I provide a more conservative estimate of stability as any transient males that were not identified were unlikely to be present long enough to contribute to the social stability of the system. NSJI values were then averaged per day for each male and ranged from 0 (unstable: all new neighbours) to 1 (stable: all neighbours returned and no new neighbours).

6.2.3 Statistical analyses

To test how neighbour stability and other spatial metrics for males on the colony changed within and between seasons, individual daily averages for NJSI, DNM and DNF (**Chapter 3.2.6**) were assessed for differences between sites at Donna Nook (RAF n = 590; PUB n = 827) and years (2011 n = 277; 2012 n = 634; 2013 n = 504) using generalized linear mixed effects models (GLMM) with male ID (n = 147) and observer ID (in 2012 and 2013, n = 2) as random effects to account for pseudoreplication and observer variance. For measures across years, only days that were represented in all three years were used for calculating means/medians (Day of Year (DOY) 309-343). In 2011, a storm-surge, tidal-event occurred on November 26th (DOY 330) which resulted in spring tide waters > 8 m (normal range 5-7 m), female-pup separations, and an increased numbers of females moving up into the soft dunes. To test for differences in NJSI, DNM and DNF at each site before and after the tidal event, I fitted similar GLMMs as above (Before n = 220; After n = 57) with NSJI, DNM and DNF as response variables, and Tidal Event as a categorical predictor variable (TDEV: Before and After).

I then predicted individual daily rates of aggression (DAI, **Chapter 2.6.2**) by fitting GLMMs (Poisson distribution; link = log) with male ID and observer ID (in 2012 and 2013) as random effects to account for repeat measures of the same male within each year and potential observer variance. The response variable was the DAI per male per day and the predictor variables included were the male's mean normalized dominance score that day (DayEloN); his average distance to nearest male (DNM) that day; average distance to nearest female (DNF) that day; and his average local neighbour similarity (NJSI) that day. These variables accounted for individual quality, density effects and social determinants of rates of aggression. The model also included SITE as an interactive, fixed explanatory variable to test for site-specific differences.

Models were fitted for 2011, 2012 and 2013 separately. An additional predictor variable of Tidal Event (TDEV) was included in the 2011 model as an interactive term to test if the continuous predictor variables differed in their effect prior to or after the tidal event. Finally, the same modelling procedure was followed to predict the probability of a male engaging in at least one aggressive interaction which involved contact per day using binomial GLMMs (logit-link). Models for all analyses were run in R 2.13.2 (R Development Core Team 2011) with the lme4 package (Bates et al. 2011). Final models were selected following AIC minimization criteria (Richards 2008).

6.3 Results

6.3.1 Patterns in local social stability and spatial distributions of males

Generally there was little difference in NJSI, DNM and DNF between sites and years. NJSI was higher in 2011 than in 2012 or 2013 but the difference was not significant; Site and Site:Year were also not retained in the best model ($\Delta AIC_{Random} = 0$). DNM tended to be shorter at the RAF than the PUB site across all three years but again there was no significant effect of Site, Year or Site:Year ($\Delta AIC_{Random} = 0$). DNF was significantly greater at the RAF site than the PUB site all three years ($\Delta AIC_{Site} = 0$; $\Delta AIC_{Random} = 3.12$). Within study sites, there was a significant effect of Year at the PUB site; with greater DNF in 2011 compared to 2012/2013 (PUB $\Delta AIC_{Year} = 0$; $\Delta AIC_{Random} = 2.64$). There was no significant effect of Year at the RAF site (RAF $\Delta AIC_{Random} = 0$).

6.3.2 Effect of stochastic tidal event

DNM did not differ pre and post-tidal event at either site ($\Delta AIC_{Random} = 0$; Figure 6.2a). Individuals' DNF pre-tidal event at the RAF site was on average 10.1 m ±1.04 SE, and 11.4 m

±1.02 SE at the PUB site. At both sites, DNF significantly increased after the tidal event to 21.6 m ±3.65 SE at the RAF site, and 23.1 ±4.48 SE at the PUB site (RAF ΔAIC_{Tidal} = 0; ΔAIC_{Random} = 17.3; PUB ΔAIC_{Tidal} = 0; ΔAIC_{Random}=18.09; Figure 6.2b). Individuals' NJSI decreased at the RAF from an average of 0.6 ±0.025 SE before the tide to 0.3 ±0.027 SE after the tidal event (RAF ΔAIC_{Tidal} = 0; ΔAIC_{Random} 25.09, Figure 6.2c). The mean value of NJSI at the PUB site was lower post-tidal event but the difference was not significant (PUB ΔAIC_{Random} = 0, Figure 6.2c).

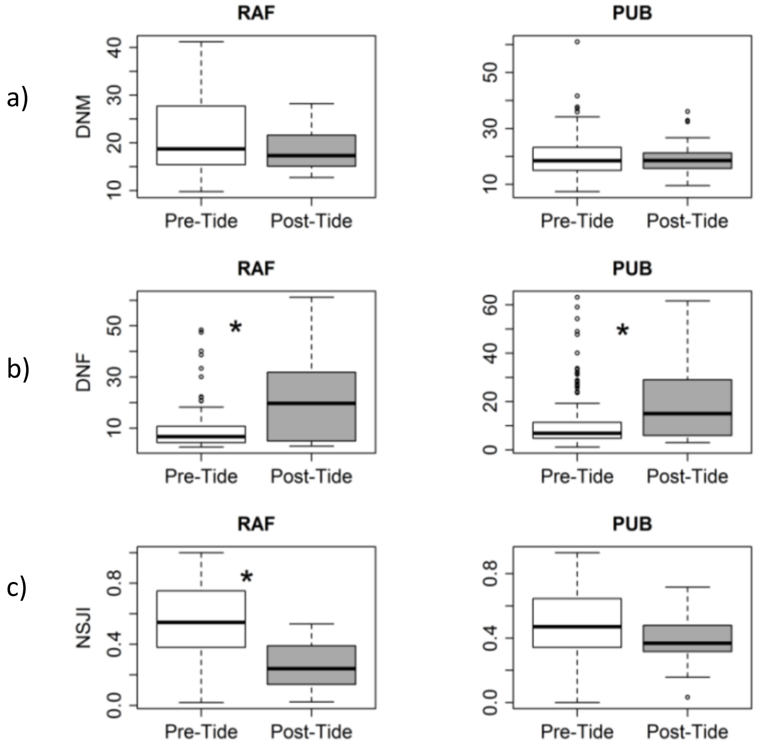


Figure 6.2: The differences in (a) mean daily distance (m) to nearest male (DNM); (b) distance (m) to nearest female (DNF); and (c) neighbour similarity (NJSI, 0 = unstable, 1 = stable) at the RAF and PUB site pre and post tidal event in 2011 (Day of year 330). Significant differences are denoted by an *.

6.3.3 Prediction of individual rates of aggression

NJSI, DNM and DNF were all retained in the best models for 2011, 2012 and 2013; DayEloN and SITE were additionally retained as predictive parameters and SITE was an interaction term in 2012 and 2013 (Table 6.1). TDEV was retained as a fixed and interactive effect in 2011.

NJSI had a negative effect on rates of aggression across all three years; however in 2012 and 2013 the effect was only apparent at the RAF site (Table 6.2; Figure 6.3a). DNM had a negative effect on aggression, and males in areas of closer male proximity (higher density) had higher rates of aggression per day (Table 6.2, Figure 6.3b). The effect was slightly lower at the PUB site compared to the RAF site in 2012 and 2013, but there was no effect of SITE in 2011. DNF generally had the weakest relationship with rates of aggression and the directionality of the effect varied across study sites and years. In the 2011 model at both sites, and in the 2012 model at the PUB site, DNF had a positive effect on aggression (Table 6.2, Figure 6.3c). In contrast, at the RAF site in 2012 and at both sites in 2013, DNF had a negative effect on aggression (Table 6.2, Figure 6.3c). Finally, DayEloN was retained in all three years' models (Table 6.1); however, the relationship between DayEloN and aggression was only significantly positive in 2013 at the RAF site and the relationship was significantly negative at the PUB site in 2012 (Table 6.2; Figure 6.3d). In all years, the effect size of DayEloN was relatively small compared to other parameters (Table 6.2).

The effect of the tidal event in 2011 on the rates of aggression was retained in the final model but was not significant (Table 6.2). TDEV was also retained as an interaction term with DayEloN and DNM. Prior to the tidal event, DNM shared a negative relationship with aggression, but this relationship was lost post-tidal event (Table 6.2; Figure 6.3b). In 2011, DayEloN had no effect on aggression prior to the tidal event; but following the event, DayEloN was found to share a negative relationship with rates of aggression (Table 6.2; Figure 6.3d).

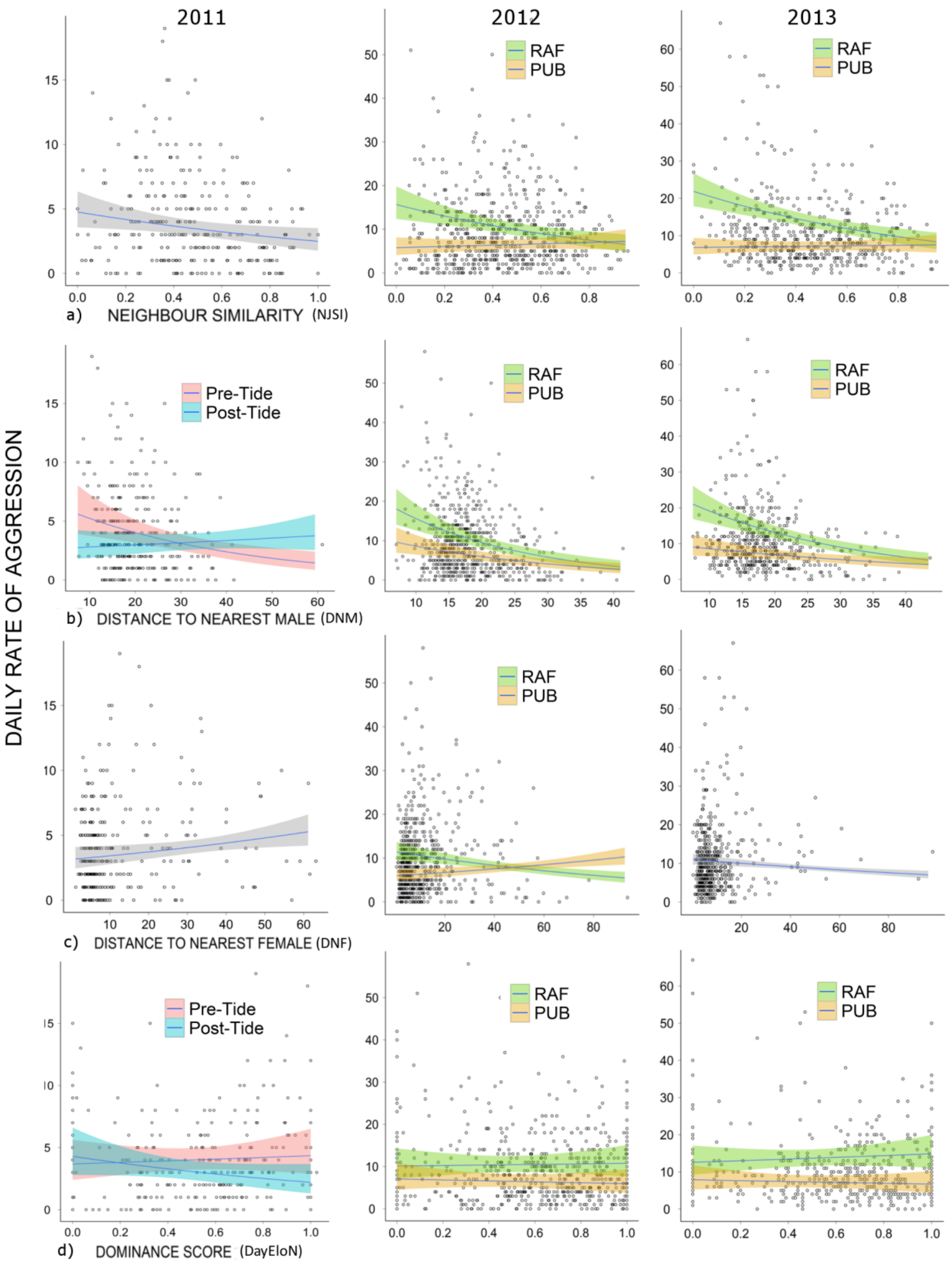


Figure 6.3: The effects of (a) NJSI (0 = unstable, 1 = stable); (b) DNM (m); (c) DNF (m); and (d) DayEloN (Elo dominance score) in 2011, 2012 and 2013 on an individual males' frequency of AIs daily. If there was an interaction effect of the tidal event, separate responses are differentiated as pre-tidal event (Pink) and post-tidal (Blue). Similarly, if SITE interacted the responses are differentiated as RAF (green) and PUB (orange). Shaded area is 95% CI.

Table 6.1: Retained GLMMs for predicting individual male DAI (daily rate of aggression), 2011-2013.

YEAR	AICc	ΔAIC	n_{samples}	RanEf: n_{MID}	RanEf: n_{OBSR}	Weight
2011						
DAI ~ TDEV + NJSI + DNF + DNM + ELO + ELO:TDEV + DNM: TDEV + (1| MID)	701.78	0	277	48	--	0.086
DAI ~ TDEV + NJSI + DNF + DNM + ELO + ELO: TDEV + (1|MID)	703.58	1.801	277	48	--	0.035
DAI ~ TDEV + NJSI + DNF + DNM + DNM: TDEV + (1|MID)	706.659	4.881	277	48	--	0.007
2012						
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNF:SITE + DNM:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	2635.12	0	634	75	2	0.356
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNF:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	2636.16	1.051	634	75	2	0.210
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + DNM:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	2636.31	1.195	634	75	2	0.196
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	2637.88	2.769	634	75	2	0.089
2013						
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNM:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1551.58	0	504	82	2	0.258
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + DNF:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1553.42	1.0301	504	82	2	0.154
DAI ~ NJSI + DNF + DNM + SITE + DNF:SITE + DNM:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1554.05	1.1904	504	82	2	0.143
DAI ~ ELO + NJSI + DNF + DNM + SITE + ELO:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1554.08	1.5884	504	82	2	0.117
DAI ~ NJSI + DNF + DNM + SITE + DNM:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1554.21	2.5983	504	82	2	0.070
DAI ~ ELO + NJSI + DNF + DNM + SITE + DNF:SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1556.59	3.1691	504	82	2	0.053
DAI ~ NJSI + DNF + DNM + SITE + NJSI:SITE + (1| MID) + (1|OBSR)	1556.67	4.5509	504	82	2	0.027

†ELO = DayEloN dominance score; NJSI = neighbour similarity; DNF = distance to nearest female (m); DNM = distance to nearest male (m); TDEV = Tidal event 2011. Random effects (RanEf): OBSR = observer (primary or secondary) and MID = male ID. All continuous predictor variables are daily averages.

Table 6.2: Coefficient estimates for the retained fixed effects in the best models across years for predicting individuals' daily rates of aggression (ΔAIC = 0; Table 6.1). All predictor variables are averages per day.

YEAR		Coefficient Estimate	Standard Error	*P*-value
2011	*Intercept:PRE TIDE*	2.021	0.159	<0.0001
	Intercept:POST TIDE	1.536	0.354	0.1700
	NJSI	-0.649	0.179	0.0003
	DNF	0.008	0.003	0.0030
	ELO: PRE TIDE	0.167	0.128	0.1940
	ELO:POST TIDE	-0.668	0.264	0.0100
	DNM:PRE TIDE	-0.026	0.005	<0.0001
	DNM:POST TIDE	0.006	0.015	0.6960
2012	*Intercept:RAF*	3.694	0.203	<0.0001
	Intercept:PUB	2.453	0.198	<0.0001
	ELO:RAF	0.061	0.074	0.4105
	ELO:PUB	-0.170	0.078	0.0302
	NJSI:RAF	-0.922	0.117	<0.0001
	NJSI:PUB	0.239	0.141	0.0850
	DNF:PUB	0.006	0.003	0.0300
	DNF:RAF	-0.007	0.002	<0.0001
	DNM:PUB	-0.037	0.005	<0.0001
	DNM:RAF	-0.493	0.005	<0.0001
2013	*Intercept:RAF*	3.694	0.154	<0.0001
	Intercept:PUB	2.393	0.194	<0.0001
	DNF	-0.004	0.002	0.0040
	ELO:RAF	0.167	0.081	0.0390
	ELO:PUB	-0.159	0.100	0.1120
	NJSI:RAF	-1.013	0.122	<0.0001
	NJSI:PUB	0.105	0.141	0.4560
	DNM:RAF	-0.037	0.006	<0.0001
	DNM:PUB	-0.022	0.004	<0.0001

† ELO = DayEloN dominance score; NJSI = neighbour similarity; DNF = distance to nearest female (m); DNM = distance to nearest male (m); Pre Tide = DOY < 330; Post Tide = DOY ≥ 330.

6.3.4 Prediction of individual daily contact aggression

NJSI and DNM were retained in the best models predicting the probability of a Contact AI for all three years (Table 6.3, Figure 6.4a-b). The probability of a Contact AI was reduced by increasing NJSI in all years at the RAF site (Table 6.4, Figure 6.4a), but in 2012 the relationship at the PUB site was lost (Table 6.4; Figure 6.4a). Smaller distances between males (DNM) resulted in greater probabilities of Contact AIs in all three years (Table 6.3), and at both sites equally (Table 6.4, Figure 6.4b). DayEloN was only retained in the 2011 model but its effect on the probability of escalation was not significant (Table 6.4). Before the tidal event, dominant males had a tendency to have relatively higher probabilities of Contact AIs and after the tidal event they tended to have lower probabilities (Table 6.4). DNF was only retained in the best model in 2012 (Table 6.3). At the RAF site, closer proximity to females increased probabilities of Contact AIs (Table 6.4); the relationship at the PUB site was not significant (Table 6.4).

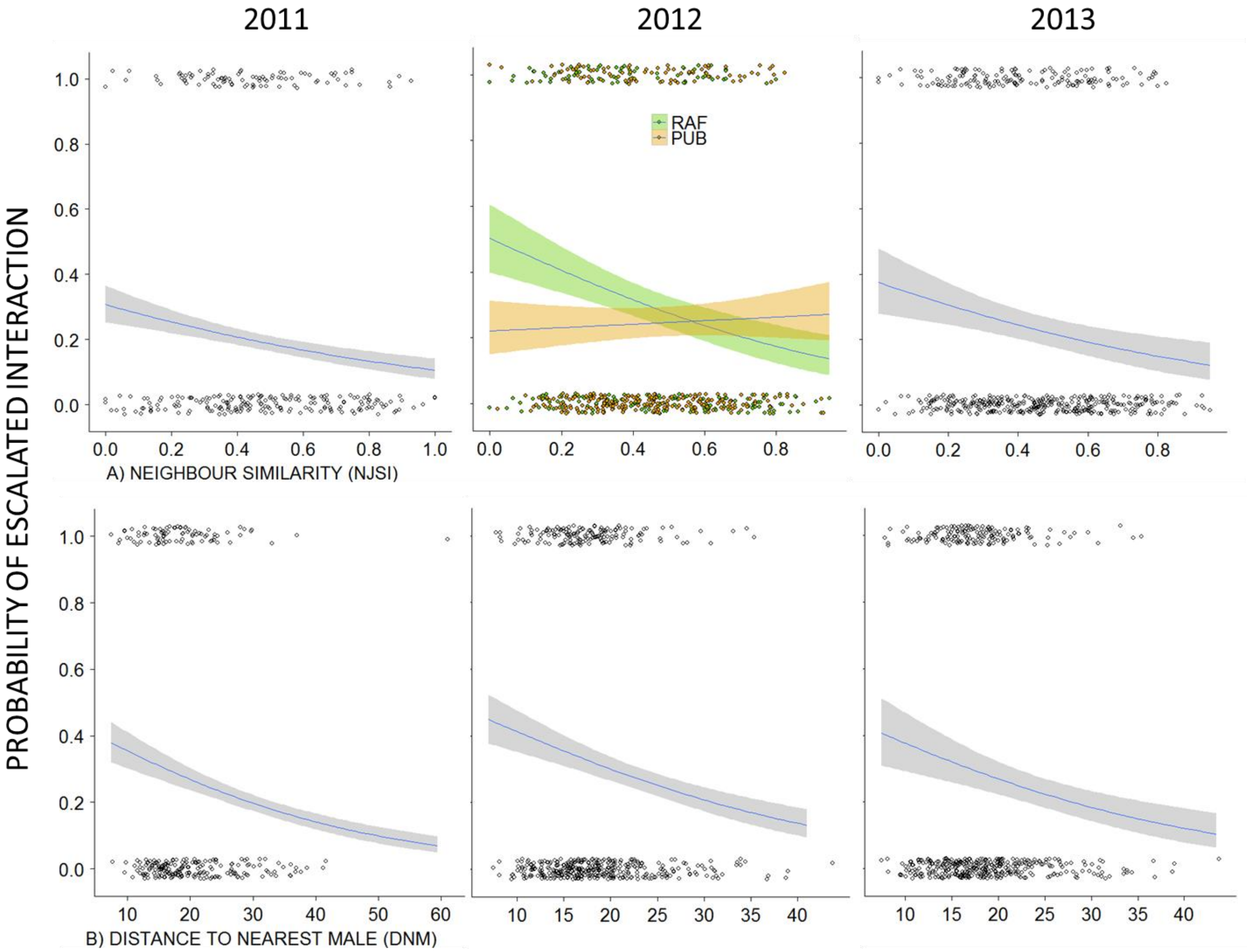


Figure 6.4: The effects of (a) NJSI (0 = unstable, 1 = stable) and (b) DNM (m) in 2011, 2012 and 2013 on the probability of a male engaging in a contact AI on a given day. When SITE was retained as an interaction term; response of RAF (green) and PUB (yellow) are separate. Shaded area is 95% CI. Points represent jittered raw data.

Table 6.3: Retained GLMMs for predicting the probability of a contact AI per day in 2011-2013.

YEAR	AICc	ΔAIC	n_{samples}	RanEf: n_{MID}	RanEf: n_{OBSR}	Weight
2011						
PF ~ ELO + NJSI + DNM + ELO: TDEV + (1|ID)	343.143	0	277	48	--	0.030
PF ~ ELO + NJSI + ELO: TDEV + (1|ID)	345.649	2.506	277	48	--	0.009
PF ~ NJSI + DNM + (1|ID)	345.687	2.545	277	48	--	0.008
PDF ~ DNM + (1|ID)	345.989	2.847	277	48	--	0.007
PF ~ NJSI + DNF + (1|ID)	347.295	4.153	277	48	--	0.004
PF ~ NJSI + (1|ID)	348.282	5.140	277	48	--	0.002
PF ~ 1 + (1|ID)	348.812	5.670	277	48	--	0.002
2012						
PF ~ NJSI + DNF + DNM + SITE + NJSI:SITE + DNF:SITE + (1|ID) + (1|OBSR)	799.689	0	634	75	2	0.195
PF ~ NJSI + DNF + DNM + SITE + DNF:SITE + (1|ID) + (1|OBSR)	803.215	3.526	634	75	2	0.033
PF ~ NJSI + DNF + DNM + SITE + NJSI:SITE + (1|ID) + (1|OBSR)	803.579	3.889	634	75	2	0.028
PF ~ DNM + (1|ID) + (1|OBSR)	802.286	3.086	634	75	2	0.027
PF ~ NJSI + DNF + SITE + NJSI:SITE + DNF:SITE + (1|ID) + (1|OBSR)	803.978	4.779	634	75	2	0.017
2013						
PF ~ NJSI + DNM + (1|ID) + (1|OBSR)	606.557	0	504	82	2	0.124
PF ~ NJSI + DNF + SITE + NJSI:SITE + (1|ID) + (1|OBSR)	610.790	4.235	504	82	2	0.015
PF ~ NJSI + (1|ID) + (1|OBSR)	611.360	4.810	504	82	2	0.011

† PF = Daily probability of escalating to a fight/contact AI. ELO = DayEloN dominance score; NJSI = neighbour similarity; DNF = distance to nearest female (m); DNM = distance to nearest male (m); TDEV = Tidal event 2011 only. Random effects (RanEf): OBSR = observer (primary or secondary) and MID = male ID.

Table 6.4: Coefficient estimates for the retained fixed effects in the best models across years for predicting the probability of an individual engaging in an escalated interaction on a given day (ΔAIC = 0; Table 6.3). All continuous predictor variables are averages per day.

YEAR		Coefficient Estimate	Standard Error	*P*-value
2011	*Intercept*	0.499	0.566	0.377
	NJSI	-1.423	0.632	0.024
	DNM	-0.042	0.021	0.039
	ELO:PRE TIDE	0.643	0.454	0.156
	ELO:POST TIDE	-0.698	0.636	0.278
2012	*Intercept:RAF*	1.629	0.628	0.009
	Intercept:PUB	-0.247	0.584	0.001
	DNM	-0.051	0.019	0.008
	NJSI:RAF	-2.063	0.724	0.004
	NJSI:PUB	0.304	0.704	0.666
	DNF:RAF	-0.035	0.012	0.005
	DNF:PUB	0.013	0.015	0.394
2013	*Intercept*	0.746	0.536	0.164
	NJSI	-1.615	0.523	0.002
	DNM	-0.051	0.020	0.010

† ELO= ELO_3Y dominance score; NJSI = neighbour similarity; DNF = distance to nearest female (m); DNM = distance to nearest male (m); Pre Tide = DOY < 330; Post Tide = DOY ≥ 330 in 2011 only.

6.4 Discussion

The results of this chapter demonstrate that the variation in aggression between individual male grey seals is associated with the local stability of neighbour identity, competitor proximity and resource (female) proximity, and not individual characteristics such as dominance rank. Neighbour stability had the strongest negative relationship with the frequency of aggression and the probability of escalated aggression. There was some temporal and spatial variability for this relationship, as demonstrated by the observed lack of NJSI effect at the PUB site in 2012 and

2013, which suggests that the importance of maintaining local neighbour similarity through draws or conflict reduction might be dependent on local conditions. The results suggest dominance rank did not predict individual frequency or probability of escalated aggression during typical breeding seasons, but after a stochastic tidal surge caused redistribution of seals and disruption of local social stability, the more dominant males had lower rates of aggression than males with more subordinate ranks.

6.4.1 Dominance and aggression

Although previous work has found that dominant males at other breeding colonies, such as North Rona, benefited in the form of reduced rates of aggression (Twiss 1991); the results of this chapter suggested that dominance was not significantly associated with reduced rates of conflict for males throughout the general breeding season at the Donna Nook colony. The contradictory results could be the product of different sampling windows: Twiss (1991) calculated dominance score as a measure across an entire breeding season while the Elo approach used in my analysis (Neumann et al. 2011) allows for sequential updates to dominance scores. Calculating a dominance score for the entire season compares males who might not have been present simultaneously and also assumes that a male's rank is unchanging throughout the season. This controls for the natural variability from the system, and thus revealed the observed overarching trends; but might not be predictive or reflect the importance of particular drivers of conflict reduction across contexts. These results highlight the need to revisit previously studied systems and to incorporate new methodologies, such as Elo ranking and local social stability measures, when attempting to discern the drivers of the variability in individual rates of aggression in natural varying contexts.

6.4.2 Neighbour stability

Instead of dominance score showing a strong correlation to rates or intensity of aggression, there was a strong association between increasing local social stability of an individuals' neighbours and lower rates and intensity of aggression at the daily temporal scale. Dominance scores reflect intrinsic characteristics of an individual and quantify his resource holding potential, or probability of winning an aggressive interaction (Drews 1993). However, for male grey seals, it has been suggested that males adopt a conflict strategy where 'not losing' a position near females is more important than 'winning' in terms of securing mating success (Anderson et al. 1975, Anderson and Fedak 1985, Twiss 1991). Similarly, length of stay, not dominance, has been found as an important driver of mating success in other pinniped breeding systems (Pörschmann et al. 2010). As such, individuals' relative dominance scores, as measures of ability to 'win', might not be driving opponent's decisions to engage in conflict if males are more concerned with 'not losing'. In regards to the apparent benefit of social stability in reducing aggression, in other territorial systems losing to a stranger often results in expulsion from a territory, but a loss to a neighbour might only result in a small loss of territory or a few resources (Husak and Fox 2003a, Husak and Fox 2003b, Bee 2003, Lachish & Goldizen 2004, Booksmythe et al. 2010, Cross et al. 2013). Male grey seals might therefore be making decisions to engage more frequently when the local social context is not stable as a means of preventing loss of a position, and conversely, when the local social neighbourhood is stable, individuals benefit from not having to defend their positions to intruders, but only maintain the boundaries with their neighbours. This could explain the previous link between dominance and lower aggression (Twiss 1991) in that dominant males on North Rona were often described as maintaining positions in the core of the colony where they are buffered from exposure to ‘roaming’ transient males (Anderson et al. 1975, Boness and James 1979, Twiss 1991, Twiss et al. 1994). Overall, the evidence suggests that the correlation of local social stability and low individual daily rates of aggression reflects the potential for greater mating success through conservation of energy and prolonged tenure found in this and other closely-related systems (Twiss 1991, Twiss et al. 1994, Lidgard et al. 2005, Twiss et al. 2006, Pörschmann et al. 2010).

While it was not explicitly tested in this study, neighbour consistency is a key requirement for the dear enemy phenomenon (DEP; Jaeger 1981, Getty 1987) and thus, the potential for this DEP in this system merits some consideration. In closely-related species, recent evidence suggests that male northern elephant seals are capable of discriminating between individuals (Casey et al. 2013). While, to my knowledge there have not been any previous rigorous attempts to investigate individual recognition capability in adult male grey seals, there is some evidence of socially-mediated behaviours for this species. Previous studies have shown that female grey seals exhibit some level of sociality not explained by spatial metrics alone (Pomeroy et al. 2000, Insley et al. 2003, Pomeroy et al. 2005 Ruddell et al. 2007, Robinson et al. 2015) and also have the capacity to identify their pups (McCulloch et al. 1999, McCulloch and Boness 2000, Insley et al. 2003). Individual recognition has also been demonstrated between weaned pups of both sexes, and pups which had previous exposure to each other in trials demonstrated reduced rates of aggression (Robinson et al. 2015). At an interseasonal scale, male grey seals exhibit some degree of site fidelity (approximately 30-40% return across years; Twiss et al. 1994), and many return to the same spatial positions on the colony across years (Twiss et al. 1994). Furthermore, in Chapter 5, it was demonstrated that the duration of escalated aggressive interactions were shorter for previously known opponents and longer for Non-Contact interactions, likely due to a shift from information gathering to nagging after prior interactions

(Stamps and Krishnan 2001). This provides some evidence that males who have previous experience with each other, though not necessarily neighbouring males, are adjusting their behaviours in a fashion similar to what would be expected under DEP. At this time it cannot be ascertained if DEP, via local social stability, is driving the observed reduction in rates and intensity of conflict for individuals, but the evidence suggests that there could be a component of individual or neighbour recognition in play. Very little is known about how DEP might emerge in wild systems which do not assort into clearly-defined territories. As controlled, paired-trials are not feasible for adult grey seals, a more comprehensive examination of the role of local social stability, and DEP would benefit by coupling neighbour similarity metrics such as NJSI with playback methods which test for individual recognition (Casey et al. 2013), or hormonal analysis which can test for physiological indicators of recognition (Robinson et al. 2015).

6.4.3 Fine-scale determinants of aggression: environment

The main objective of this study was to examine the fine-scale factors contributing to the variability in male aggression, and examining individual rates of aggression in a wild species across three discrete breeding seasons allowed for the incorporation of natural variation in the spatial and environmental variables in the models. In the present study, the overall patterns of male aggression appeared to be conserved across years; however some factors still varied in their importance as a correlate or in the direction of their effect between years. For example, at the RAF site in 2012-2013, relative DNF (not absolute proximity) increased rates of aggression, suggesting that during these years the benefits of maintaining a proximity as close as possible to a female was more important than absolute proximity and might explain why subordinates would compete to be on the outskirts of the colony even though it would be costly to do so. The effects of neighbour stability on rates of aggression also differed across years with particular differences noted for 2011: a year which was atypically warmer and drier than usual prior to the atypical tidal event. Due to only three seasons of data being available, additional years of data would be needed for any firm conclusions to be drawn between the observed patterns and the broad weather variables, but the literature on the effects of thermal constraints can provide some potential links to the findings of this chapter.

Thermal stress, and the associated physiological responses such as a decrease in water economy and increased corticosterone levels, has been suggested as a driver for selecting against high levels of aggression in warm environments for animals such the mole-rat *Spalax ehrenbergi* (Ganem and Nevo 1996). Although grey seals breed in the autumn in temperate climates, they share a direct relationship between individual behaviours and weather patterns, and exhibit variation in behaviour patterns in relation to thermal stress (Twiss et al. 2000, Redman et al 2001, Twiss et al. 2002, Twiss et al. 2007). For example, female grey seals prefer breeding sites in close proximity to pools of water not only for the presumed function of thermoregulation, but also as a source of drinking water (Stewart et al. 2014). Twiss et al. (2007) found that in years with increased rainfall, the variation in mating success was greater between males due to females not traveling to gain access to pools for thermoregulation and thus facilitating greater monopolization of mating opportunities by the more dominant males. Studies of other pinniped species have also highlighted the role of air temperature and thermoregulatory processes on behaviours. For example, the location of aggressive behaviours was more likely in or near the water during high temperatures for California sea lions (Bohórquez-Herrera et al. 2014), male Galapagos sea lions congregate in shaded areas during periods of thermal stress (Wolf et al. 2005), and California sea lions have also shown behavioural plasticity in their response to temperatures dependent on the location of the colony and the ‘typical’ range of temperatures experienced (Bohórquez-Herrera et al. 2014). Weather effects are also likely coupled with the topography of the colony (Twiss 1991). In the present study, the wetter and colder years (2012-2013) at the PUB site corresponded with reduced female-male distances (**Chapter 3**), and there was a corresponding loss of the effect of NJSI on aggression at this location during those years.

The links between topography, weather, and female distributions noted above suggests that the observed differences in the importance of NJSI across site and years could be the result of changes in relative resource availability at this site as driven by individuals' response to weather parameters. This supports the findings of other studies in which mechanisms driving conflict reduction were context-dependent (Graham and Herberholz 2009, Tierney et al. 2013, Monclús et al. 2014); specifically, for male pupfish (*Cyprinodon variegatus*) the presence of a female in the test arena reduced the effect of DEP (Leiser 2003). Therefore, the findings of this Chapter have shown that analyses at fine temporal and spatial scales can reveal the relative importance of mechanisms of conflict reduction under differing contexts of resource availability. Similar methods can be applied to systems in which previous analyses have only integrated data at large scales.

6.4.4 Context-dependent effect of dominance on rates of aggression

An extreme tidal event in 2011 allowed for the unique opportunity to examine how the effects of the variables influencing grey seal behaviour under undisturbed conditions changed in the presence of stochastic, natural disturbances. Studies have indicated that when features of the environment are highly variable, inter-individual differences can be masked or their effects diminished (Killen et al. 2013). At Donna Nook, in comparison to colonies such as North Rona, individuals are exposed to greater environmental variability in the form of daily tidal fluctuations due to open access to the sea. Individuals are also exposed to relatively greater anthropogenic presence due to the colony's position on the mainland coast. While dominance rank was found to be an important driver of conflict reduction at North Rona (accepting the different scales of analysis, Twiss 1991), the generally variable environment at Donna Nook could be masking or increasing the costs of relying on dominance under normal conditions, and thus be selecting for mechanisms such as the behavioural maintenance of local social stability instead. Following the disturbance effect of the tidal event in 2011, measures of individuals' average local social stability were greatly reduced and males appeared to be relying more strongly on their individual dominance ranks as a mechanism of conflict reduction, even though under 'normal' conditions this would presumably have a greater cost. This could again be evidence of the strong selection for 'not losing' in this system (Anderson and Fedak 1985).

6.4.5 Conclusions

This study has identified the importance of local social stability in explaining inter-individual variation in aggression for polygynous pinnipeds and provides evidence for the importance of both average levels of environmental variability as well as stochastic disturbance events on the selection of conflict reduction mechanisms. Further work which links these changes to direct measures of costs will be vital for predicting the differences in responses between individuals, colonies or populations to potential stressors such as anthropogenic presence or climate change.

Chapter 7

Within-season timing of reproductive effort suggests alternative mating tactics for male grey seals

7.1 Introduction

7.1.1 Male alternative mating strategies and tactics

Emlen and Oring (1977) suggested that mating systems arise as a function of the spatial and temporal distribution of receptive females and the ability of males to monopolize mating opportunities. In polygynous mating systems, due to the increased conflict and competition for access to females, species are often sexually dimorphic (Bartholomew 1970) and individuals have exaggerated characteristics such as size (Carlini et al. 2006, **Chapter 5**), mass (Crocker et al. 2012), ornamentation (Brodsky 1988), behavioural displays (Sanvito et al. 2006, 2007a, 2007b, **Chapter 4**), or social dominance (McElligott et al. 2001, **Chapter 6**) which can enhance individual fitness. While the above characteristics represent the general trends for males in polygynous systems, there is also variation in individual mating strategies which can reflect the maximization of fitness across specific life-history stages or present conditions (Gross 1996, Shuster and Wade 2003, van Parijs et al. 2003, Lifjeld et al. 2011, Lidgard et al. 2012). In the literature, the term “mating strategy” is often used interchangeably with alternative mating tactic (Lidgard et al. 2004, 2005, Carlini et al. 2006, Pörschmann et al. 2010) and alternative mating strategy (Gemmell et al. 2001).

In polygynous mating systems, two of the main mating strategies males adopt are “Stay” or “Roam”, which represent female-defence and scramble competition respectively (Emlen and Oring 1977, Thornhill and Alcock 1983, Sandell and Liberg 1992). The “Stay” strategy consists of males monopolizing access to receptive females for prolonged periods of time, and this strategy is often associated with the greatest mating success and extreme phenotypic traits (Emlen and Oring 1977). Due to the energetic and physical requirements of this strategy, these individuals are typically larger, older, and more dominant (Lidgard et al. 2012). The effectiveness of this strategy is largely constrained by resource distribution in that patchy environments facilitate the monopolization of clusters of females (Anderson et al.

1975, Anderson and Fedak 1985, Twiss 1991, Sandell and Liberg 1992, Twiss et al. 1994, Arnould and Duck 1997, Apollonio et al. 2013). The most common alternative strategy, “Roam”, consists of peripheral males which do not maintain direct access to females, but gain mating opportunities through opportunistic copulations, intercepting females, or by timing their reproductive effort to periods outside of the time when the most females in the local population are in oestrus (Thornhill and Alcock 1983, Sandell and Liberg 1992, Lidgard et al. 2004). Roaming can be a life-history tactic, wherein young, smaller or novice males are the primary adopters, but it can also persist as an alternative, adult strategy where the mean fitness each individual achieves at equilibrium does not differ from other strategies in the population (Maynard-Smith 1982, Gross 1996, Shuster and Wade 2003, van Parijs et al. 2003, Lidgard et al. 2004, Lidgard et al. 2012). While these two mating strategy classifications provide explanations for the variation in behavioural phenotypes for polygynous males, recent studies have begun to suggest that this is not necessarily the finest level of distinction for mating strategies in some systems (Lidgard et al. 2005, Mason et al. 2012).

7.1.2 Pinniped mating strategies

Many pinniped species exhibit moderate to extreme polygyny (Bartholomew 1970). For terrestrial breeding species, the males exhibit varying degrees of female monopolization either through territorial or harem defence, and also exhibit both the Roam and Stay strategies, with increasing ability to prolong territory or harem defence associated with increased mating success (Anderson and Fedak 1985, Twiss 1991, Arnould and Duck 1997, Gemmell et al. 2001, Lidgard et al. 2005, Carlini et al. 2006, Pörschmann et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Franco-Trecu et al. 2014). Less is known about the mating systems of pinnipeds with primarily aquatic mating, as observations in this environment are difficult to obtain, but again there is some evidence that males still attempt to monopolize access to females by holding underwater territories through vocalizations (van Parijs et al. 2003).

For grey seals, male mating strategies are typically broadly classified as either Tenured (present for ≥ 2 days and partaking in ≥10 AIs) or Transient (present for < 2 days; Boness and James 1979, Boness 1984, Anderson and Fedak 1985), based on whether or not a male adopted a resource defence or scramble strategy. While admittedly the two day criterion has been critiqued as arbitrary (Twiss 1991), evidence has shown that males adopting the Tenured mating strategy have the greatest relative mating success (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2004). Furthermore, recent work has suggested that the Transient strategy is divided into multiple forms or behavioural phenotypes such as sneaking copulations, copulating with neighbouring males' females, failed attempts at Tenured strategies, and aquatic mating due to a range of underlying causes (Worthington-Wilmer et al. 1999, Lidgard et al. 2003, 2004, 2005, 2012). Lidgard et al. (2012) further suggested that mating success for male grey seals is not responsive to environmental variation, and that certain alternate mating strategies for male grey seals might be linked with life-history stages until a threshold size is met (Lidgard et al. 2012).

While multiple strategies have been identified within the Transient paradigm for grey seals (Lidgard et al. 2003, Lidgard et al. 2004), until now it has been assumed that the variation of mating success within the Tenured class of males is attributed to differences in length of stay on the colony (Twiss 1991, Twiss et al. 1994, Lidgard et al. 2005, Lidgard et al. 2012). However, when observing the development of a grey seal colony from the start of a breeding season, it is apparent that some males arrive in a particular geographic location, or on the colony in general, at different points in the breeding season (pers. obs). Also, the quantification of variation in male energetic expenditure, such as mass loss over time within a breeding season, has proven difficult for pinnipeds. Predictions of mass change are typically based on early capture and late capture (Crocker et al. 2012), or using 3-4 captures throughout the season (Twiss 1991). This provides a total energetic budget but very little information on the subtleties of the trajectory of that energy loss over time. For example, it has been demonstrated that dominant elephant seal males that are able to maintain tenure for the longest time were found to have the greatest energy expenditure, and were able to derive that energy almost entirely from blubber fats and not lean mass (Crocker et al. 2012). Crocker et al.'s (2012) study further provides rationale for why mass is selected for, even if length if associated with contest outcome success (**Chapter 5**; Carlini et al. 2006), but it does not address variation in energy expenditure across time or inter-individual differences in mass loss.

In other polygynous systems, intra-seasonal variation in male reproductive success has been linked to timing of reproductive effort (RE) within a breeding season (Smith and Moore 2005, Robinet et al. 2008, Mason et al. 2012). For example, for ungulate species such as the alpine chamois (*Rupicapra rupicapra*), different age-classes of males differ in their timing of RE, such that younger males exhibit greater RE later in the season when competition with dominant, older males is reduced (Mason et al. 2012). Similarly, the peak in RE for prime-aged male red deer coincides with female oestrus, while younger males peak later (Mysterud et al. 2008). In pinniped systems, work on Galapagos sea lion males found mating success increased with attendance, but found males which spent more time on the colony in pre- and peak season had the greatest success (Meise et al. 2014). While the Meise et al. (2014) study is one of the first to consider mating success relative to timing of attendance on the colony for pinnipeds, they admittedly did not consider post-season success or variation in RE beyond a measure of attendance. Variation in intra-seasonal timing of RE, as a potential alternate male strategy or tactic which explicitly accounts for inter-individual differences in timing and not just longer stays, is a topic still requiring much attention, and has not previously been investigated within the Tenured strategy for pinnipeds.

7.1.3 Aims and Objectives

The purpose of this Chapter is to utilize modern dominance-score calculation techniques (**Chapter 6**) to test for strategies or tactics within the Tenured male classification based on the hypothesis that timing of RE influences mating success. As direct mass-loss estimates were not feasible at Donna Nook, dominance might be a suitable proxy for RE for grey seals. Dominance is strongly related to rates of mass loss in capital breeding pinnipeds under the assumption that more dominant males exert more energy in defending territories or females, or on reproductive activities while fasting (Twiss 1991, Crocker et al. 2012). Anderson and Fedak (1985) further proposed that larger males might be able to sustain a high level of reproductive activity for longer periods, while for smaller males, staying for the same time might require individuals to adjust their behavioural activities. Their suggestion posits that perhaps there is a decoupling of length of stay and behaviours not yet assessed in these capital breeding systems.

As mentioned in **Chapter 6**, Elo scores for dominance can be calculated in sequence. This method ‘tracks’ a male’s rise and fall throughout a season and between seasons at a much finer scale and can be used to quantify how a male’s RE is expressed and changes throughout a breeding season. While initially, Elo calculations require approximately 10 interactions to provide accurate rankings (Neumann et al. 2011, **A6.1**), following this, temporal changes in dominance have been associated with biologically meaningful changes in individuals’ reproductive or behavioural output (Neumann et al. 2011, **A6.1**). As males engaged in an average of 4-12 AIs daily in 2011-2013, this would suggest that after 1-2 days, changes in dominance should reflect biological differences and are less likely to be stochastic or due to small sample sizes. Therefore,

Therefore changes in dominance within a breeding season, as captured by Elo provided the ability not only to assess how variations in timing or duration of RE, within two identical lengths of stay might reflect alternate mating strategies within the grey seal breeding system. Specifically, I hypothesized that the longevity of maintaining dominance status and/or the timing of an individual's peak in dominance will represent distinct categories of males within the Tenured classification. Some males will be able to maintain dominance for long periods and males that cannot achieve long durations of dominance will time their RE to non-peak oestrus periods, either before or after, to avoid conflict with more dominant males (Mysterud et al. 2008, Mason et al. 2012). To examine this, I investigated if males could be categorized based on their timing of dominance within a season and on the duration for which a male could maintain high dominance status. These categories of males were then assessed for differences in total mating success across and within years, as well as differences in peak dominance status within a season, phenotype (length), and the average local social stability and average rate of aggression during the period of high dominance within each season. This provided an examination of how factors contributing to conflict and conflict reduction examined previously in this thesis associate with individual differences in fitness. Finally, as a follow-up to Lidgard et al.'s (2012) study, I tested to see if any males adopting similar strategies between years exhibited consistent individual differences in their behaviours or fitness to start to examine if these categories represent fixed or flexible, mating strategies or tactics.

7.2 Methods

7.2.1 Dominance peak and duration

Elo scores were calculated in sequence for each male using the Elo_3Y method described in **Chapter 6.2.1**, and there is inter-individual variation in the patterns of dominance trajectories within and across seasons (Figure 7.1). To attempt to quantify this pattern, for each male I extracted his peak Elo score (EloPeak) and day of peak Elo, (PeakDay) per year as measures of individual quality and timing of RE. Then, to quantify the duration for which a male was able to maintain high reproductive effort, I used the entire range of dominance scores for each male per year, and generated cut-off values representing the upper 10%, 20%......90% of his range. For example, a male who's Elo scores ranged from 600 to 1200, would have a cut-off at 1140 to represent the top 10% of all his achieved scores. Due to potential gaps in sightings for individual males due to differing sampling methods across years, the duration of a male's dominance, DurDomX%¸ was calculated as the number of days in which the male was present in the study area, and where his Elo score exceeded his cut-off value. If a male exceeded the threshold-value, then lost ranking, then increased above the threshold again, his dominance run would be represented by two or more time periods. When this occurred, DurDomX% was the sum of all separate duration periods.

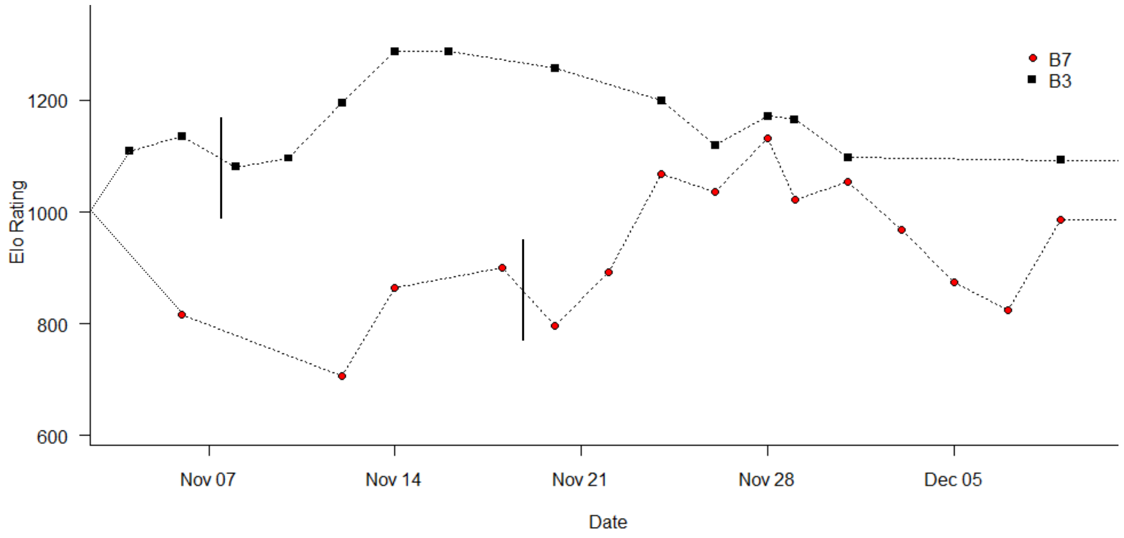


Figure 7.1: Examples of two males' dominance patterns across the 2011 breeding season; points represent the males' average Elo at the end of a given day. "B3" peaked in dominance around Nov 14, after which his score gradually declined; whereas "B7" started with a low Elo score, and then surged and peaked around Nov 28. Vertical lines represent the point where each individual had partaken in 9 AIs, as it has been suggested comparing relative rankings prior to this point should be done 'provisionally' (Neumann et al. 2011).

7.2.2 Determining percentile threshold for dominance duration

Threshold values could not be selected at extremely large percentiles (*e.g.*, 90% of the range) as this would encompass the entire time a male was present and not specifically provide information on the partitioning of RE; however, they needed to be sufficiently large so as to not represent only a single day (*e.g.*, 5% of the range). A goal of this study was to identify how the variation in mating success reflects the trade-offs between aggression and conservation of energy. Therefore, in order to select the percentile at which to create the threshold value, I compared a male's mating success per year (MS_TOT) to his total duration of dominance above the threshold value (DurDomX%) for the range of threshold percentiles previously generated (**7.2.1**). This was done by fitting a generalized linear mixed-effects model with Poisson error distribution using the {glmmADMB} package. To account for the high number of males that did not achieve any mating success (**Chapters 2 & 3**), a zero-inflation model parameter was also included from the glmmADMB package. Male ID was included as a random effect to account for pseudoreplication across years and for males with multiple peaks. A separate model was fitted for each threshold value from 10% to 50% and the model with the threshold which best explained the variance in mating success, and had the lowest AIC value, was selected. This process determined the threshold used subsequently; 50% was chosen (**7.3.1**).

7.2.3 Grouping males by their duration and timing of dominance

One way of partitioning data into groups is a classification tree, such as the one used by Franco-Trecu et al. (2014) to divide male South American fur seals, *Arctocephalus australis*, into groups based on their aggression, number of copulations, or length of tenure. This method uses one explanatory variable at a time and requires a response variable (e.g. in the Franco-Trecu et al. 2014 example, the response variable was male paternity). When partitioning data without response variables and across multiple predictor variables simultaneously, the K-means method, which aims to minimize the sum of squares from points to assigned centres, is often used (reviewed in Steinley 2006, R Core Team {stats} package). However, this method requires the user to specify how many divisions to apply to the data. There are multiple methods available for determining the number of divisions such as (1) visualizing the within-groups sum of squares across the number of clusters and manually assigning the position at which the plotted pattern ‘kinks’ or generates an elbow, (2) hierarchical clustering methods such as Ward’s method (Ward 1963), or (3) model-based, maximum-likelihood estimations (Fraley and Raftery 2002, Fraley and Raftery 2007). The {mclust} package, and *mclust* function in R (Fraley et al. 2014) is an example of this third method which selects the best number of clusters based on Bayesian Information Criterion, BIC, expectation and hierarchical clustering for parameterized Gaussian mixture models (Fraley et al. 2014). This method iteratively increases the number of clusters until BIC peaks and any further addition of clusters reduces BIC. It does so simultaneously across 10 model types (*e.g.,* ellipsoidal, equal volume and shape, or diagonal, varying volume and shape). Also, the *mclust* method combines the steps of determining the number of clusters and data partitioning thus eliminating the need for a secondary step. I selected the *mclust* method in combination with visual inspection of within-group sum of squares to determine the number of supported clusters based on: length of dominance (DurDom50%) and timing of dominance (PeakDay). This method resulted in each male being assigned a Cluster-ID (CLUSTER), based on the above two parameters.

7.2.4 Mating success across clusters

To determine the importance of clustering based on dominance duration and timing, relative to other predictors of mating success, I used a GLMM with male ID as a random effect and fitted a model to predict observed mating success (standardized by the maximum observed, Pörschmann et al. 2010). Fixed factors were CLUSTER, DOC, PeakRank, and uNJSI_DOM (see Table 7.1 for definitions of these parameters). Seasonal rates of aggression were a significant component of mating strategy classifications and predictions of male paternity for male South American fur seals (Franco-Trecu et al. 2014), but uDAI_DOM was not included for the present study due to its co-linearity with uNJSI_DOM (**Chapter 6**). This model was fitted first across all years combined to look for broad determinants of mating success, then fitted again with YEAR interacting with DOC and CLUSTER to examine if the effect of these variables on males' fitness differed under various contexts such as weather and seal distributions, as indicated by gross year effects (**Chapter 3**). The GLMMs were fitted with {glmmADMB}; error structures were set as negative-binomial error distribution (overdispersed Poisson) with zero-inflation again to account for the large proportion of males with no mating success. I also investigated differences in the total mating success across the population for each CLUSTER to determine if these resulted in equal total mating success, due to numbers adopting a particular strategy, as opposed to only assessing the average success per male. Finally, for males present across multiple breeding seasons, I examined the consistency in their strategies and mating success across years.

Table 7.1: Definitions of additional variables included in the mating success models, and in comparison across CLUSTERs.

Variable	Method or Reference	Abbreviation
Mean NJSI during DurDom50%	Chapter 6.2.#	uNJSI_DOM
Mean DAI during DurDom50%	Chapter 6.2.#	uDAI_DOM
Days seen on colony	Number of days mapped	DOC
Number of males with greater Elo on peak day	Maximum Rank	PeakRank
Percentage of days on colony above threshold	DurDom50% /DOC	PercDOC
Mating success during DurDom50%	#Cops while above threshold	MS_DOM
Total mating success whole season	Total number of cops	MS_TOT

7.3 Results

7.3.1 Threshold determination

Mating success had the strongest positive association with how long a male's dominance score was maintained in the upper 50% of his range (Table 7.2). This threshold was used in the cluster analyses to determine the duration of dominance, start date of dominance period, and the percentage of total DOC in which a male remained in the upper 50% of his range. Using the 50% threshold, males with a PercDOC of 100% accounted for 19.2% of all males (*n* = 46/239). DurDom ranged from 1-23days (Median = 3), and PeakDay ranged from DOY 301 to 346 (Median = 323).

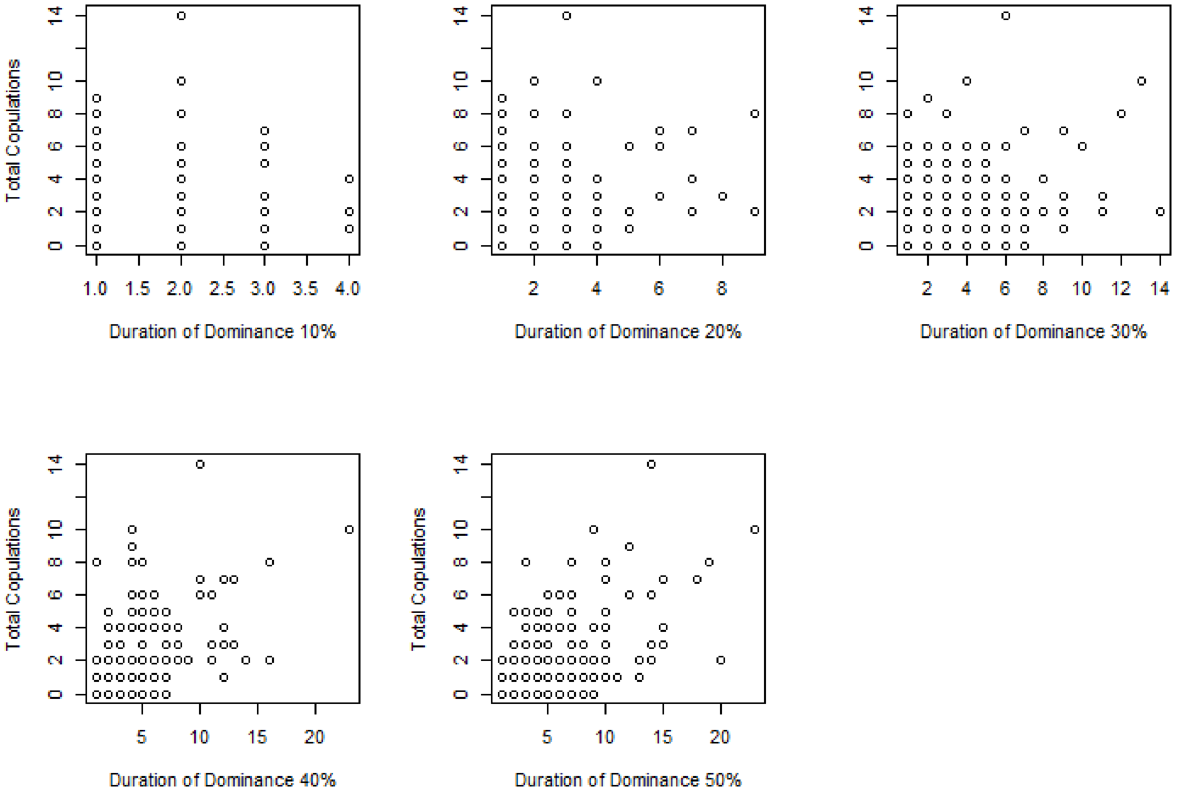


Figure 7.2: Relationship between number of copulations and duration of dominance, when duration is defined by 10-50% thresholds (Table 7.2)

Table 7.2: Results of GLMMs examining the relationship between DurDomX% and MS_TOT depending on different threshold values used to calculate DurDomX%. Best model was 50% (Richards 2008 criteria).

X	Est. DurDom	n	n_{males}	AIC$_c$	ΔAIC	P-value ∑DurDomX%
10%	0.002	239	177	850.0	60.6	n.s.
20%	0.093	239	177	845.9	56.5	0.024
30%	0.110	239	177	834.1	44.7	<0.0001
40%	0.095	239	177	818.5	29.1	<0.0001
50%	0.149	239	177	789.4	0	<0.0001

7.3.2 Clustering males by dominance timing and duration

The optimal model for determining the clusters of males for all years combined was a VVI (diagonal, varying volume and shape) model with three clusters (log.likelihood = -1507.857, n = 239, df = 14, BIC =- 3092.385; Figure 7.1, Table 7.3). The VVI model suggests that an unequal number of males were included in each of the clusters, and each cluster represented a different proportional spread of the data (Fraley and Raftery 2002). Clusters 1 and 3 were similarly characterized by males who are dominant for < 5 days; however, males in Cluster #1 peaked early in the season and males in Cluster #3 peaked late in the season (Figure 7.1, Table 7.3). Males in cluster #2 were characterized by midseason peaks in dominance and durations of dominance typically >5 days. The variation in PeakDay and DurDom50% is greatest for males in cluster #2 (Table 7.3). Males in cluster 3 were significantly shorter in MSL (ΔAIC = 0) and tended to have greater DAI (ΔAIC = 0, Table 7.3).

Table 7.3: Averages (±SE) for the DurDom50%, PeakDay, MSL, DAI and Rank on peak day for each of the three clusters determined by the Gaussian finite mixture model {mclust} and log-likelihood maximization. The breeding season typically runs from DOY 300-346.

Cluster	DurDom50%	PeakDay	MSL	DAI	Rank	MS_TOT	∑MS	n	% Total males
1	2.6 (0.2)	315.1 (0.7)	199.9 (1.1)	9.7 (0.7)	4.2 (0.4)	0.60 (0.1)	61	102	42.7%
2	8.8 (0.4)	327.3 (1.0)	203.5 (1.4)	10.2 (0.6)	2.6 (0.4)	3.1 (0.3)	271	89	37.2%
3	2.3 (0.1)	336.7 (0.7)	195.3 (2.5)	12.8 (1.5)	4.0 (0.6)	0.9 (0.2)	43	48	20.1%

∑MS = the total number of copulations observed by males in this category; % of Total males = cluster (n) / total males (n).

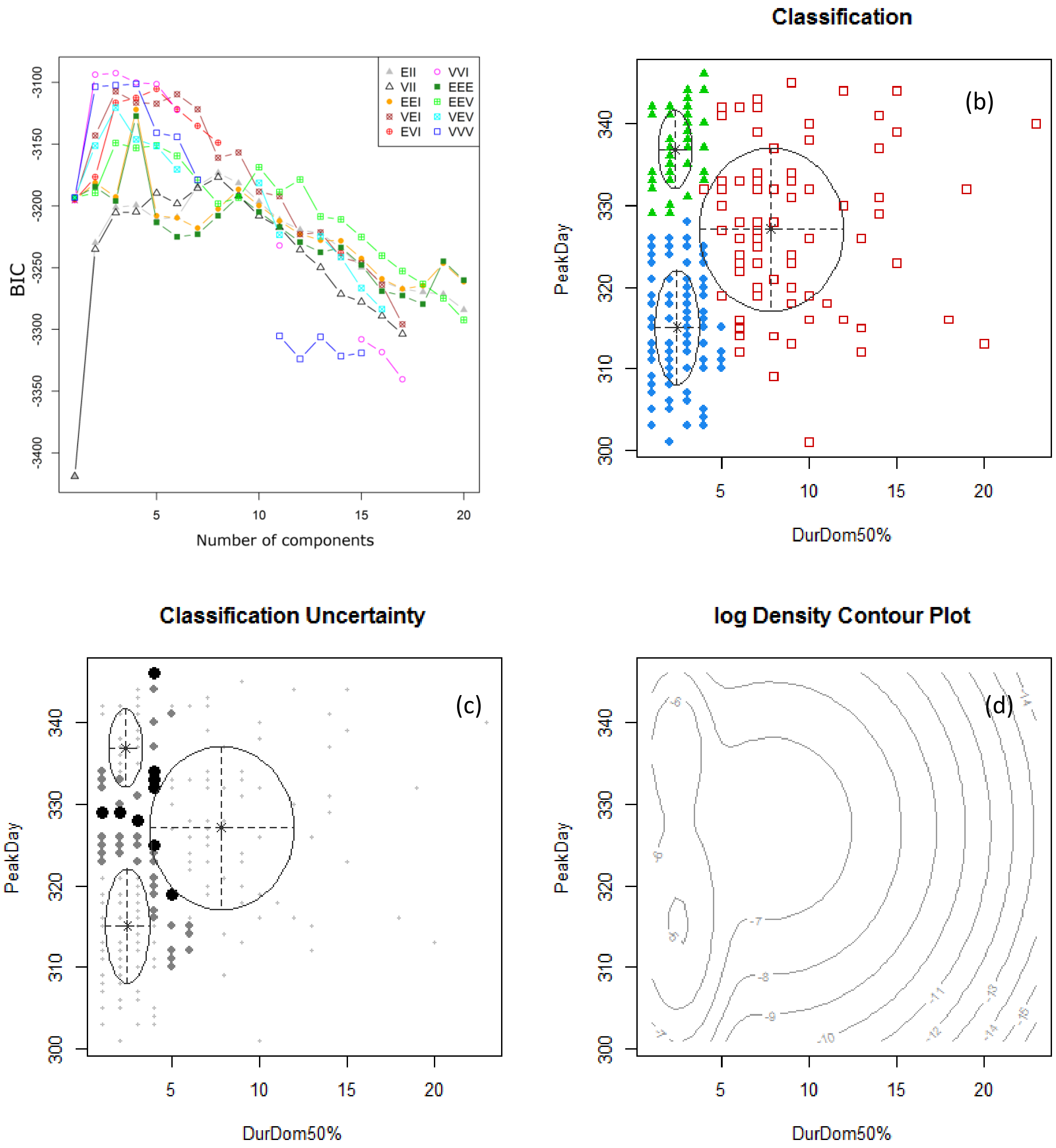


Figure 7.1 From top left clockwise: (a) BIC estimates compared to the number of components (clusters) for each of the 10 cluster-type models. The VVI model (pink circle) was selected as it had the greatest BIC of all the model types and achieved this at three clusters. (b) Classification clusters of males across two parameters of timing (PeakDay) and duration of dominance (DurDom50%) where blue is cluster 1, red is 2, and green is 3. (c). Uncertainty plot of cluster assignments. Data points that are larger and darker represent classifications with greater uncertainty. (d) Density contour plot depicts the density of data points assigned to each cluster classification (Fraley et al. 2014).

7.3.3 Does timing and duration of dominance predict individual mating success?

7.3.3.1 All years combined

The model that best predicted observed mating success across all years combined retained DOC, CLUSTER, and uNJSI_DOM (Table 7.4). CLUSTER and uNJSI_DOM were not included in the second and third best models respectively, but both of these models had a ΔAIC value close to the criteria limit suggesting the evidence for excluding either of these two variables is weak (Table 7.4). From the best model, observed mating success shared a significant positive relationship with DOC and uNJSI_DOM (Table 7.5). In regards to timing and duration of RE, when DOC and uNJSI_DOM were accounted for in the model, observed mating success was greater for males in Cluster 2 than males in Cluster 1 for all years combined (2-1: *P* = 0.008 Figure 7.3). Males in Cluster 3 had greater mating success than males in Cluster 1 (3-1: *P* = 0.024), but males in Cluster 3 and Cluster 2 did not differ in mating success across all years combined (3-2: *P* = 0.864).

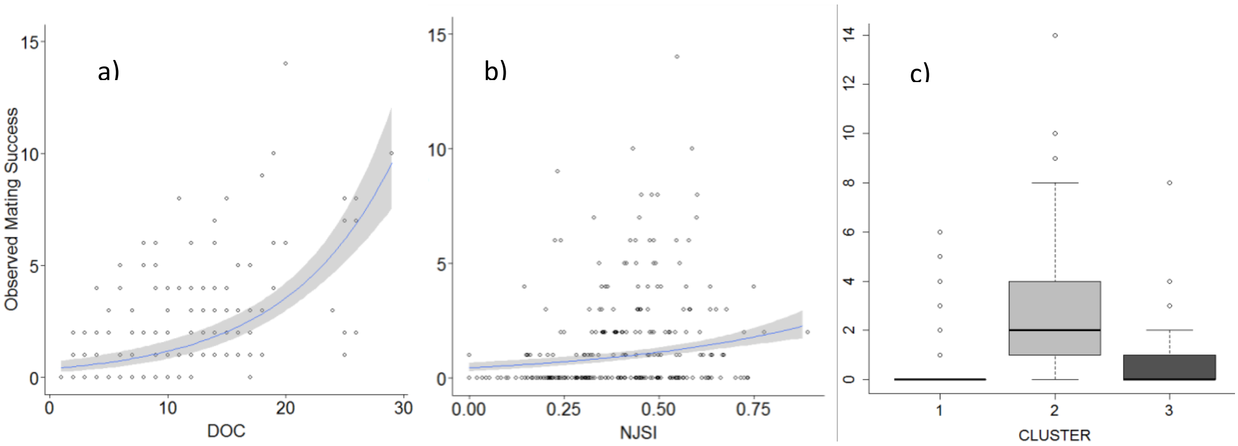


Figure 7.3 The fixed effects a) Days on Colony (DOC) and b) local social stability (NJSI = uNJSI_DOM) share a positive relationship with reproductive effort (RE). Differences in RE across c) CLUSTER (based on timing and duration of dominance during breeding season) were supported by the best model predicting observed mating success across all years combined. Shaded areas = 95% CI.

Table 7.4: Model selection and variable inclusion for predicting mating success across all years (models without year) and when allowing for interannual variability in the effects of the predictor variables (models with year interaction). Model with ΔAIC = 0 was selected as best model; all other retained models are the result of selection criteria (Richards 2008).

	Intercept	CLUSTER	DOC	uNJSI_DOM	Rnk	Yr	CLUSTER:Yr	DOC:Yr	df	logLik	AICc	ΔAIC	weight
Models without year[1]													
1	-1.8	+	+	+	--	NA	NA	NA	7	-344.4	703.36	0.00	0.63
2	-1.6	--	+	+	--	NA	NA	NA	5	-349.1	708.49	5.13	0.05
3	-1.2	+	+	--	--	NA	NA	NA	6	-348.1	708.54	5.18	0.05
Models with year interaction[2]													
1	-0.9	+	+	--	--	+	+	+	14	-317.2	664.31	0.00	0.40
2	-0.7	+	+	+	--	+	+		13	-321.1	669.75	5.45	0.03

Table 7.5: Coefficient estimates for the three clusters, uNJSI_DOM and DOC from the best model predicting mating success without year as a parameter (Table 7.4[1]).

	Est.	Std. Error
uNJSI_DOM	1.8	0.57
DOC	0.1	0.02
INTERCEPT		
CLUSTER 1	-2.1	0.32
CLUSTER 2	-1.5	0.26
CLUSTER 3	-1.5	0.25

Table 7.6: Coefficient estimates (± SE) from the best model with year as an interaction term across cluster. Cluster values represent intercepts. DOC was also retained in this model and the effects across years are shown (Table 7.4[2])

Year	Cluster 1	Cluster 2	Cluster 3	DOC
2011	-1.2 (0.33)	-2.2 (0.41)	-1.3 (0.31)	0.2 (0.04)
2012	-1.4 (0.48)	-0.1 (0.53)	-2.7 (1.12)	0.1 (0.04)
2013	-3.2 (0.62)	-1.2 (0.72)	-0.9 (0.65)	0.1 (0.05)

7.3.3.1 Interannual variation

When examining the model which included interannual predictors of observed mating success, it was apparent that the effect of predictor variables DOC and CLUSTER varied by year (Table 7.4). PeakRank was not retained in any of the separate years' models and while uNJSI_DOM was retained in the second best model the ΔAIC value was again close to the cut off value of 6 (Table 7.4).

DOC had the strongest effect on mating success in 2011, followed by 2013 then 2012 (Table 7.6, Figure 7.4). The effect of CLUSTER also varied across years and within years (Table 7.6). Strangely, in 2011, males in cluster 2 had significantly lower mating success than males in cluster 1 or 3, but males in 1 and 3 did not differ (Tables 7.6 & 7.7, Figure 7.5); while in 2012 males in cluster 2 had significantly greater mating success than males in cluster 1 or 3 (Tables 7.6 & 7.7, Figure 7.5). In 2013, there was no significant difference between males in cluster 2 and 3, but males in cluster 1 had the least mating success (Tables 7.6 & 7.7, Figure 7.5). When considering variability in mating success by cluster type: males in cluster 1 did equally well in 2011-12 but significantly worse in 2013; males in cluster 2 did equally well in 2012-13 but significantly worse in 2011; and males in cluster 3 had equal success across all three years (Tables 7.6 & 7.7, Figure 7.5).

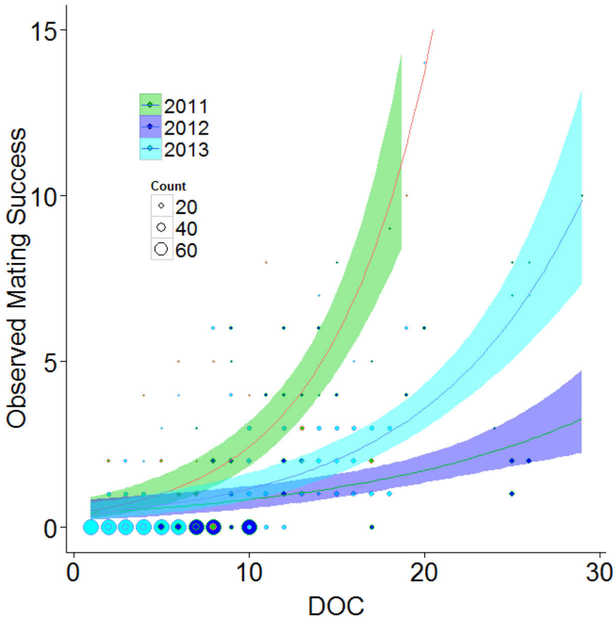


Figure 7.4 The effect of DOC on observed mating success in 2011-2013. DOC had the strongest effects in 2011 and 2013. Point size represents the count, or number of observations at the same coordinate (*e.g.*, more than one male with the same DOC and MS_TOT).

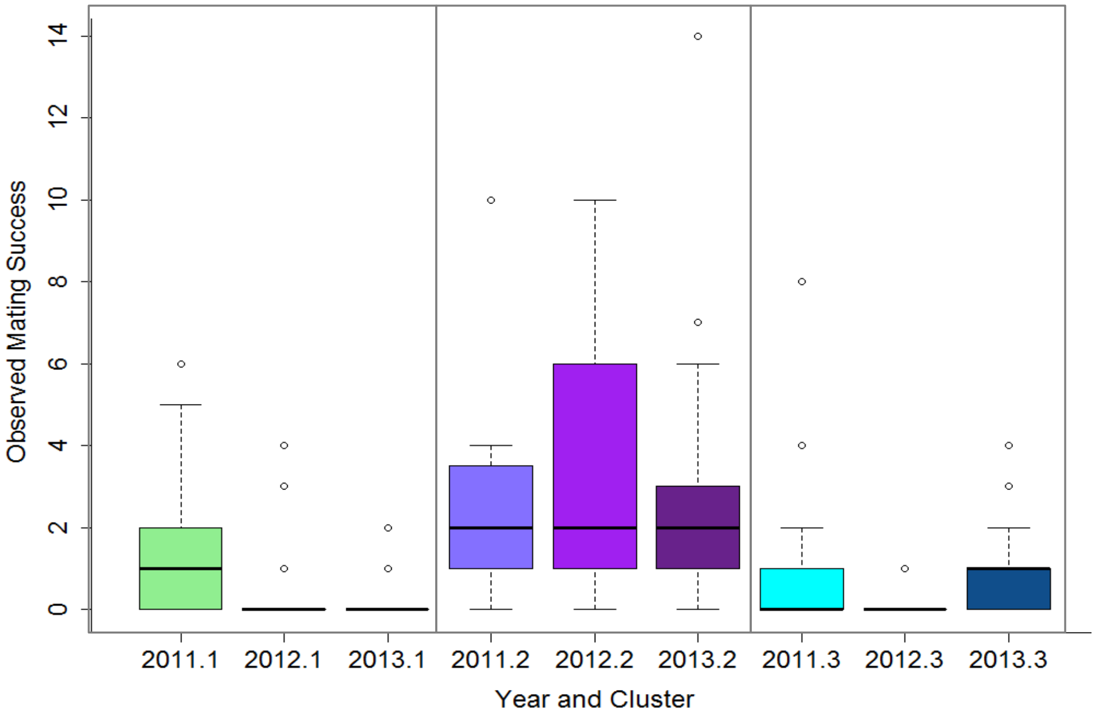


Figure 7.5 The observed mating success by year and cluster category (YYYY.cluster) demonstrates interannual variation in the success of males adopting each of the three RE duration and timing clusters: 1 = early peak, short duration; 2 = mid peak, long duration; 3 = late peak, short duration.

Table 7.7 Average observed mating success per Cluster across years, total MS for each cluster per year (SUM) and the number of males in each cluster per year (n). [Sums in 2012 and 2013 are greater due to full observer coverage and longer field seasons—see discussion].

Cluster	Year	Mean	SE	SUM	*n*	% in each cluster
1	2011	1.55	0.34	45	29	50%
2	2011	2.66	0.75	32	12	21%
3	2011	1.29	0.53	22	17	29%
1	2012	0.44	0.21	12	27	36%
2	2012	3.48	0.46	136	39	53%
3	2012	0.125	0.13	1	8	11%
1	2013	0.09	0.05	4	46	43%
2	2013	2.71	0.44	103	38	36%
3	2013	0.87	0.23	20	23	21%

7.3.4 Consistency of tactics for individuals across years

There were 49 males who were seen in more than one season from 2011 to 2013. Of that number, 20 were classified by the same cluster in subsequent seasons; only three males were categorized into the same cluster for all three years (Table 7.8). Of the males that were present for more than one season but changed cluster category, five were categorized as either cluster 1 or 3; suggesting they consistently had short durations of RE but changed timing. There were 10 males which either switched from cluster 1 to 2, or 3 to 2, suggesting a ‘progression’ in tenure ability. Seven males switched from 2 to 1 or 2 to 3, suggesting a shortening of tenure ability. Seven males were classified once in each category.

Table 7.8 The number of individual males categorized into each cluster for multiple years.

	Cluster 1	Cluster 2	Cluster 3
2 years	8	8	1
3 years	0	2	1
Total	**8**	**10**	**2**

For males returning in subsequent years with the same Cluster assignment in both years, the consistency in the day of peak dominance was fairly strong across all males combined (*Pearson’s Corr* = 0.47, df = 20, *P* = 0.027; Figure 7.6a). The consistency in duration of dominance was fairly strong for all males (*Pearson's Corr* = 0.52, df = 20, *P* = 0.013), but became more variable for males with durations longer than 10 days in either year (Figure 7.6b).

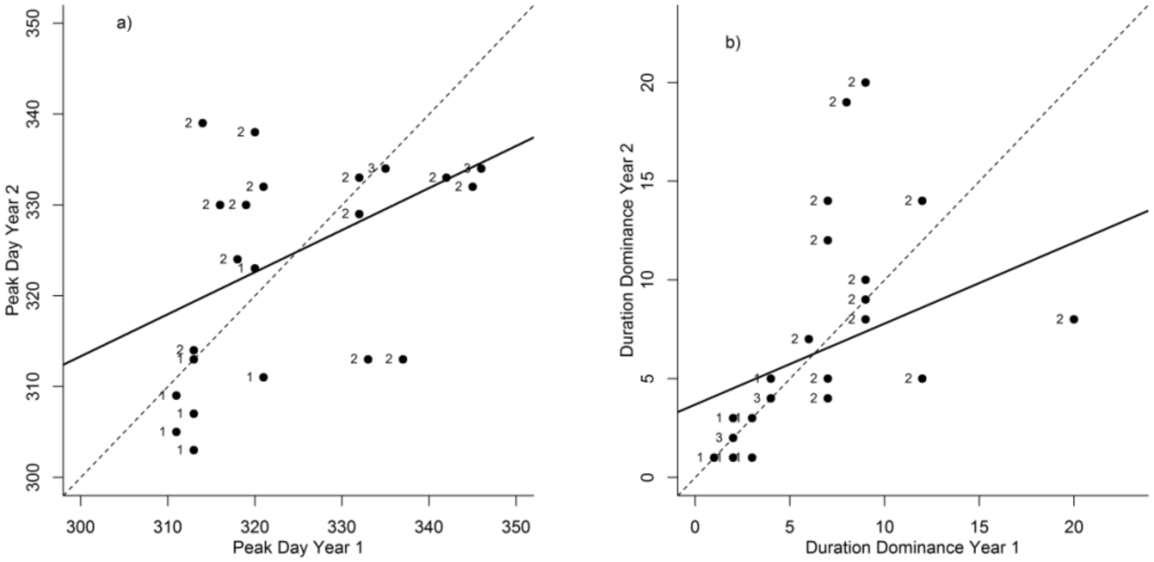


Figure 7.6 a) The consistency between peak day in year 1 and year 2 for returning males; b) the consistency between duration of dominance in year 1 and year 2 for returning males. Dashed line = 1:1 relationship, solid lines = visualization of linear correlation, and labels = cluster type (n= 20).

To see if the correlations across years are upheld within Cluster categories and not just across all categories, separate tests were run for each Cluster. For Cluster 2, there was no consistency in duration of dominance (*Pearson's Corr* = -0.07, df = 11, *P* = 0.81) or Peak Day (*Pearson's Corr* = -0.09, df = 11, *P* = 0.76; Figure 7.6a); however, when considering Cluster 1 and 3 together (due to sample size constraints), males showed consistency in duration of dominance (*Pearson's Corr* = 0.76, df = 7, *P* = 0.02) and in peak day (*Pearson's Corr* = 0.909, df = 7, *P* = 0.0007; Figure 7.6b).

7.4 Discussion

7.4.1 Main findings

This is the first study for pinnipeds, and one of few studies in general, which has demonstrated a link between timing of reproductive effort (RE) and mating success. The results confirm that length of stay was positively associated with mating success, but in addition to this, duration and timing of reproductive effort contributed to explaining the variation in individual mating success between and within years. Some males maintained RE for over 5 days ("Long"), and achieved relatively high mating success across all years. Males who were not able to maintain dominance for long periods ("Short") were split into two categories based on the timing of their RE as "Early" or "Late" in the season (Figure 7.7). The observed differences in mating success and phenotypes across male classification clusters, within and between years, suggests that these are alternate mating tactics within the 'conditional strategy' of Tenureship (Gross 1996).

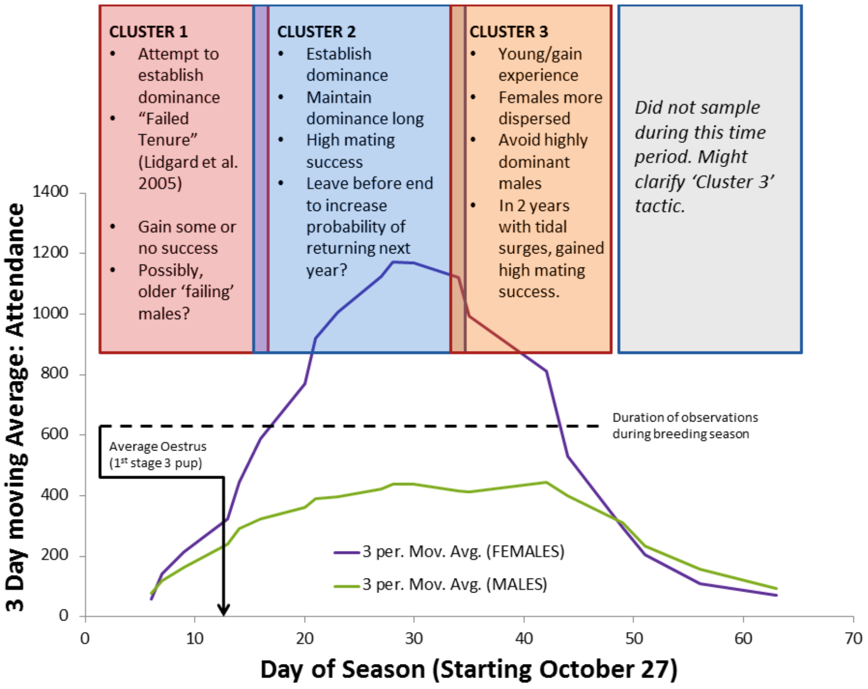


Figure 7.7: Schematic of the three identified male tactics based on duration and timing of dominance, overlaid on the average numbers individuals ashore for females and males in 2011-2013. Date of oestrus and timing of observations are also denoted. Notes on each cluster reflects discussion topics in sections **7.4.3—7.4.5**.

7.4.2 Duration of tenure and mating success

Mating success for many polygynous mammals is positively associated with length of tenure, or the ability to maintain a position of access to females (Clutton-Brock and Albon 1979, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2001, McElligott et al. 2001, Fabiani et al. 2004, Lidgard et al. 2004, Twiss et al. 2006, Pörschmann et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Meise et al. 2014). Increased mass, or energy stores, facilitates prolonged fasting and duration on the colony, which in turn would allow males to be exposed to high numbers of reproductively receptive females and increase mating success. For some pinnipeds, including grey seals, there appear to be some trade-offs between the selection of increased mass for fasting (Pörschmann et al. 2010) and intermediate size for manoeuvrability in fighting (Lidgard et al. 2005, **Chapter 5**), both of which would play key roles in maintaining a position near receptive females. This study confirmed previous findings that that length of stay was positively associated with mating success, but timing and duration of RE clusters were also retained as significant predictors. This suggests that it is not only the total energetics available for fasting driving mating success, but rather, the dynamics of male RE as expressed as dominance behaviours seem to explain some of the intra-seasonal trade-offs between fighting, fasting, and mating.

7.4.3 Timing and duration of RE as predictors of mating success

Timing of RE has been demonstrated as a determinant of mating success in many species with temporally- or spatially-restricted breeding (Smith and Moore 2005, Mason et al. 2012, Cordes and Thompson 2013, Meise et al. 2014). For some species, early arrival for both sexes is associated with greater reproductive fitness (Smith and Moore 2005, Cordes and Thompson 2013), while for other species late arrival might be an adaptive strategy for certain life-history stages (Mysterud et al. 2008, Mason et al. 2012).

7.4.3.1 Early RE

Females arrive on the colony typically at the end of October and for the first week female and male densities are relatively low (**2.4**, Figure 7.7). Oestrus occurs for females on approximately day 16 of the lactation (Figure 7.7, Kovacs and Lavigne 1986, Twiss et al. 2006). In our study, males who maintained dominance for a short period early in the breeding season had similar rates of aggression and standard lengths to the males exhibiting the long RE duration tactic but with relatively lower dominance ranks. Lidgard et al. (2012) suggested males with short durations of tenure might have failed at their attempt at the Tenured, or consortship, strategy. However, we found that males which had short durations of RE early in the season ranged in total length of stay from 1-14 days, which suggests that males peaking in RE early might subsequently remain as a tenured male, but with lower relative rank, once the more dominant males exert RE. In this context, the early, short-RE tactic might be adopted by older males who are losing competitive ability but are still attempting to express the primary mating tactic or by males who do not have the mass to stay for a long period, but can be competitive. Early breeding females generally have longer lactation periods and greater fitness (Boness et al. 1995, Cordes and Thompson 2013). Therefore it could be an adaptive strategy to maintain RE until these early females come into oestrus, and then subsequently ‘retreat’ to sub-optimal positions and attempt to gain marginal benefits of mating success through the remaining length of stay. Further investigations could attempt to tease out which of these scenarios is occurring through monitoring long-term consistency in tactics, age, experience and size of individuals, and the potential for early females to express mate choice based on quality of males present.

7.4.3.2 Late RE

Late arrival might alternatively be an adaptive strategy for certain life-history stages (Mysterud et al. 2008, Mason et al. 2012). Male grey seals categorised by short RE durations peaking late in the season, were relatively smaller, had the greatest rates of aggression, but had relatively high mating success in some years. Age estimations were not available for this study, but, assuming that smaller males are typically younger (Hewer 1964, Lidgard et al. 2012), there is the suggestion that male grey seals expressing their RE later in the season are young males. Peak RE for prime-aged male red deer, Cervus elaphus, coincides with female oestrus, while younger males peak later (Mysterud et al. 2008). Similarly, young male alpine chamois appear to time their RE to the end of the breeding season as a strategy to minimizes interactions with older, stronger males and maximize individual fitness during a particular life-history stage (Mason et al. 2012).

Contrastingly, in our study, males which peaked in RE late in the season exhibited relatively greater rates of male-male aggression. The ‘late’ season is particularly protracted at Donna Nook (Figure 7.7) and this study did not encompass the entire period. Therefore, the expected benefits of reduced aggression might not come until later towards the end of the breeding season. Considering the time frame of our data, the observed increased rates of aggression associated with late males could have instead been driven by increased male-male competition as the sex-ratio became increasingly male biased (**2.4**), or through the increased frequency of male-female harassment late in the season triggering male-male competition (Boness et al. 1995). It is also possible that the increase in aggression for Late males could be an artefact of the atypical, stochastic natural events which occurred late in two of the studied breeding seasons distupting social and spatial distributions on the colony (**Chapter 6**). It was in these two years that the Late males had the relatively greatest mating success. It is still possible that under natural conditions, aggression for Late males might be relatively lower and reflect the cost-aversion strategy that maximizes fitness and minimizes intrasexual competition, suggested to be used by young chamois (Mason et al. 2012), but additional data from ‘non-disturbed’ years would be necessary to confirm that hypothesis.

Males expressing RE late in the breeding season could also be immigrant males looking for additional mating opportunities. Grey seals around the UK show considerable movement between geographic regions during non-breeding periods (Matthiopoulos et al. 2004, Russell and McConnell 2013). Some level of dispersal during the foraging season is expected due to changing prey availability, but less is known about dispersal during the breeding season. Peripheral males New Zealand sea lions (*Phocarctos hookeri*) with no harems also exhibit high rates of dispersal between breeding colonies during the breeding season, potentially as a strategy to gain multiple breeding opportunities (Gross 1996, Robertson et al. 2006). Such inter-colony dispersals during the breeding season have not previously been considered for grey seals, but are possible around the UK, as breeding seasons on the west coast of Scotland occur approximately one month prior to the start of breeding in England. Anecdotal evidence suggests this could be happening. In 2013, I observed a satellite tagged male arrive at Donna Nook and persist on the periphery of the colony for an entire day. After the season it was discovered that this male had originally been tagged in the Netherlands (*pers corr:* S. Brasseur). The marginal benefits for males adopting such a dispersal tactic would depend on the male's energy stores, the costs of immigration, and the relative difficulty of gaining access to females. Future work incorporating satellite telemetry or comprehensive photo-ID networks would be required to assess if this is occurring across UK populations and if so, to what degree or under what contexts it is most supported.

Figure 7.8: Male at Donna Nook, November 20th 2013 arrived with satellite tag attached (orange arrow pointing to device). Photo has had brightness increased by 40% to aid in visualization.

7.4.4 Inter-year variability in mating success

7.4.4.1 Duration of tenure vs duration of RE and thermal stress

While interannual environmental variability has been linked to differences in variation in mating success (Twiss et al. 2006, Apollonio et al. 2013) it has not been considered a driving force for the adoption of alternative grey seal mating strategies (Lidgard et al. 2012). Long duration of tenure has consistently been correlated with increased mating success across species, colonies, and mating seasons exposed to varying environmental conditions (Twiss 1991, Carlini et al. 2006, Pörschmann et al. 2010, Lidgard et al. 2012, Meise et al. 2014).

In the present study, this was not the case; length of stay was retained as a strong predictor of mating success in all years, but the effect was strongest in 2011; a year characterised as relatively warmer, drier and with fewer seals present (**2.4, 3.4.1.3**). Furthermore, in 2011, males with long durations of RE had the highest mating success on average, but when length of stay was corrected for, this tactic had the lowest mating success. These interannual differences might reflect the trade-offs between fasting and fighting when males are exposed to eco-physiological stress. For grey seals, under dry, warm conditions, the ability to monopolize females is reduced, leading to subsequent reductions in the variation in male mating success (Twiss et al. 2007), and under similar conditions, aggression was greatly reduced across all individuals at Donna Nook (**3.4.1.3**). Aggression is required to establish and maintain dominance; therefore it can be assumed periods of high RE are more costly in terms of metabolism (Copeland et al. 2011), stress (Lidgard et al. 2008), and potential physical damage. Perhaps then individuals which maintained long durations of RE as well as long lengths of stay faced greater costs under the thermally stressful conditions of the warm years, leading to the lower mating success for that category across all values of length of stay. In contrast, in the year with the coldest and wettest weather, 2012, length of stay alone had very little effect on mating success, and males who were able to maintain RE for the longest durations under these conditions had the greatest mating success of all three tactics. The 2012 breeding season also did not experience an atypical tidal event to disrupt social structure, perhaps limiting the opportunistic nature of the late RE males.

While very little research has found similar across season variation in mating tactic success (Lidgard et al. 2012), this pattern merits further investigation as other pinnipeds have exhibited variation in behaviours driven by thermal stress, which reflect the relative trade-offs of costs and benefits of aggression (Bohórquez-Herrera et al. 2014) and environmental variability is known to promote multiple behavioural phenotypes within a population for salmonids (Hoogenboom et al. 2013). With only three years to compare across, it is difficult to say if the observed differences in tactic success are driven by the weather or other factors, but this study provides some evidence that the success of various mating tactics might be context dependent under the natural fluctuations in environmental conditions experienced at breeding colonies.

Longitudinal studies of otariids have begun to tease apart broad patterns in interannual mating tactics for territorial males (Meise et al. 2014), but the interannual consistency of individuals' mating tactics merits further investigation. For example, male Galapagos sea lions are exposed to a variable environment, driven by El Niño events, and alternative mating tactics might be an adaptation which enables males to maintain high levels of fitness across interannual fluctuations (Gross 1996, Meise et al. 2014). While this finding suggests that under poor conditions, alternate mating tactics can allow young or smaller males mating opportunities they otherwise might not have had, other studies have shown that dominant male Galapagos sea lions exhibit consistency in behaviours and mating success across years (Pörschmann et al. 2010). In the present study, there was some evidence of consistency in RE tactics for individuals across years. It will be interesting to consider in future work if male grey seals are flexible in the mating tactics they exhibit within seasons in relation to natural fluctuations in weather such as the North Atlantic Oscillation, or if individuals are more fixed in their behavioural patterns (Twiss et al. 2012). Particularly, investigations into patterns of weather stochasticity would be interesting to apply to the males on the North Rona colony, as it has recently been found that the top males are not returning in subsequent breeding seasons and no previously subordinate males are filling in their positions (unpublished data, SDT & AMB). Further work discerning if this pattern is driven by the current ecological and social conditions could reveal at what point in a colony's decline do the benefits of achieving a relatively enhanced RE fail to outweigh the associated costs. This information would be of use for population modellers, managers and conservationists concerned with the within-colony and population-level genetic and social consequences of a colony decline.

7.4.4.2 Implications of phenological shifts

A phenological mismatch is a shift in the timing of the onset of the breeding season due to environmental variation or climate change (Crick et al. 1997, Forrest and Miller-Rushing 2010, Cordes and Thompson 2013). Variance in nesting date for birds in the UK (Crick et al. 1997), ringing date for seabirds (Møller et al. 2006), and pupping date for harbour seals (Cordes and Thompson 2013) have shown advances over time which can be attributed to various factors such as climate change, the North Atlantic Oscillation, or population density, respectively. The findings of this chapter suggested that males peaking in RE early and for a short duration in 2013 had strikingly lower mating success relative to males adopting that tactic in previous years. When considering overall attendance patterns for 2013, female attendance and pup production appeared to lag by about 5-7 days relative to the two previous years. If males are actively scheduling their short duration of RE to a specific time of the breeding season based on previous experience, and not the current conditions, a delayed season could reduce or eliminate an opportunity for mating for some males and produce the pattern observed in 2013. The early RE tactic could still represent a stable strategy if the variation in mating success averages out over an individual's lifetime.

However, if weather patterns become increasingly stochastic, it is possible this environmental variation might impact the diversity of mating strategies feasible within a grey seal breeding colony. Due to the intricacies and conflicting variables, predicting shifts in female pupping dates and attendance at grey seal breeding colonies is difficult (Coulson 1981, Cordes and Thompson 2013), but it appears that male grey seals are not able to predict interannual shifts in female pupping either. Therefore, long-term studies monitoring changes in individual tactics and timing of RE might provide more accurate predictions of how populations will respond to changing environments.

7.4.5 Conclusions

In conclusion, this study is the first for grey seals, and one of few for mammalian males, to consider the effect of timing of RE on mating success. Variation in mating success among Tenured individuals was explained by the timing and duration of reproductive effort. These findings are preliminary, in the sense that longitudinal data over a much longer time period would be necessary to confirm if the interannual patterns of RE represent consistent, individual stable strategies (Parker and Maniscalco 2014). However, this study highlights the often-overlooked concept of non-uniform RE during a breeding season and individual differences in timing of male RE for non-territorial males. The potential for interannual differences in the effectiveness of these tactics, whether through environmental conditions or phenological shift, further suggests that the topic of male timing of RE requires further investigations to discern: 1) the continued success of each tactic, and 2) the plasticity of males in their response to future environmental change scenarios and future phenological shifts, as predicted by Forrest and Miller-Rushing (2010).Furthermore, combining behavioural observations of RE and mating success with molecular data would help clarify the questions of timing of ejaculation, female choice, sperm competition, or induced ovulation in terms of individual mating success (**Chapter 2.6.3**).

Chapter 8

General discussion

8.1 Summary of main findings

This thesis has utilized a diverse set of objectives and techniques to investigate male grey seal breeding behaviours, and specifically, the behavioural mechanisms of conflict and conflict reduction. The findings have furthered our understanding of the evolutionary drivers of individual male grey seal behaviours. It has also provided insights into the variability in behaviours in systems with polygynous mating patterns at the scale of the breeding colony and individual. Specifically, conflict behaviours differ in response to social, spatial and environmental conditions, and individuals' behaviours at the daily scale can reveal alternate tactics and strategies which are likely to have fitness consequences.

8.1.1 Main findings

1) Behavioural studies at (relatively) newly formed breeding colonies, and/or at colonies with atypical environmental characteristics, can further our understanding of behavioural continuums and selection pressures, and can reveal new behaviours.

2) Males at Donna Nook breeding colony fall into the middle of the known spectrum for a range of ecological factors and breeding behaviours such as: sex-ratio, variation in mating success (I_s), aggression (frequency and activity budget), and time spent in Non-Active behaviours.

3) Colonies with lower aggression and lower variation in mating success also had greater female to male sex-ratios; the role of topography, specifically the increased ease of access to the breeding sites from the sea, appears to drive increased rates of aggression amongst males.

4) Males at breeding colonies on the mainland, exposed to anthropogenic activities relatively more often than males at offshore colonies, showed no behavioural evidence of disturbance relative to males at offshore, isolated colonies.

5) The apparent lack of a cross-colony indicator of a behavioural response to human activities suggests the evolutionary imperative for conservation of energy is either

counteracting the selection for acute disturbance responses, and/or that males at mainland colonies have habituated to the present levels of anthropogenic activities.

6) The Body Slap has been identified as a geographically-isolated, male threat behaviour. It consists of a prone, stationary male arching his back or pushing his torso off the ground with his fore-flippers then letting his ventral surface fall to the ground emitting a distinct slapping sound.

7) Body Slaps are pervasive in aggressive interactions at Donna Nook breeding colony, and do not appear to be submissive. Winners displayed at higher rates than losers, and proportionally more than losers; and the displays were positively associated with other known aggressive behaviours.

8) The substrate vibrations of the Body Slap contain information regarding male length, a known correlate of RHP for grey seals. Furthermore, the reliability was not altered by the surface dampness of the substrate.

9) Investigating the trade-offs between potential for fasting duration (mass) and fighting ability (length) has revealed that assessment strategies are context dependent.

10) For male grey seals, mid-sized length is associated with greater probability of success in aggressive interactions; mass was not found to be important for fighting success but has previously been linked to mating success. This suggests that size and mass might be selected for separate evolutionary processes or for different purposes.

11) During aggressive interactions, male assessment strategies varied across the contexts of contest escalation and outcome. Self-assessment was the primary assessment strategy in high-cost, escalated interactions with clear winners and losers, while mutual assessment was supported as the assessment strategy used in low cost, Non-Contact interactions resulting in a draw.

12) Males that have previously interacted with each other had fights of shorter durations, but longer duration Non-Contact interactions. This suggests prior knowledge is important in high-cost interactions but might promote ‘nagging’ in the form of low cost interactions of extended durations.

13) Investigating the variation in aggression between individuals at the daily temporal scale was feasible with the use of recent techniques such as Elo dominance score ranking calculations.

14) At the daily scale, males with higher average neighbour stability had lower rates of aggression and lower probability of aggression.

15) Individual dominance score had no correlation with aggression at the daily scale, but after stochastic natural disturbances, which disrupted the local social stability, males with high dominance ranks did have lower rates of aggression than males of lower dominance ranks.

16) There was some between-season and spatial variability in the relationships between neighbour stability and aggression suggesting that the importance of specific variables in conflict reduction might be context dependent.

17) Timing of reproductive effort (RE) is linked to the variability in individual mating success within breeding seasons and could represent alternative mating tactics within the Tenured male strategy.

18) Males timing their RE towards the end of a breeding season were potentially younger or smaller males, adopting a life-history mating tactic to maximize trade-offs between fitness and the costs of aggression or maintaining positions.

19) Males timing their RE towards the start of the season had relatively less success, possibly due to the greater potential for a temporal mismatch with female ovulation date when breeding seasons were delayed.

This chapter will discuss how these main findings have contributed to the broader literature of conflict, pinniped ecology and evolution. I will also identify paths for further research which have developed from this thesis.

8.2 The importance of draws as a contest outcome

It has now been demonstrated that draws are pervasive in wild grey seal mating systems, and ‘not losing’ is more important to male mating success and fitness than winning (Anderson et al. 1975, Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998). The occurrence of draws in this system has been attributed to the strong selection pressure for conservation of energy (Anderson and Fedak 1985), the high costs of losing a position near females (Anderson et al.

1975, Anderson and Fedak 1985, Lidgard et al. 2005), and the apparent benefits of maintaining stable local neighbourhoods (**Chapter 6**). Yet, even though the prevalence and importance of draws has been consistently demonstrated in the grey seal system, it is rare that other studies acknowledge the occurrence of draws as a valid conflict strategy, and not just as a failed contest outcome (see review in **5.1.1**).

In his original models of conflict strategies, Maynard-Smith (1982) demonstrated the evolutionary reasoning behind why we do not see total wars in nature. His work also determined that while the 'Hawk' strategy could be an ESS, the 'Dove' strategy on its own should not be persistent in a population because individuals which are willing to risk greater costs associated with escalating conflict interactions would always win. To further tease apart this pattern, Maynard-Smith and Price (1973) modelled a third strategy, the 'Retaliator', in which an individual might adopt Dove if their opponent does as well, but if faced with a Hawk they will appropriately escalate ('Retaliator') or retreat ('Bully'). Under this model, there were two ESSs, the 'Retaliator' and the 'Hawk/Dove' dimorphism (Maynard-Smith and Price 1973, Maynard-Smith 1982). While Maynard-Smith and Price (1973) demonstrated the evolutionary stability of a 'Retaliator' strategy on a theoretical basis, most empirical behavioural studies at present have focused on the 'Retaliator' or 'Bully' (Hsu et al. 2008, Arnott and Elwood 2009). The lack of empirical studies on draws might be attributed to criticisms of the original Hawk-Dove game, in which it was argued that the Dove-Dove scenario, whether the pure strategy or as a part of the 'Retaliator' strategy, is biologically implausible; two individuals should only settle a contest with minimal costs (primarily time-wasting) if the resource is divisible-equally which is rare in natural systems (Maynard-Smith 1982). In many systems though, including the grey seal mating system, individuals are found to engage in what appears to be 'Dove-Dove' interactions, where neither escalates, no change in resource division is observed following the interaction, and where neither side retreats (Anderson and Fedak 1985, Jennings et al. 2005).

The current knowledge of draws suggests that they are likely selected for in systems where the costs associated with losing access to resources on the breeding colony are high and/or where RHP asymmetries are low (Anderson and Fedak 1985, Jennings et al. 2005). This thesis has attempted to provide some of the first empirical work investigating the decision-making that occurs in contests which result in draws, using male grey seal conflict as the model system. In **Chapter 5**, it was demonstrated that decisions in threat contests ending in a draw were based on mutual assessment, and that this differed from the strategies males employed in win-loss contests with an escalated phase. In **Chapter 6**, it was also reported that social stability engendered a reduction in aggression for individuals at a fine-temporal scale. Based on these findings, it is likely that the presence of draws in a moderately polygynous system might be selected for as a mechanism for extending an individual’s tenureship of existing resources, or duration of RE, which in turn increases mating success (Twiss 1991, **Chapter 7**). Under this hypothesis, draws would not be considered a failed win-loss interaction. Instead, in systems where (1) ‘not losing’ is important, (2) there are excess males ready to fill vacant positions amongst females, and (3) pushing for a ‘win’ yields little marginal net value and high risk, males adopting the long stay, long RE tactic might initially resolve contests with clear outcomes to attain a position or access to resources. Subsequent to this, individuals might switch to a system of repeated draws with neighbours as this both reduces the costs of expelling neighbours and maintains social stability. Therefore, draws should be considered a behavioural mechanism which promotes the conservation of energy by reducing the costs of energy and risk of damage associated with high rates of aggression, escalated aggression or changes in local social structure, and not simply a failed contest.

Under this hypothesis, one would draws to persist in other wild systems where social stability aids in prolonging tenure (Getty 1987, Booksmythe et al. 2010, Cross et al. 2013) or where resources cannot be harvested simultaneously, leading to a strong selection for conservation of energy as a way to prolong tenure and capitalize on the 'latent' resources held (Jennings et al. 2005). In both cases, draws could be considered a risk averse, or risk mitigation strategy, which minimizes the potential for losing resources which are held already. References to draws in animal contest literature are few (**5.1.1**). This could potentially be due to restrictions of methods (only win-loss allowed), omission, or limitations in the available methods for analyzing draws in a meaningful manner. Alternatively, other biological factors such as resource distribution or relatively greater RHP asymmetries could restrict the expression of draws. Further work is therefore needed to investigate the prevalence of draws across taxonomic groups in the wild as a mechanism for promoting a 'not-losing' strategy, social stability, and conservation of energy. Currently, meta-analyses have been used to investigate the evolutionary drivers of broad behaviours such as cooperative-breeding (Lukas and Clutton-Brock 2012). Similar methods could be applied to examine the evolution of the conflict outcome of draws, assuming the literature actually represents the true presence/absence of draws in wild systems. Additionally, the work of this thesis clearly indicates that draws are a meaningful result of animal conflict; however, some assumptions had to be made in order to use the presently available models for discerning decision-making and the role of RHP. Future work investigating animal decision-making in contests will benefit from the generation of models which explicitly allow for draws as an outcome. The development of such models was beyond the scope of this thesis, but would provide essential information on the broader patterns and evolutionary similarities between taxa which resolve contests in draws, and would expand our current knowledge of the decision-making of animals in naturally occurring contests.

8.3 Conservation of energy and breeding behaviours

8.3.1 Assessment and physiological thresholds

Tor capital breeders, the importance of the conservation of available energetic resources has long been suggested as a primary driver of the observed patterns of animal conflict in systems with polygynous mating patterns (Maynard-Smith and Price 1973, Anderson et al. 1975, Anderson and Fedak 1985, Twiss 1991, Sandell and Liberg 1992, Twiss et al. 1994, Arnould and Duck 1997, Taylor and Elwood 2003, Apollonio et al. 2013). Particularly, individual energetics have been shown to play a strong role in contest assessment when costs are high but not when costs are low (Briffa and Elwood 2004, Briffa 2008, Hsu et al. 2008). In the self-assessment, or war of attrition, model of animal decision-making, individuals will continue a contest until some energetic threshold is met (Briffa and Elwood 2004). For this reason, self-assessment has been suggested as the better adapted strategy in high-cost, high-benefit interactions as it reduces the probability of an incorrect decision being made from unreliable information or from cheating during signaling (Arnott and Elwood 2009). This thesis supports this hypothesis, and has shown that for male grey seals, self-assessment is the strategy males adopt during physical, contact fights between two opponents with no prior knowledge (**Chapter 5**). As a capital, polygynous breeder, if no information has been gained from prior interactions with mutual-assessment, a physiological threshold which determines a male's decision to give-up in contact contests would reduce the potential for over-extending energy stores. As male grey seals typically become reproductively competitive around the age of 10, and their average lifespan ranges from 25-30 years (*pers. corr*: S. Twiss), this strategy might reduce a male's seasonal fitness, but could be selected for as a way to maximize life-time success.

This potential for energetic conditions to trigger fitness-related behavioural decisions provides a platform for further exploration of the links between physiology and behaviour in capital breeding species. Hormonal pathways for energy acquisition, metabolism and conservation have been suggested to be conserved throughout life-history stages in northern elephant seals (Ortiz et al. 2006), but little is known about what physiological mechanisms trigger specific behavioural changes (*e.g.* ending an escalated aggressive interaction between adult males). Some current research is investigating these types of links, using weaned grey seal pups as the model system (Bennett et al. 2007). Upon weaning, grey seal pups remain on the colony for 1-4 weeks of fasting before going to sea for the first time (Noren et al. 2008) and ~94% of their energy appears to be metabolized from subcutaneous fat stores (Nordøy and Blix 1985). Similar to the benefits of mass, length and RHP in adults (**Chapter 5**), the benefits of mass for weaned pups are relatively well understood. Pups which are heavier at weaning have greater rates of mass loss; primarily from metabolism of fats (Bennett et al. 2007). Therefore, being heavier at weaning can benefit individuals by increasing diving capabilities in post-weaning periods (Bennett et al. 2010). While it is largely accepted that some energetic trigger at the end of the post-weaning fast determines when weaned pups head to sea to learn to forage, it is still unknown what mechanism drives that decision to terminate fasting in phocid seal pups (Bennett et al. 2012), or if a similar mechanism is conserved and expressed in adult males during contest decision making and when deciding to give up tenure.

The implications of identifying such signaling pathways would extend beyond phocid seals, to broader ecological and conservation issues for any capital breeding species. For example, determining what physiological mechanisms trigger individual males to express ‘giving up’ behaviours during a breeding season, and to what energetic threshold they are willing to exert themselves to, would be of interest in modeling post-breeding foraging distributions. Perhaps, males which have higher thresholds and can ‘push themselves’ further during a breeding season are more restricted in the distances or depths at which they can forage immediately following return to the sea, while males which give up more readily might not require such rapid recovery, and thus can forage at greater distances or depths. Identifying the individual differences in these thresholds during and post breeding, and the physiological underpinnings of the individual behaviours, could then inform protected area managers concerned with spatial distributions of animals, spatially-explicit foraging models, and temporally specific predictions of interactions with industry or anthropogenic developments.

8.3.2 Cross-colony resilience to disturbance

In addition to contest decision-making and draws, the selection pressures for energy conservation seem to drive species’ resilience or ability to cope with natural and anthropogenic stressors (**Chapter 3**). The capital breeding male grey seals appear to be robust to environmental perturbations such as anthropogenic disturbances (**Chapter 3**, Perry et al. 2002). In contrast to many studies which only look at acute responses to disturbance events or disturbance outside of the breeding season (Curtin et al. 2009), this thesis (**Chapter 3**) has provided a distribution-wide investigation into potential drivers of male behaviours which allowed for assessment of the relative severity of cumulative acute behavioural responses. Due to the similarity of activity budgets across colonies of grey seals, each exposed to various degrees of anthropogenic disturbances and natural environmental conditions, I suggested that the strong selection for conservation of energy in grey seal breeding ecology could be overriding individuals' responses to local acute stressors (**Chapter 3**). This is further backed up by the evidence that grey seals do respond to anthropogenic activities during the non-breeding season and in acute time-scales (Perry et al. 2002, Curtin et al. 2009).

While the evidence in this thesis suggests that male grey seal behavioural patterns are unaffected by human activities during the breeding season, the hypothesis that this pattern is driven by strong selection for conservation of energy has identified a potential focus for future investigations into disturbance. Specifically, physiological and behavioural assessments will need to be conducted concurrently in order to tease apart trade-offs between conservation of energy and selection for responses to disturbance. For example, I found that the amount of time spent 'Non-Active' was similar across colonies (**Chapter 3**), but it is possible that behavioural 'rest' (*e.g.*, Non-Active) might be expressed in different physiological ways across individuals in terms of heart-rate variability, a measure used to assess stress and welfare of farm animals (von Borell et al. 2007). Some studies have already begun to incorporate physiology and behaviour into assessments of disturbance (Perry et al. 2002, Christiansen et al. 2013), but often such work is limited to pre- and post-exposure measures at small spatial and temporal scales. Therefore, assessments of disturbance on wild populations of animals will benefit from adopting behavioural approaches at acute and cross-colony scales to examine broader evolutionary drivers of response behaviours (**Chapter 3**). Furthermore, if energetic conservation or similar selection pressures are identified as potentially strong drivers of the behaviours in a system, studies might then benefit from incorporating a measure of physiological stress into these models to identify non-overt expressions of stress. Such work will further provide a platform for questions regarding (1) individual differences in responsiveness to natural and anthropogenic triggers of stress, (2) the consequences on life-span (*e.g.,* telomere length; Monaghan 2010), (3) the implications for population models, (4) the ontogeny of decision-making, and more broadly, (5) the adaptations allowing facilitating fasting for many capital breeding mammals.

8.4 Consistency and flexibility in individual behaviours

Recently in ethological research, there has been a burgeoning interest in the study of the flexibility or consistency of individual behaviours and tactics (reviewed in Dingemanse and Wolf 2010, Schuett et al. 2010). A wide range of taxa ranging from cnidarians to mammals are now known to exhibit consistent individual differences in their behaviour patterns (Réale et al. 2000, Estes et al. 2003, Sinn and Moltschaniwskyj 2005, Briffa 2008, McGhee and Travis 2010, Twiss and Franklin 2010, Briffa and Greenaway 2011, Huckstadt et al. 2012, Twiss et al. 2012). Subsequently, the focus shifted from looking exclusively for only individual consistencies in behaviours, but also looking at the inter-individual variation in the range of behaviours or degree of behaviours expressed in response to their environment (McGhee and Travis 2010, Twiss et al. 2012, Killen et al. 2013). For example, female grey seals can either be categorized as proactive, in which they consistently display the same rate of pup-checking behaviours across disturbed and non-disturbed situations, or reactive, in which they are more flexible and adjust their behaviours to suit the level of disturbance (Twiss et al. 2012). Such studies which have investigated inter-individual differences typically investigated the flexibility and consistency of individuals across whole breeding seasons or two discrete situations (*e.g.,* disturbed and non-disturbed) in the wild, or across a series of laboratory-regulated trial contexts. However, the ability of individuals to express consistency and flexibility can be driven by the environment, and conditions such as environmental stochasticity can potentially mask the appearance of consistent individual differences (Killen et al. 2013). In this thesis, I demonstrated that at a grey seal breeding colony exposed to interannual variations in weather, a range of anthropogenic stressors (**Chapter 3**), and stochastic disturbance events (**Chapters 6**), males demonstrated individual consistency in vigilance behaviours and male RE tactics showed some evidence of consistency across individuals (**Chapters 3 and 7**). As this study was limited to observational measures of consistency, further experimental work is still needed to determine individual differences in "flexibility", tolerance, and stress. However, the methods used in this study have broader applications for investigating the drivers of flexibility in conflict and conflict reduction in systems with varying levels of natural environmental fluctuation.

8.4.1 Context dependent decision making

Previous research has suggested that decision-making strategies in contests are context-dependent, in relation to the level of escalation and costs (Hsu et al. 2008). The findings of this thesis provide the first investigation into assessment strategies for pinnipeds, and have demonstrated that male grey seals follow a similar context-dependent pattern to that identified by Hsu et al. (2008). When engaged in low-cost, threat contests, individuals spend more time information gathering, and subsequently base decisions to retreat on the RHP of their opponent either on its own (Opponent-only assessment; Prenter et al. 2008), or in relation to their own RHP (mutual-assessment; Taylor and Elwood 2003). When escalated to high-cost behaviours such as physical fighting however, individuals appear to base their decision to retreat on some individual threshold, matching the self-assessment or war of attrition models but only when the combatants have not engaged previously (Arnott and Elwood 2009). The support for this pattern in male grey seal contests again fits the conservation of energy paradigm, but also demonstrates the flexibility in the behavioural mechanisms male grey seals employ within contests. Furthermore, the dependency of the differences in assessment processes on the degree of prior contact between individuals, and the unclear and mixed assessment strategies that were found in some contexts suggest male grey seals could be an ideal model species for future investigations into the drivers of decision-making flexibility. Along these lines, it would be interesting to conduct comparison studies of assessment strategies, and the flexibility in strategies, across additional grey seal colonies where the costs/benefits of winning/losing or draws may differ due to topography, spatial distribution, and behaviour of females. Ideal locations to test for potential environmental drivers of strategy selection would be the Isle of May, North Rona, or Sable Island.

Further studies examining assessment strategies across additional pinniped species would also provide an evolutionary perspective on contest decision-making. Based on the aforementioned characteristics of this type of context-dependent assessment, I would hypothesize that other polygynous capital breeding species with strong selection for ‘not losing’, and species which may have reliable methods of mutual assessment would exhibit this type of flexibility. Ideal target species for taxonomic comparisons would thus be territorial otariids (*e.g.*, Galapagos sea lions, California sea lions, Steller sea lions), aquatic breeding phocids (*e.g.*, harbour seals), and the elephant seals for comparison. Such a study would require information on individual identities, contest durations, and measures of RHP for individuals as well as information regarding prior experience with combatants. Although this would be difficult for some species, particularly the aquatic breeders, such an endeavor would allow for a comprehensive review of decision-making during the breeding season from an evolutionary perspective in regards to the degree of polygyny, environmental conditions, and sexual-size dimorphism within and across phylogenies. Furthermore, such methods could also be applied to non-breeding contexts such as feeding patches, limited haul-out locations, or inter-species interactions to examine how these decision-making processes are conserved or differ across the behavioural ecology of a species or across taxonomic groups.

8.4.2 Consistency and flexibility across environments

By definition, mating patterns are determined by the distribution of resources in space and time, and the ease of monopolization of those resources (Emlen and Oring 1977). For example, in the polygynous grey seal system, female distributions are driven by water or pool availability at some colonies like North Rona (Twiss et al. 2007, Culloch 2012, Stewart et al. 2014) and therefore it would be expected that male behaviours and the opportunity for sexual selection should likewise reflect these patterns (Emlen and Oring 1977, Twiss et al. 2007, **Chapters 6 and 7**). In the same way that interannual variation in weather has been shown to drive female behaviours (Twiss et al. 2007), in this thesis, it was found that interannual fluctuations in weather patterns in relation to the local topography were driving inter-individual variation in rates of aggression amongst males (**Chapters 3 and 6**), and the variation in the effectiveness of alternate mating tactics (**Chapter 7**). It was also shown that stochastic perturbations in the environment can shift the importance of dominance as a measure driving the amount or intensity of conflict for individuals (**Chapter 6**).

While the distribution of the resources, in this case oestrus females, might be the driving force for the variability in male behaviours, the expression of this variability in both sexes is likely driven by past and present grey seal ecological constraints (Bartholomew 1970). For example, compared to other pinnipeds such as harp seals, which breed exclusively on landfast ice during the winter, grey seals are a relatively widely-distributed species which breeds across many substrates and environmental conditions. Over evolutionary time, this has likely selected for some flexibility in the expression of behaviours within and across seasons, and across individuals and colonies. For example, male and female grey seal breeding at Sable Island in Canada are generally larger than seals in the UK population, and females also have relatively shorter lactation periods (Twiss pers. corr., Boness and James 1979, Twiss 1991). It is uknown what is driving the size differences between these regions of grey seal distribution, but short lactation periods are typically associated with ice-breeding seals (Riedman 1990, Krüger et al. 2014). Therefore, the shorter lactation period at Sable Island might reflect how recently in their evolutionary history grey seals in that region switched from breeding on ice (Boness and James 1979, Krüger et al. 2014). Differences in sizes and behavioural patterns have been described in other species, such as stickleback fish (*Gasterosteus aculeatus*) populations (Bell and Sih 2007). Individual fish from the population which experienced relatively greater predation risk had heavily plated armor. They also were on average behaviourally more ‘timid’, expressing more antipredator behaviours than the individuals from the other population (Bell and Sih 2007). It is clear local environmental and evolutionary conditions can shape the behavioural and morphological variability expressed across individuals and populations, and further work investigating the drivers of this variability would likely be valuable for modelling population dynamics across species distributions.

Some behaviours, and the effectiveness of certain conflict reduction mechanisms, appeared to be context dependent, but other aspects of the breeding behaviours of grey seals were inflexible or predictable across variable environments. Activity budgets were largely conserved across the three breeding colonies in this study (**Chapter 3**). A recent addition to the behavioural repertoire, the Body Slap, appears to be a reliable source of information regarding

RHP regardless of the temporal and spatial variability in substrate dampness due to rain and tidal inundations (**Chapter 4**). Also, the evidence from **Chapter 7** regarding mating tactics suggests that some males might express their RE at a consistent time across years regardless of the local current conditions (sex-ratio, density, weather), even if the relative success of a particular strategy is reduced. Such consistencies might represent the selection for some behavioural syndromes, or consistent individual differences, within a population (Twiss and Franklin 2010). Additionally, there was still unaccountable variation in the models predicting mating success by RE and in models predicting individual rates of aggression. This variation might be attributed to such consistent differences between individuals (*e.g.*, how flexible they are in response to the environment or how constrained they are in their behaviours; **Chapters 3, 6, and 7**). Finally, while there was evidence of consistency in activity budgets across populations (**Chapter 3**), how individuals achieve this might vary dependent on the local environment. For example, as seen in **Chapter 6**, males might achieve a similar reduction in aggression pre- and post-tidal flood events, but the mechanisms driving those rates appeared to switch from a social stability to one based on individual dominance. With the time constraints of a three year study, any conclusions to be drawn about consistencies in individual differences in male aggression or RE tactics are somewhat limited. However, my results suggest that future studies investigating the consistency or flexibility that individuals can express, in regards to aggression or RE across contexts, should be done taking into account the environment at a fine-temporal and spatial scale. Furthermore, as mentioned in **Chapter 6**, a future step will also be to attempt to combine physiological and behavioural metrics of these fine-scale dynamics to identify the potential individual costs of behavioural flexibility or consistency in aggression or RE. Fitness consequences and population level assumptions can then be made which might be masked by approaches which rely strictly on observed behavioural patterns.

8.4.3 Future investigations into flexibility and consistency

Within-season variation in RE, aggression, and attendance has been acknowledged as a part of the behavioural ecology of grey seal breeding systems (Twiss et al. 1994, Pomeroy et al. 1994, Pomeroy et al. 2000), but more often than not, aggression and RE have been averaged across an entire season and inter-annual variation has been explored (Twiss 1991, Twiss et al. 1998, Twiss et al. 2007, Lidgard et al. 2012). As capital breeders, the decision-making processes regarding the relative trade-offs and benefits of aggressive, or costly, behaviours are likely taking place for individuals at a much finer temporal scale, as the physical and social environment changes throughout the course of a season (Twiss et al. 1994, Pomeroy et al. 1994). In this thesis, the process of investigating individual behaviour at a fine temporal and spatial scale has revealed new information for grey seals regarding the flexibility of behavioural decision-making in contests (**Chapter 5**), changed the perceptions on what intrinsic and extrinsic characteristics drive individual rates of aggression on a daily scale (**Chapter 6**), and revealed the potential for individually-consistent alternate mating tactics based on timing of RE within a season (**Chapter 7**). Similar methods, capitalizing on newer methodologies such as Elo calculations for dominance score (Neumann et al. 2011), can be applied to other systems with polygynous mating patterns which may not have considered the behavioural ecology of individuals at such a fine temporal scale previously. Particularly, such investigations will likely be of interest in species that experience variability in social or environmental conditions within a breeding season, species that are capital breeders and energetically limited, species that have experienced relatively recent evolutionary changes in breeding patterns, or species that are predicted to experience environmental or social changes in response to future climate change.

8.5 Review of male grey seal sexual selection: size and strategies

The trade-offs between size and reproductive success has been examined extensively in the literature, often with the phrase ‘Bigger isn’t always better’ in the title (Kirkpatrick 1989, Knapp and Warner 1991, Zamudio et al. 1995, Sadowski et al. 1999, Vanpé et al. 2010, Jones et al. 2011, Regnier et al. 2013, Young and Bennett 2013). These studies have explored the somewhat contradictory observations that in species which are sexually dimorphic, the larger sized individuals do not always achieve the greatest fitness or lowest aggression. For example, male *Drosophila melanogaster* which were phenotypically smaller but developed under optimal thermal conditions had greater territorial success through physiological vigour (Zamudio et al. 1995). Standard length, not mass, in male sword-tails was the strongest predictor of RHP (Moretz 2003) and while mass was a good predictor of RHP for large male maritime earwigs, smaller males benefited from weapon asymmetry as a possible enhancement of maneuverability (Munoz and Zink 2012). These findings suggest that the adaptive significance of being larger in a highly competitive system, such as the grey seal’s polygynous system, might not be as clear as once assumed.

A recent review of sexual size dimorphism (SSD) in pinnipeds has suggested that the degree of SSD, when the two elephant seal species are excluded, is not correlated with the variation in reproductive success across species (González-Suárez and Cassini 2014). The authors suggest that instead of sexual selection, size differences between sexes might be driven by differing constraints in endothermy across sexes. For example, females are constrained in energy by lactation and gestation; while males can invest more energy in body size and their increased size might further allow for exploitation of colder or deeper waters for foraging (González-Suárez and Cassini 2014). In their study, González-Suárez and Cassini (2014) only considered differences in SSD in relation to variation in mating success, without considering the local topography or environmental conditions where breeding occurs (**Chapter 3**). All of the species of Otariidae they tested are terrestrial breeders, but some species, such as the Galapagos sea lion, males and females are both known to spend some time at sea foraging and some on land during the breeding season (Meise et al. 2014). In contrast, of the phocid species examined, the species which are known to have either primarily aquatic mating (*e.g., Phoca vitulina richardsi*, van Parijs et al. 2000) or some indication of aquatic mating (*Halichoerus grypus* Lidgard et al. 2004) had much smaller SSD values than the Otariidae, and much smaller SSD than the elephant seals (González-Suárez and Cassini 2014). Therefore, it is more likely that SSD might still be under sexual selection pressure, but that the degree of expression is dependent on the mating strategies present in the system, which, in turn, are likely driven by the environmental context (**Chapter 3**).

Although González-Suárez and Cassini (2014) found a relatively low SSD coefficient for grey seals adults: males were typically larger, both by mass and length, on average than females (Reidman 1990). The relatively larger mass for males likely increases their fitness by increasing the duration of fasting and/or residency on a colony (Twiss 1991). Throughout this thesis, the theme of the importance of conservation of energy, and arguably mass, has been supported strongly as a factor driving male aggressive breeding behaviour either through reduced response to disturbance (**Chapter 3**), through the prevalence of draws and the mutual assessment in draws (**Chapter 5**), and through social stability reducing the amount of aggression individuals engage in on a daily basis (**Chapter 6**). However, investigations into the determinates of male success have shown that mass does not directly correlate to dominance (Carlini et al. 2006) and that male grey seals of intermediate length were found to have the greatest mating success at Sable Island, Canada (Lidgard et al. 2005). I further provides evidence supporting the greater apparent fitness of males of intermediate length, in that these males were more likely to win aggressive interactions (**Chapter 5**).

The apparent contradiction in the importance of mass and length could be explained by the evolutionary history of the grey seal breeding system and the polygynous mating pattern. Until the last glacial maxima, grey seals were likely exclusively ice-breeding and probably exhibited relatively more aquatic mating (Krüger et al. 2014). It is therefore possible that there have been strong selection pressures promoting traits which increase manoeuvrability in aquatic fighting, but after terrestrialization, selection has also promoted phenotypes (including behavioural phenotypes) and behavioural mechanisms which facilitate prolonged fasting. Presently, most grey seal males adopt a terrestrial mating strategy; however, the grappling and wrestling involved in fights might be better suited for males with intermediate lengths, as bulk or mass would likely hinder maneuverability (Twiss 1991, Lidgard et al. 2005). Consequently, I hypothesize that these trade-offs might have contributed to the relatively reduced sexual dimorphism in this species, as selection has worked in opposite directions balancing the trade-offs between increased competitive abilities and increased fasting capabilities. These contrasting selection pressures might also explain the finding that while length of RE is an important determinant of mating success overall, timing of RE also appears to be a contributing component of male mating success, with some evidence of differences in tactics across size within tenured males (**Chapter 7**).

This hypothesis extends beyond grey seals to other pinniped species. González-Suárez and Cassini (2014) found that the species of Otariidae which had the lowest SSD was the Galapagos sea lion. Recent research has suggested that for this species, which exhibits a semi-aquatic mating strategy, absolute mass is not as important as body length in predicting mating success (Pörschmann et al. 2010). Much of the comparative work examining the evolution of species mass and length, and the tradeoffs between mass and manoeuvrability has been done via meta-analysis (González-Suárez and Cassini 2014). A goal of future research might therefore be to link the fields of behavioural evolutionary ecology and animal kinematics (*e.g.*, Halsey et al. 2011) to examine these evolutionary trade-offs between size and manoeuvrability. This could be done at the intra- or inter-specific levels by (1) testing for genetic and phenotypic differences within and across species; (2) determining how individual body size relates to the local physical environments, (3) testing how these size differences relate to individual strategies, and subsequently, (4) linking behavioural and energetic measures through the use of modern technology such as accelerometers (Halsey et al. 2011).

8.6 Conclusions

In conclusion, this thesis has provided new insights into the evolution of conflict and conflict reduction, variation within and across polygynous mating systems, grey seal behaviours, including signalling, and has suggested how these features might have implications for conservation and management. However, it has also identified gaps in the theory (assessment in draws) and empirical methodologies (*e.g.*, ignoring or omitting draws) used to assess contests and conflict reduction in wild systems which will be of interest to future explorations of conflict in wild systems. Furthermore, it has highlighted that whenever possible, future studies which examine individuals' behaviour should be done *in situ*, with fine-scale spatial and temporal data. This allows for the incorporation of the natural variation across a wide range of breeding conditions into models of individual behaviours. Such approaches can not only reveal the plasticity and variability in how individuals deal with the tradeoffs between costs and benefits, but can also allow for observing behavioural conditions that might have been 'artificially selected out' in controlled, laboratory settings (e.g. not allowing for draws).

Grey seals and elephant seals have routinely been used as model systems for investigating the behaviour and physiology of individuals under varying degrees of polygyny. Grey seal breeding behaviours were extensively investigated in the 1970s-1990s, with recent increasing movement away from natural history studies and behavioural observation studies, and towards genetic assessments of fitness (Lidgard et al. 2004, Twiss et al. 2006), consistent individual differences in behaviours (Twiss and Franklin 2010, Twiss et al. 2012), or physiological underpinnings of behaviours (Bennett et al. 2012, Robinson et al. 2015). While it common to progress towards investigating the finer-components of a system (as this thesis itself does in **Chapters 6 and 7**), this emphasis on novelty and cutting edge science can often be at the expense of continuing the study of natural history, *e.g.*, revisiting old systems or pursuing similar studies at new locations or for new species. It is often only through graduate work that such studies are possible, due to lack of direct funding for such broad monitoring projects (*e.g.*, Twiss 1991, Lawson 1993, Deakos 2002, Culloch 2012). For example, since no previous study gathered information for colonies of grey seals breeding on the mainland of England, one of the first requirements of this thesis was to attempt to examine the overarching trends in the breeding behaviours of males at Donna Nook, relative to other colonies for which extensive behavioural information has previously been gathered (Boness 1984, Boness and James 1975, Anderson and

Fedak 1985, Anderson and Harwood 1985, Twiss 1991, Twiss et al. 1994, Pomeroy et al. 1994). By first gathering this information for Donna Nook, I set the groundwork for subsequent fine-scale examinations and discussions of local and broader ecological mechanisms in **Chapters 5, 6 and 7**. Furthermore, by taking this initial broad natural history approach, I was able to raise awareness of a behaviour previously overlooked in the repertoire of grey seals for 15 years and begin to examine its form and function (**Chapter 4**). Finally, this thesis has shed light on the broad drivers of sexual selection and the overriding nature of sexual selection with regards to anthropogenic stressors (**Chapter 3**). Ultimately, I suspect that although the realm of natural history science has been shifted to amateur naturalists and postgraduate students, the work is still continuing at some level in many systems. The challenge therefore, is to shift the views of scientific funders and publishers which express aversion to publishing studies which are local in scope, or without paradigm shifting results, and to re-affirm the importance of such studies for expanding and updating our information on the behavioural and evolutionary ecology, population dynamics, conservation issues and modeled predictions for the future.

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APPENDIX CHAPTER 3

A3.1 Activity Budgets

A3.1.1 Selecting the cut-off number of scans

If males were present on the colony for a short period there was the potential that some males' activity budgets could be skewed due to a sampling of anomalous behavioural events. To address this, previous studies have selected cut-off values for a minimum number of sample scans, to ensure that the males included in subsequent analyses have an adequate sample of scans and thus confidence that their measures are robust to anomalies. Twiss (1991) used 180 scans while Culloch (2012) used 200. I selected 200, as this removed much of the extreme variation seen in Figure A3.1 but still included a range of variability (Figure A3.2). Also, 200 scans represented approximately two days of observations, which meant any males selected fit the definition of a 'Tenured' male (Boness and James 1979). A similar pattern was found and used for 2012 (Figures A3.3, A3.4).

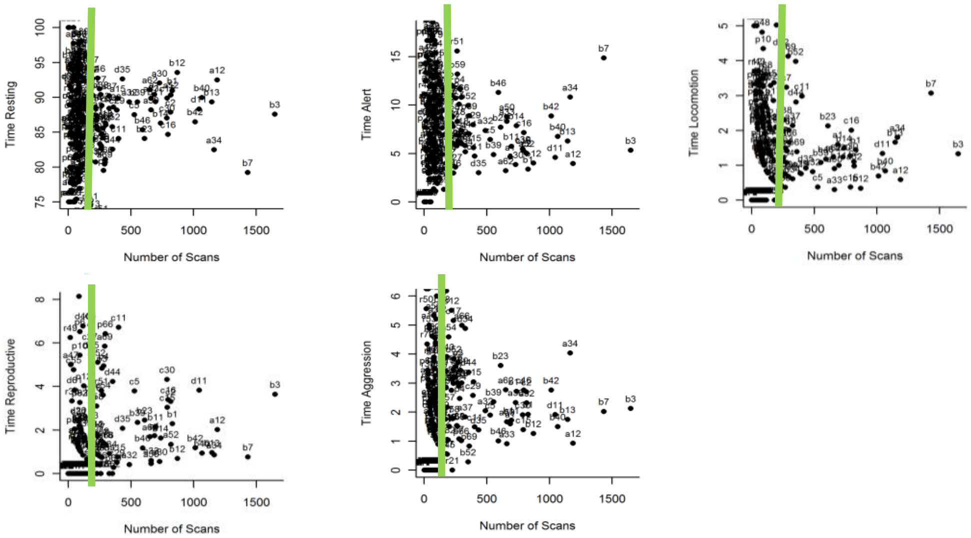

Figure A3.1 The percentage of time each individual male spent in the five broad behavioural categories, both sites combined, in 2011. Labels represent male IDs. Green lines represent the 200 scan cut-off criteria (Culloch 2012).

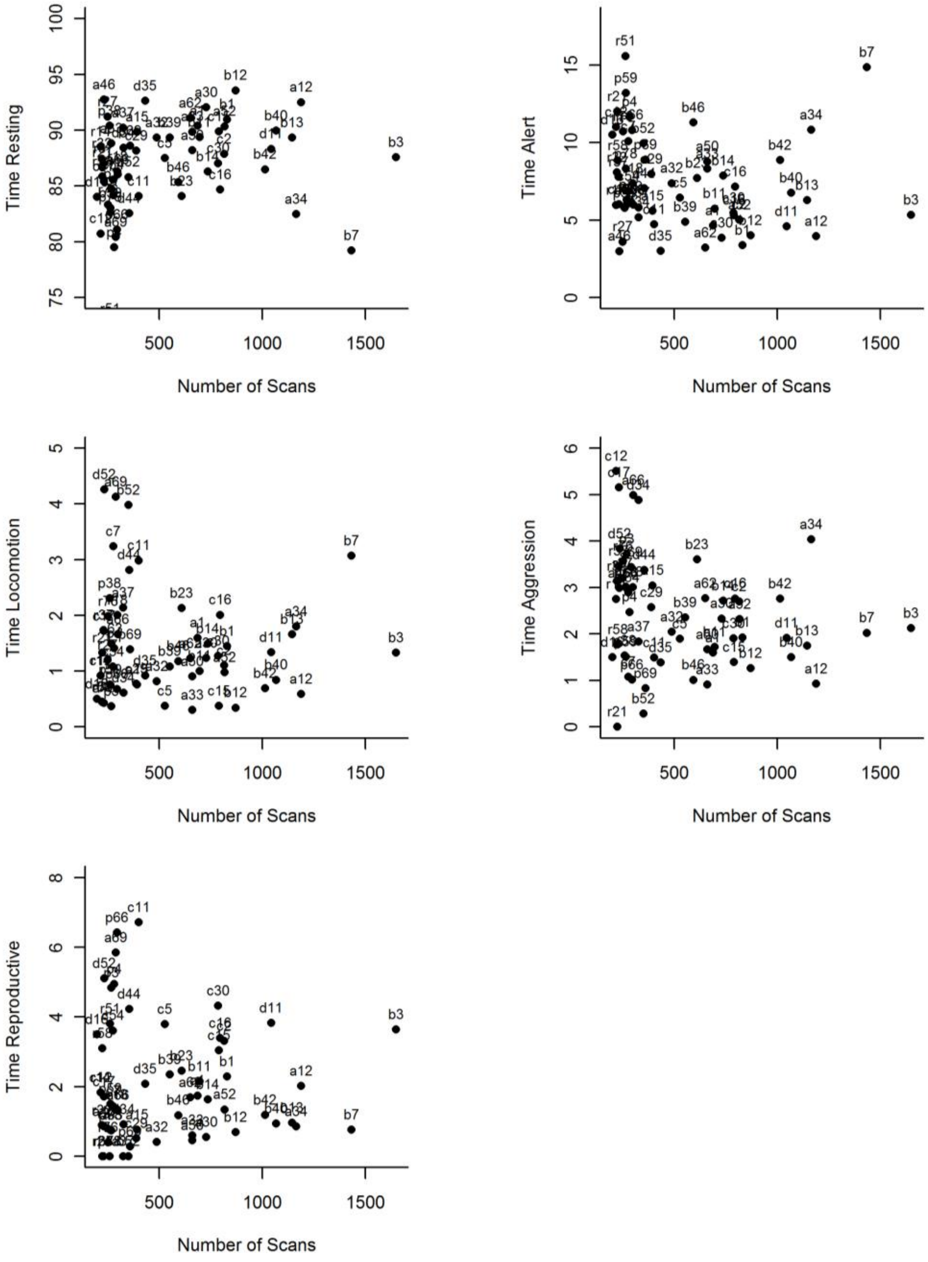

Figure A3.2 For males with ≥200 scans, the percentage of time each individual male spent in the five broad categories, both sites combined, in 2011. Labels represent male IDs.

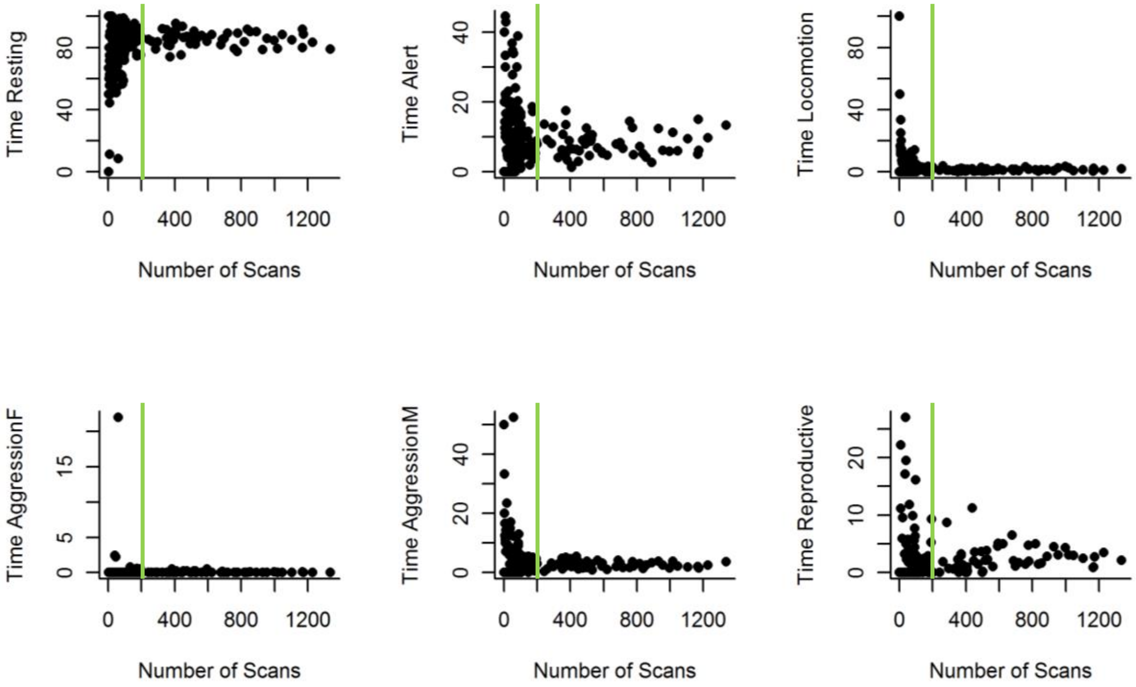

Figure A3.3 The percentage of time each individual male spent in the five broad behavioural categories, both sites combined, in 2012. Aggression was split by aggression towards females (AggressionF) and males (AggressionM). Green lines represent the 200 scan cut-off criteria (Culloch 2012).

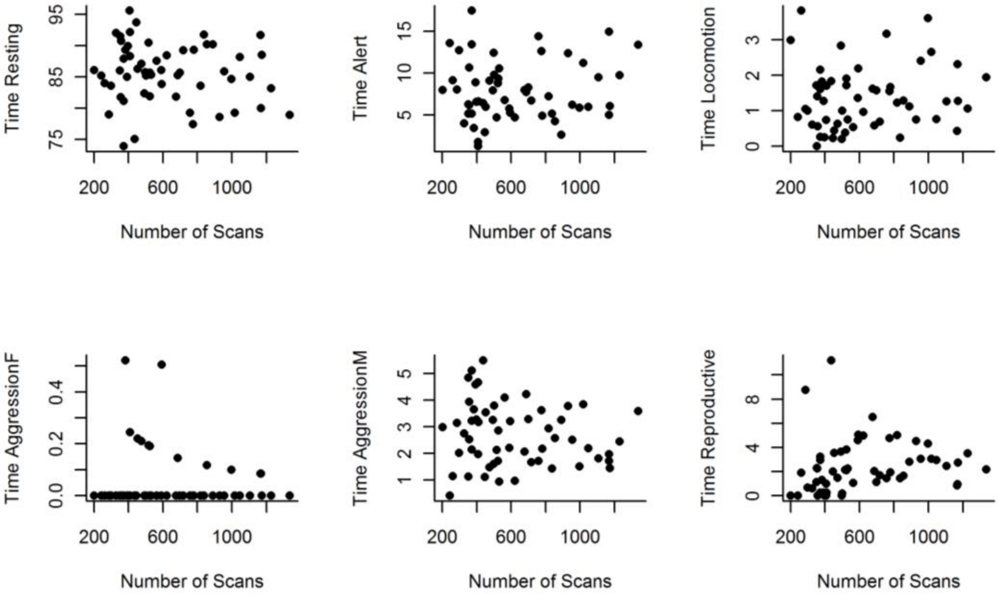

Figure A3.4 For males with ≥200 scans, the percentage of time each individual male spent in the five broad categories, both sites combined, in 2012. Aggression was split by aggression towards females (AggressionF) and males (AggressionM).

A3.2 Spatial distributions at Donna Nook and comparison colonies

A3.2.1 Male and Female Spatial Distributions and Densities at Donna Nook

Males were fairly consistent in their distribution and densities (#males / m^2) among years at both sites (Fig A3.5). At the PUB site (Fig A3.5), males seemed to use similar areas across all three years with areas of high male usage (high kernel density) forming discrete clusters. In contrast, the areas of highest male density at the RAF site seemed to be along the dune line in all three years; particularly 2012 evidenced extremely high male density in this area (Fig A3.5). Comparing between sites, maximum values of male density were greater at the RAF site in 2012 and 2013 and greater at the PUB site in 2011. The low whole-season densities in 2011 at both sites compared to 2012 and 2013, are likely in part due to the alternate day sampling regime that year reducing the number of points used to calculate densities (*e.g.*, PUB 2011 n = 3271; 2012 n = 8865 data points).

Maximum values for female density were greater than male density in all years and in contrast to males, female spatial usage did not span the entirety of the study area in any year (Fig A3.6). At the PUB site, females were clustered along the vehicle track and key features like muddy wallows, while females at the RAF site tended to cluster at the dune line (Fig A3.6). Spatial distribution of females at the PUB site did not appear to be different among years while at the RAF site, females were more dispersed throughout the study area in 2011 than in 2012 and 2013 (Fig A3.6). Again, the low densities in 2011 at both sites compared to 2012 and 2013 are likely due to the alternate day sampling regime that year reducing the number of points used to calculate densities.

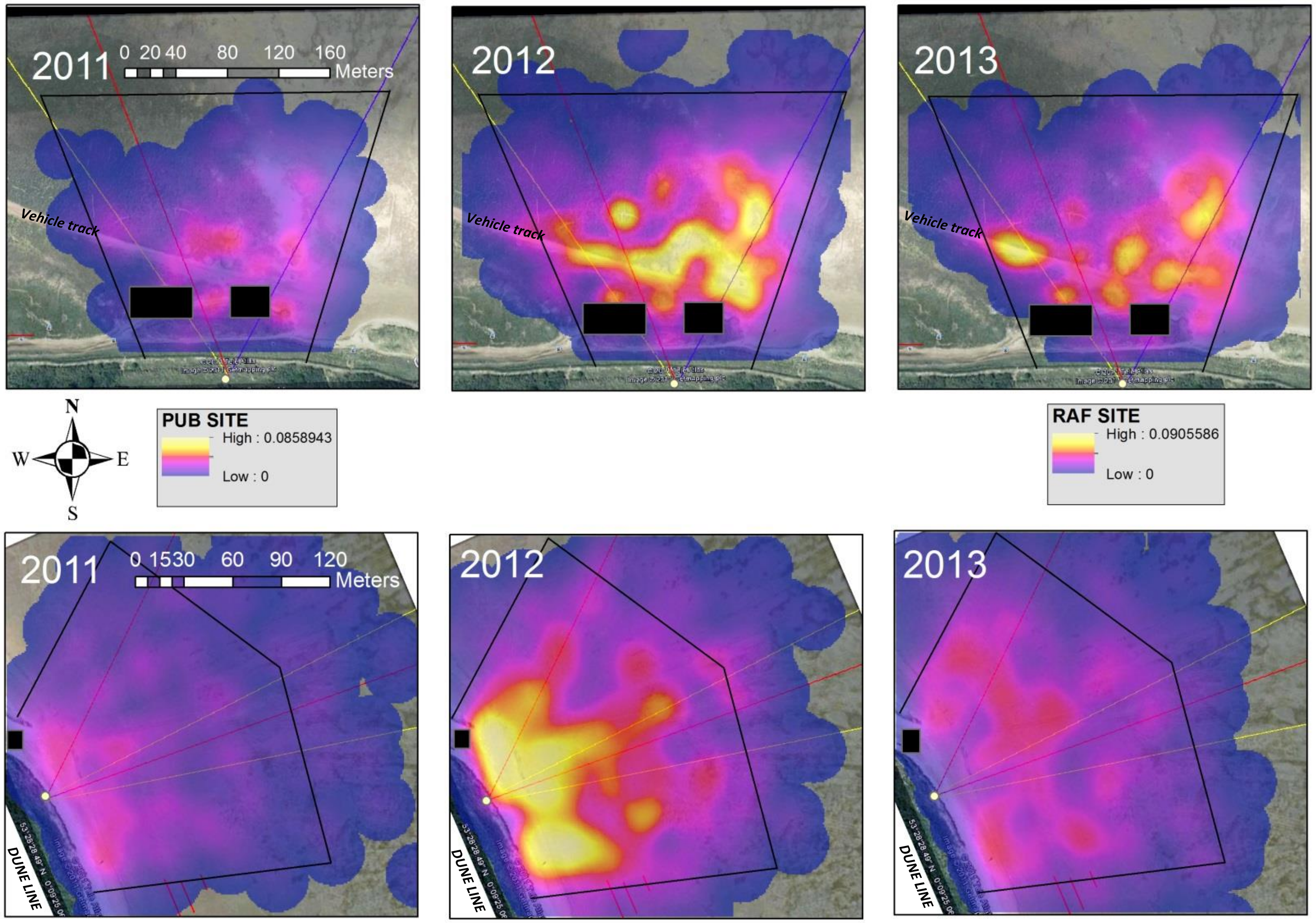

Figure A3.5 Density of males at PUB (top) and RAF (bottom) sites in 2011-2013. Density was calculated with the Kernel Density tool in ArcGIS 10.1 (20 m search radius). Coloured lines are artefacts of map used for orienting and converge at location of hide (yellow point). Study areas are inside outlined boxes. At the PUB site, blind spots due to dune elevation are denoted by filled boxes. At the RAF site, the entrance to the RAF site, where tractors and JCB enter the colony, is denoted by a filled box. Open water is to the North at the PUB site and to the North-North East at the RAF.

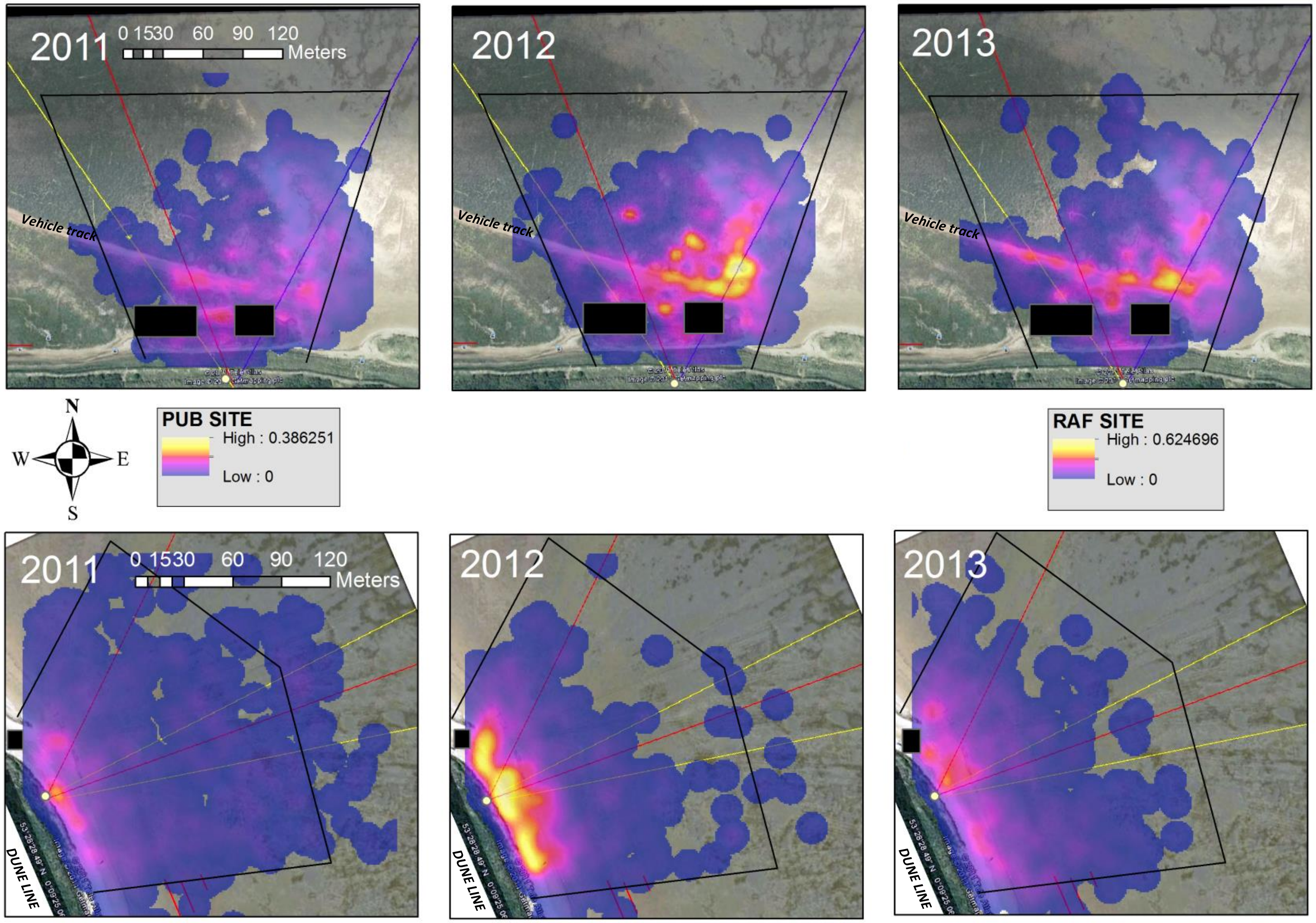

Figure A3.6 Density of females at the PUB (top) and RAF (bottom) sites 2011-2013. Density was calculated with the Kernel Density tool in ArcGIS 10.1 (10 m search radius). Coloured lines are artefacts of map used for orienting and converge at location of hide (yellow point). Study areas are inside outlined boxes. At the PUB site, blind spots due to dune elevation are denoted by filled boxes. At the RAF site, the entrance to the RAF site, where tractors and JCB enter the colony, is denoted by a filled box. Open water is to the North at the PUB site and to the North-North East at the RAF.

A3.2.2 Density of contact aggression

Aggressive interactions containing a contact phase at the PUB site were clustered around features characterized as low-lying and non-vegetated and were generally in the centre of the study area (Fig A3.7). At the RAF site, contact aggression seemed to occur most commonly near to the dune line in 2012 with fewer occurrences further seaward. In 2013, the highest density of contact aggression appeared to occur further seaward (Fig A3.7). In both years at the RAF site, a lack of contact aggression was apparent near the opening in the dunes to the RAF base (Fig A3.7). No data were available for 2011 as aggressive interactions were not mapped in this year.

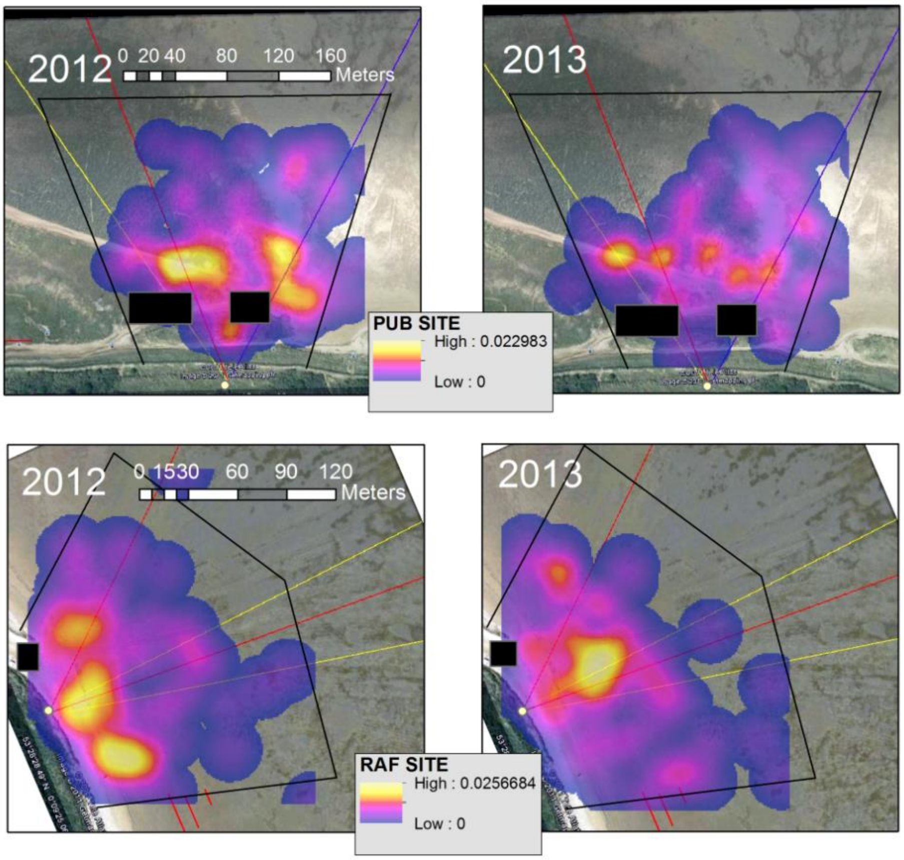

Figure A3.7 Density of aggressive interactions containing a contact phase at the PUB (top) and RAF (bottom) sites 2012-2013. Densities (fights/m^2) calculated with the Kernel Density feature in ArcGIS 10.1 with 20 m kernel. Coloured lines are artefacts of map used for orienting and converge at location of hide (yellow point). Study areas are inside outlined boxes. At the PUB site, blind spots due to dune elevation are denoted by filled boxes. At the RAF site, the entrance to the RAF site is denoted by a filled box. Open water is to the North at the PUB site and to the North-North East at the RAF.

A3.3 Seasonal changes in behaviour and spatial metrics

A3.3.1 Seasonal changes in rates of aggression

While the average rate of aggressive interactions varied among years, rates of aggressive interactions within years also varied on a smaller time-scale (Fig A3.8). In 2011, on day of year (DOY) 330 a tidal event occurred with abnormally high storm surge coupled with a spring tide. A similar event occurred on DOY 341 in 2013. None of the nearby tidal gauges were in operation during the 2011 events, so height of water is unknown, but this timing does correspond with a secondary peak in aggression in 2011 (Fig A3.8). In 2012 and 2013, the pattern is more typical with low rates of aggression early and late in the season, with rates plateauing during the majority of the season. No observations were made early (prior to DOY 308) in 2011.

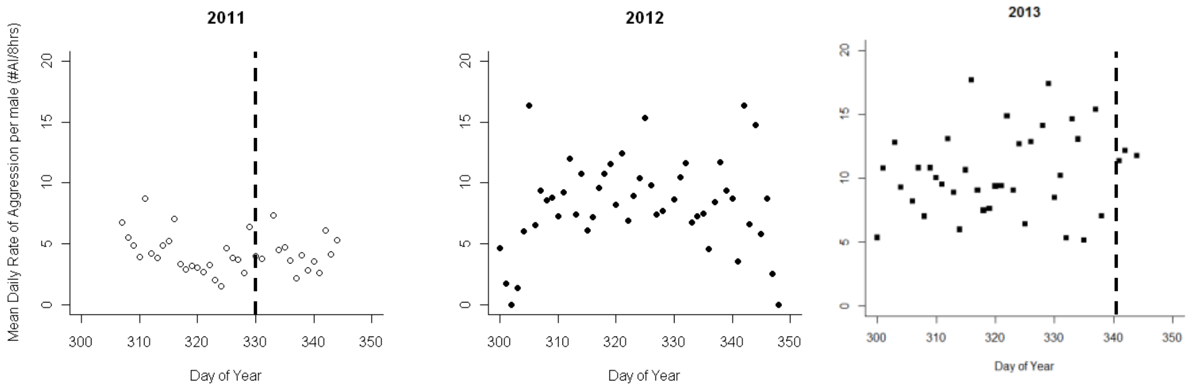

Figure A3.8 Mean daily rate of aggression per male by Day of Year (DOY) in 2011 (left), 2012 (centre) and 2013 (right). Dashed line represents the date of abnormal tidal events in 2011 and 2013.

A3.3.2 Seasonal changes in neighbour proximity within Donna Nook

Neighbour proximity on the colony varied within a season and between study sites (Figs A3.9 and A3.10). Particularly, after the extreme tidal events mentioned above, the mean distance to nearest male and female shifted at the RAF and PUB sites; this resulted in closer proximities between males and greater distances to nearest females on average (Figs A3.9 and A3.10).

In periods that were not affected by extreme tidal events, the patterns in these measures at the PUB site were relatively uniform across years. Patterns at the RAF site in 2012 and 2013 were also similar over time, but the seasonal fluctuations in 2011 showed increasing distance between males as the season progressed, reaching anomalously high average distances until DOY 330 (Figs A3.9 and A3.10) after which the spatial distributions matched those observed in 2012 and 2013. Speaking to the local wardens, this year was particularly dry (**3.3.2.1**) and the lead warden commented on the unusual spacing of the seals that year. Since mapping protocols did not differ over the course of the study, and the qualitative comments of local experts matches my observed pattern, this suggests the difference between years is not a sampling error but captured a real pattern.

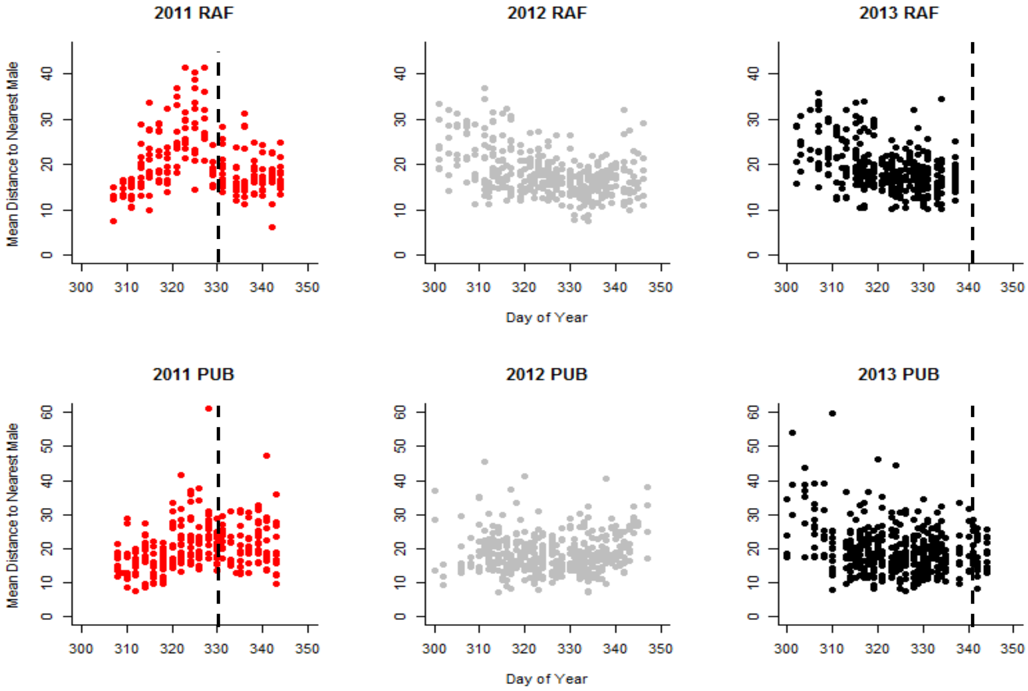

Figure A3.9 Seasonal changes in mean distance to nearest male neighbour show that as the season developed, male proximity decreased in 2012 and 2013, with an abnormally high increase in proximity distances up to the tidal event in 2011. Each dot is the average distance for a particular male on that Day of Year. Days of anomalous tidal events displayed in 2011 and 2013 plots with dashed lines.

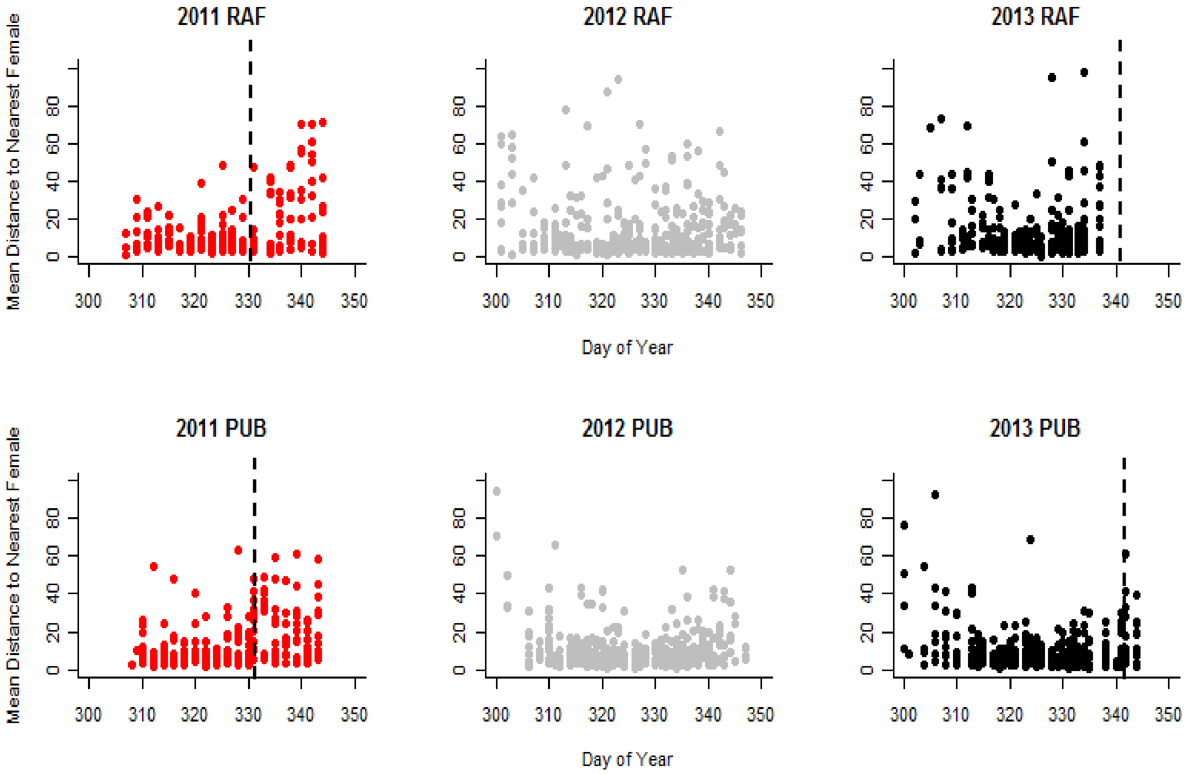

Figure A3.10 Seasonal changes in mean distance to nearest female neighbour show that as the season develops, female proximity did not vary in its temporal pattern between 2012 and 2013, however there was an increase in proximity distances after the tidal event in 2011. Each dot is the average distance to the nearest female for a particular male on that Day of Year. Days of anomalous tidal events displayed in 2011 and 2013 plots with dashed lines.

APPENDIX CHAPTER 6

A6.1 Dominance score calculations: some of the options

In previous studies (Twiss 1991), the metric used to calculate dominance ranks and scores for individual males was that used by Boyd and Silk (1983) which qualitatively ranked each male in an interaction by the intensity in which the two males displayed clear winning or losing (-4 loser was chased away, 0 draw, +4 winner chased away the loser). This calculation was deemed suitable for grey seal aggression in that, unlike other systems, 46-61% of grey seal AIs (defined in **Chapter 2**) result in draws (Twiss 1991). However the Boyd and Silk (1983) methodology does not deal with incomplete interaction matrices well and required a large sample of interactions per male to adequately calculate the average score for each male. Currently, David's Score (DS) (David 1987; Gammell et al. 2003; de Vries et al. 2006) has received support as one of the best static dominance measures for small systems where not all individuals interact with each other (Gammell et al. 2003). To calculate David's Score, a sufficiently large sample size is still required to avoid anomalous events from skewing an individual's score, but one particular benefit of this method, and an improvement on Boyd and Silk's method, is that the calculation weighs the outcome of contests by the opponent's relative dominance; for example, winning against a highly ranked male would improve a males' own rank more than if he won against a low-ranked male (Gammell et al. 2003):

> "*The proportion of wins by individual i in his interactions with another individual j (Pij) is the number of times that i defeats j (ij) divided by the total number of interactions between i and j (nij), i.e. Pij=ij/nij. The proportion of losses by i in interactions with j, Pji=1–Pij. If nij=0 then Pij=0 and Pji=0 (David 1988; de Vries 1998). DS for each member, i, of a group is calculated with the formula:*
>
> $$DS=w+w2-l1-l2$$
>
> *where w represents the sum of i's Pij values, w2 represents the summed w values (weighted by the appropriate Pij values, see below) of those individuals with which i interacted, l represents the sum of i's Pji values and l2 represents the summed l values (weighted by the appropriate Pji values) of those individuals with which i interacted (David 1988, page 108; de Vries 1998).*"

In early parts of this thesis I used David's score, which provides a whole-season estimate of dominance as this allowed comparisons to previous studies on male grey seals. To calculate individual males' scores, I first only selected males who were sighted for a minimum of two days and were involved in a minimum of 10 agonistic interactions throughout the breeding season. This matched previous studies (Twiss 1991, Twiss et al. 1998) and also matched the criteria set for determining for which males I calculated daily rates of aggression. Setting these criteria undoubtedly limited the number of 'transient males' included, so to try to account for this, the two day condition used in previous studies to classify males as 'tenured' (Boness and James 1979; Twiss et al. 1998) was relaxed to any two days sighted, not specifically two consecutive days, thus enabling a broader inclusion of male "strategies".

One of the aims of this thesis was to investigate fine temporal and spatial drivers of aggression and conflict reduction. David's score proved unsatisfactory for investigating the changes in behaviours and strategies within breeding seasons, as it was only capable of generating one score per male for a breeding season that was an average of all of the male's interactions. This ignored temporal variation within individual male's scores and ignored the variation in presence on the colony among males. For example, a male who was only present for the final week of the season but won every interaction could have a higher David's score than a male who was present all season and lost a handful of interactions. This temporal disconnect has rarely been considered in dominance literature due to lack of appropriate methodology, but was an aspect of the behavioural ecology which was of interest for this thesis. In order to address this, I utilized a relatively new method for calculating Dominance Scores in ecological systems, as suggested in 2011 by Neumann et al.: Elo Ranking (see: **Methods Chapter 6.2**).

Elo rating is calculated after each interaction. The points gained or lost depend on the expectation of the outcome and the relative difference in opponent scores. When the higher-ranked individual wins, Elo scores are calculated as:

$$\text{WinnerRating}_{\text{new}} = \text{WinnerRating}_{\text{old}} + (1\text{-}p)*k$$

$$\text{LoserRating}_{\text{new}} = \text{LoserRating}_{\text{old}} - (1\text{-}p)*k$$

where p is the expectation of winning for the higher-ranked individual as a function of the absolute difference in the two opponents before the present interaction, and k is a constant that determines the number of points gained or lost (Neumann et al. 2011). The value of k can determine how quickly Elo rating increases or decreases, but will only have minor influences on long-term rankings obtained (Neumann et al. 2011; Figure A6.1). If the lower rated individual wins, Elo scores are calculated as:

$$\text{WinnerRating}_{\text{new}} = \text{WinnerRating}_{\text{old}} + (p)*k$$

$$\text{LoserRating}_{\text{new}} = \text{LoserRating}_{\text{old}} - (p)*k$$

The initial scores are defined by the user, but this value selected has no effect on the differences in individuals' ratings, nor on the relative ratings (Neumann et al. 2011). Elo ratings can be applied to groups of any sizes, allow for individuals to leave and enter the groups without having to interrupt the rating process or restart building an interaction matrix, and are calculated independent of the number of individuals present (Neumann et al. 2011). It is suggested that ratings based on fewer than 9 interactions are 'provisional'; this matches the 10 AI criterion implemented in **Chapter 4**. Since males at Donna Nook had on average between 4 and 12 aggressive interactions per day, after 1-2 days of observations, accurate ratings, and changes in ratings, could be assessed. Once this provisional period is accounted for, changes in Elo over time have been shown to capture biologically meaningful changes in dominance such as individuals rising in dominance rank before leaving a natal group, or an individual losing position half-way through a breeding season (Neumann et al. 2011).

A6.2 Examining the differences in dominance hierarchies across DS and Elo methods

Male grey seal dominance hierarchies take on a non-linear, ogee curve shape: where first a few males appear to be distinctly dominant with steep differences in scores. This is then followed by a large group of males which have similar scores and low steepness of differences. Finally, the curve again steepens as the remaining males become increasingly subordinate. From the evidence of variation in mating success, this pattern makes biological sense, as only a few males achieve the majority of mating successes (**3.3.6**) .To see if using DS or Elo calculations resulted in different patterns of the hierarchy curve, a log-likelihood (LL) maximization test was conducted to determine how many segments best described the hierarchy curve and at what point the breaks occur. LL values for 3-segment and 2-segment curves were compared to determine which model had the best fit. This was done for hierarchy curves generated by David's Score and mean Elo score per male in 2011 and 2012, at the RAF and PUB sites separately.

The inclusion, exclusion, or omission of aggressive interactions which result in draws (**Chapter 5)** also presents a potential factor influencing the seasonal shape of a dominance hierarchy. To examine this, the above analysis was also used to compare the curves for mean Elo when the calculation either (1) included Draws or (2) omitted all contests which resulted in a draw.

A6.2.1 Results: Comparisons of dominance score calculation methods

A6.2.1.1 DS vs. mean Elo

Results of a GLM indicated that David's Score and rank by David's Score share a positive, linear relationship with mean Elo and rank by Elo, respectively, for 2011 at both sites (Figures A6.1; statistics in figure legend). Data for 2012 also showed similar patterns (RAF 2012**:** Mean Elo vs. DS ($R^2 = 0.63$, $P < 0.0001$); Rank DS vs. Rank Elo ($P < 0.0001$);

PUB 2012 Mean Elo vs DS ($R^2 = 0.46$, $P < 0.0001$); Rank DS vs Rank Elo ($P < 0.0001$). This matches findings of Neumann et al. (2011) and suggests the two measures are interchangeable at the individual level for analyses looking to describe broad, whole-season dominance scores. It also validates setting *k* in the Elo calculation at 200 for this system, as this resulted in similar dominance outputs as the David's Score method.

A6.2.1.2 Hierarchy structure: Mean Elo vs DS

Dominance hierarchy structure for grey seals is typically characterized by a non-linear, ogee curve that is best described by three segments (unpub data: Twiss et al. 2013). When qualitatively comparing the structure of the dominance hierarchies using Normalized mean DS and normalized mean Elo, the patterns appeared relatively similar between sites and years (Figures A6.2). Both methods resulted in similar ogee curve hierarchy structures; though mean Elo seemed to result in a more linear and less pronounced curve than DS (Figure A6.2).

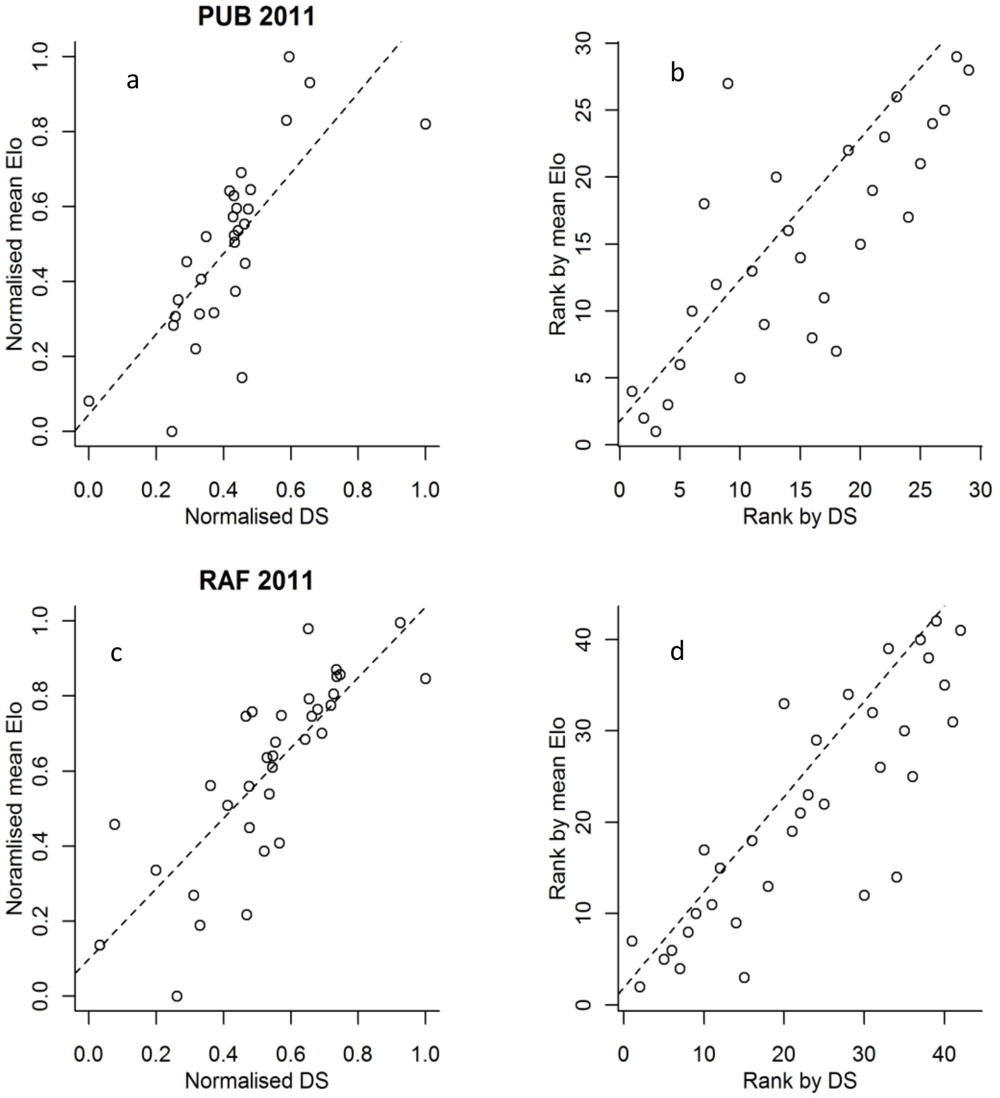

Figure A6.1 a) Mean normalized DS and Elo scores per male at the PUB site in 2011 (Spearman's: t = 6.07, df = 27, R^2 = 0.76, P =<0.0001); b) Final dominance rank per male by DS and Elo calculations at the PUB site in 2011 (GLM (*Poisson*) $P < 0.0001$); c) Mean normalized DS and Elo scores per male at the RAF site in 2011 (Spearman's: t =7.56, df = 32, R^2 = 0.80, P =<0.0001); d) Final dominance rank per male by DS and Elo calculations at the RAF site in 2011 (GLM (*Poisson*) $P < 0.001$). All calculated with draws. Increasing normalized DS or Elo represents an increase in dominance (Normalized DS 0 = low dominance). Increasing rank by DS or Elo represents a decrease in dominance (rank 0 = high dominance).

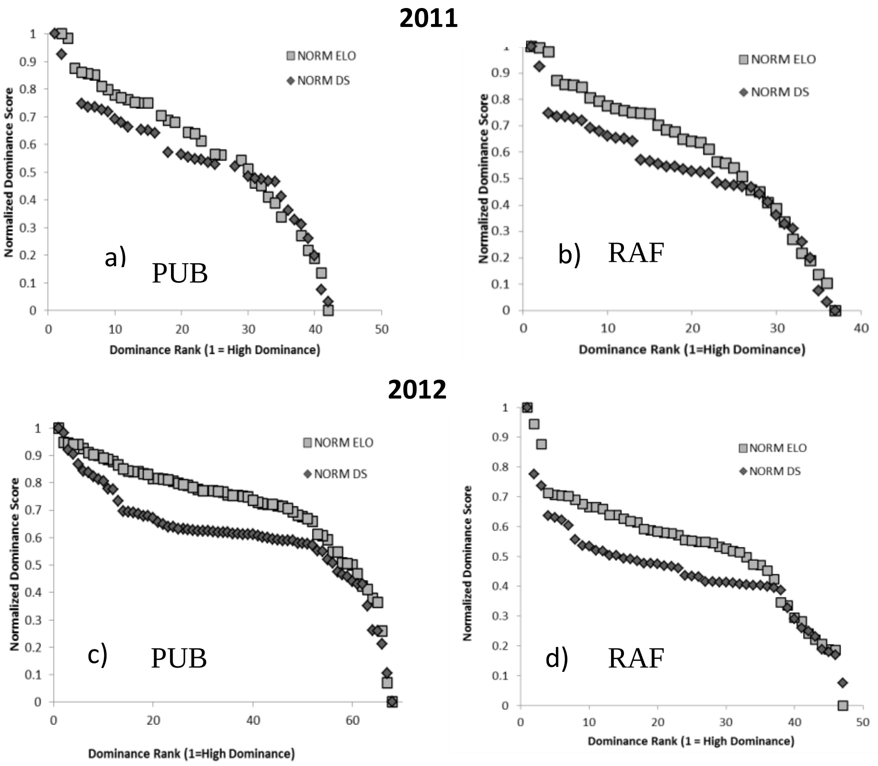

Figure A6.2: Hierarchy curves for a) PUB 2011, b) RAF 2011 c) PUB 2012 and d) RAF 2012; all with draws. Normalized David's Score and normalized mean Elo for each male. Structure of hierarchy was conserved.

Results of log-likelihood maximization tests revealed that for 2011 the curves for normalized DS and normalized mean Elo at the PUB and RAF were all best described by three segments (PUB DS: G = 55.45, *P* < 0.0001; PUB Elo: G = 34.40, *P* <0.0001, Figure A6.2a; RAF DS: G = 79.64, *P* <0.0001; RAF Elo: G = 85.97 *P* < 0.0001, Figure A6.2b). Although both methods resulted in the characteristic 3 segment curve, for the RAF and PUB curves in 2011, David's Score had fewer males in the top segment and more males in the bottom segment compared to Elo. At the PUB site in 2012, the DS and Elo curves were both best described by three segments (Elo: G = 39.35, *P* < 0.0001; DS: G = 118.47, *P* < 0.0001) but at this site, the DS included more males in the top and bottom segments than the Elo curve (Figure A6.2c). In 2012, at the RAF site curves for Elo and DS were both best described by three segments (Elo: G = 56.22, *P* < 0.0001; DS: G = 72.95, *P* < 0.0001) and the

Elo curve included more males in both the top and bottom segments than the DS curve (Figure A6.2d).

The other assessment of differences in methods of dominance score calculation was done by comparing the mean normalized scores for each method of calculation within individual males as both of these measures would give a relative position of a male from 0-1 (Figure A6.3). In 2011, the mean normalized DS was significantly lower than the mean normalized Elo at the RAF site (paired T-test: $t = 2.03$, df = 36, $P = 0.015$) and at the PUB site ($t = 2.05$, df = 28, $P = 0.014$). In 2012, the mean normalized DS was also significantly lower than the mean normalized Elo at the RAF site ($t = 2.01$, df = 47, $P < 0.0001$) and at the PUB site ($t = 1.99$, df = 67, $P < 0.0001$) (Figure A6.3).

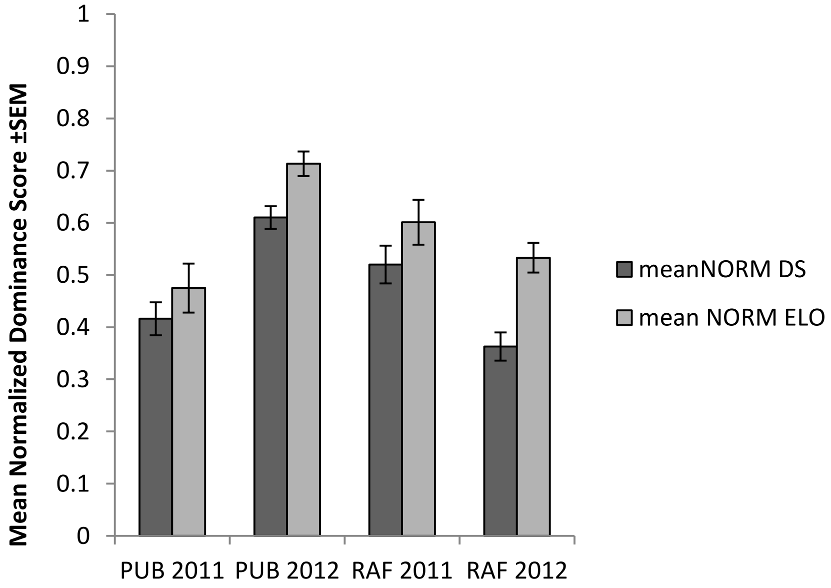

Figure A6.3 Mean dominance score using normalized David's Score (NORM DS) and normalized mean Elo score (NORM ELO) by site and by year. All differences were significant.

A6.2.1.3 Hierarchy structure: Inclusion or omission of draws

Both Elo and DS allow for inclusion of draws in the calculations. When draws were included in calculation of mean Elo per male, the hierarchy was less steep (Slope= -0.007

with; -0.0134 without) and less linear (R^2= 0.78 with; 0.96 without) compared to calculations of dominance which excluded interactions resulting in a draw (PUB 2012 as an example: Figure A6.4). The assessment of structure however revealed that when draws were not included, the curve was still best fit by three segments (G = 22.99, $P < 0.0001$). When omitting draws, the inflection points for the three segment curve were at 19 and 44 individuals compared to at 9 and 55 when the calculation including draws. This suggests that when draws are not included, more males are considered ‘dominant’ and ‘subordinate’ and fewer are categorized as ‘mid-ranked’ males, and would falsely imply the overall hierarchy increased in linearity and steepness due to omission of draws.

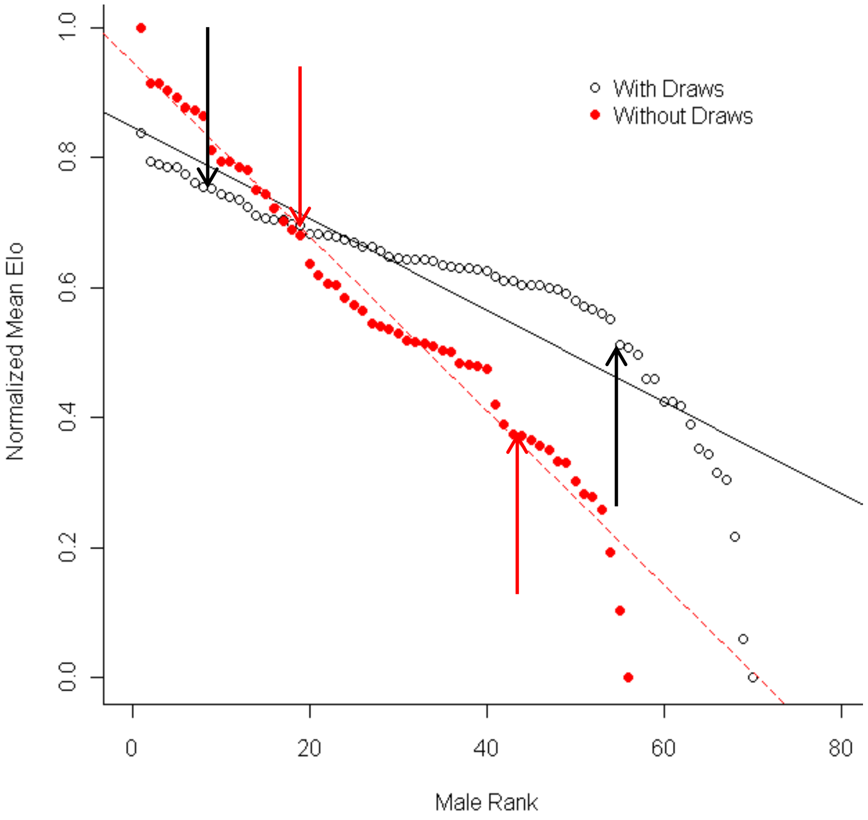

Figure A6.4 Plot of dominance curves for normalized mean Elo scores at the PUB site in 2012 with draws in the calculation (black, solid line) and when draws were omitted (red, dashed line). Arrows denote locations of segment differentiation; for the red, no draw, curve the inflection points are more evenly spaced with less males in the middle segment relative to the curve with draws. (*Number of males is slightly different across contexts as more males had >10 AI when including draws than when only considering contests with clear winners and losers).

A6.3 Relationship between dominance and aggression

Previous studies conducted at coarser temporal scales suggested that males with greater dominance ranks had relatively reduced aggression (Twiss 1991). Before looking at the finer scale of **Chapter 6**, I was first interested in seeing if the same pattern was present at Donna Nook. I used David's Scores as a measure of a male's whole-season dominance and fit GAMs with a Gaussian distribution and identity link to see if the average rate of aggression per male across the whole season was predicted by his David's Score of dominance. Best models were selected via AIC selection criteria (Richards 2008).

A6.3.1 Results: Does average dominance predict average aggression at DN?

Similar to the findings of Twiss (1991) when using whole-season averages for dominance (DS) and aggression, there was a trend suggesting a negative relationship between these two variables at Donna Nook. In 2011, the relationship between normalized DS and aggression was not significant (GAM: $P = 0.13$, $n = 59$, $R^2 = 0.08$; Figure A6.5a) and in 2012, DS did share a negative relationship with aggression (GAM: $P = 0.01$, n = 87, $R^2 = 0.12$; Figure A6.5b). From inspection of Figure A6.5, the reduction was only apparent for males with normalized David's Scores less than 0.3. While the relationship was only significant in 2012, in both years it appears that males with a Normalized David's Score of less than 0.3 had higher average rates of aggression but the negative relationship was lost above this threshold. Males with Normalized David's Scores greater than 0.3 did not gain any further reduction of aggression due to increases in their dominance score (Figure A6.5). Both of the R^2 values are lower than those observed at NR and SI (linear regression Twiss 1991: R^2=0.35 NR, 0.16 SI) suggesting that for DN, average rates of aggression and dominance scores do not share a strong predictive relationship.

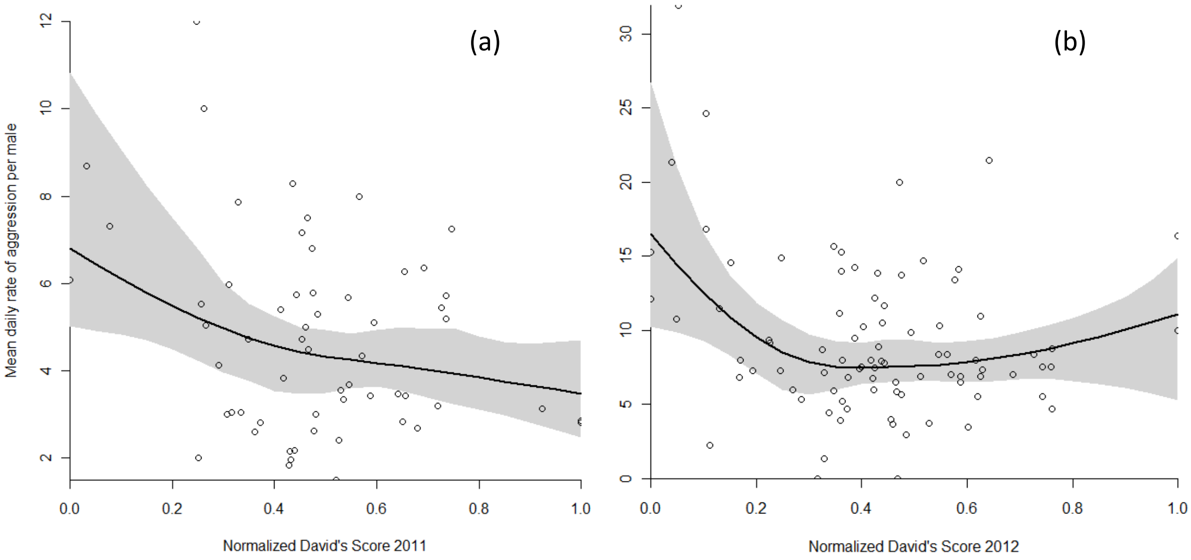

Figure A6.5: GAM outputs for 2011 (a) and 2012 (b) comparing an individual's Mean Daily Rate of Aggression across the whole season with his Normalized David's Score (>NormDS = >Dominance). In both years, males with ≤ 0.3 DS had higher than average aggression, however males with DS > 0.3 did not have any relationship between their mean aggression and their dominance.

A6.4 Discussion

These analyses confirm that Elo (with *k* of 200) and DS are interchangeable for the purposes of calculating whole season dominance scores. Using Elo does result in higher values for normalized dominance scores, but at the individual level the pattern of dominance ranking and the hierarchy structure is upheld. The exclusion of draws did significantly influence the hierarchy structure; specifically, omitting interactions with draw outcomes resulted in steeper or more linear hierarchies. Many animal systems are reported as having significantly linear, and steep hierarchies (Rosenthal et al. 1992, Drews 1993, Goessmann et al. 2000, Ang and Manica 2010), but if draws have not been accounted, for the reported linearity could be masking the more subtle dynamics of the social system. Thus, there is still a pressing need to investigate the topic of draws in animal contests and how ethologists should deal with them when addressing concepts such as dominance.

Finally, most of the analyses in this appendix were exploratory in the sense of investigating different methodological options for calculating dominance; however, the results of the final analysis, investigating the role of dominance on aggression, also provided the rationale for the main question of **Chapter 6**. Until now, for grey seals and other polygynous mammalian systems, dominance and aggression have been investigated at the scale of the whole breeding season, but from Twiss (1991) and the results of **6.3**, it is clear that this relationship was not explained thoroughly with this broad approach. One potential reason was that calculating dominance as an average across the whole season, and comparing it to an average rate of aggression across the whole season, masked the changes in dominance over time or potentially masked the effects of environmental and social variables on aggression, both of which are known to fluctuate throughout the season at fine temporal and spatial scales. This directly led to the questions addressed in **Chapter 6**.