

Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity

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ABSTRACT: Human–wildlife interactions can be incidental or direct through activities such as wildlife tourism. In the presence of anthropogenic activities, some animals exhibit behavioural alterations such as increased vigilance or spatial displacement. Thus, chronic exposure could be adverse to individual fitness through loss of energy or time. Pinnipeds are exposed to human activities in the aquatic environment and on land, but the degree of exposure varies across a species' geographic distribution. For example, breeding colonies of grey seals *Halichoerus grypus* along the mainland coast of England are exposed to anthropogenic disturbance in the forms of tourism and military activities; however, many offshore colonies are relatively undisturbed. Due to the recent expansion of mainland colonies, the impacts of human presence during the breeding season are of urgent interest for managers. Therefore, the aim of this study was to test for any behavioural adjustments associated with anthropogenic presence by comparing the activity budgets of individual male grey seals at a mainland colony with activity budgets from 2 isolated colonies. We found no evidence of differences in the male activity budgets for time spent in non-active behaviours across colonies, and of the 3 colonies, males on the mainland spent the least amount of time alert. This indicates that as capital breeders, selection for conservation of energy is potentially overriding short-term costs of local stressors or that males at the mainland colony have habituated to human presence. Our results demonstrate the importance of understanding species- and life-history-stage-specific selection pressures when considering management actions.

KEY WORDS: Wildlife tourism · *Halichoerus grypus* · Behaviour · Conservation · Management

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INTRODUCTION

Human population growth has been associated with increased human–wildlife interactions (Treves & Karanth 2003, Converse et al. 2005), particularly 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; NOAA 2012). This overlap of human and wildlife spatial usage in coastal regions drives unintentional interactions such as manatee strikes (Jett et al. 2013) and fisheries bycatch (Lewison et al. 2014), but also can promote intentional interactions such as wildlife

tourism (Hardiman & Burgin 2010, Velando & Munilla 2011, Curtin 2013, Le Boeuf & Campagna 2013, Mustika et al. 2013). Marine wildlife tourism is a multi-million dollar industry worldwide. For example, in 2010, reports from Scotland indicated that marine wildlife tourism had a net economic impact of around £65M (equivalent to US \$110M; SGSR 2010). In most cases, organized wildlife tourism operates under the ethos of sustainable, non-invasive and conservation-minded wildlife viewing, and the public responds positively to these measures (Ballantyne et al. 2009, Le Boeuf & Campagna 2013). To ensure sustainability, many government organizations, non-profit organizations and associations of tour opera-

tors 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 a 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 that has high exposure to human interactions is the phocid seals. Species within this group face exposure to human activities at sea while foraging (Skeate et al. 2012) and on land during breeding, moulting and resting periods (Perry et al. 2002, Curtin et al. 2009, Le Boeuf & Campagna 2013, Granquist & Sigurjonsdottir 2014). Many studies have focused on determining the effects of disturbance during critical periods such as pupping or moulting. Altered behavioural states during these times could be placing an energetic cost on seals, resulting in long-term repercussions or a reduction in fitness (Suryan & Harvey 1999, Lewis & Mathews 2000, Engelhard et al. 2002, Perry et al. 2002, Stevens & Boness 2003, Curtin et al. 2009, Granquist & Sigurjonsdottir 2014). At sea, disturbances can lead to lost foraging opportunities and/or increased energetic costs through physiological or behavioural alterations associated with avoidance behaviours (Williams et al. 2006, Christiansen et al. 2013). As capital breeders, the potential for increased energy expenditure due to disturbance while on land is also

important to consider, as most 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 and reproductive success (Twiss 1991, Lidgard et al. 2004, Twiss et al. 2006), and any disturbances during these discrete life history periods could lead to reduced individual fitness. How individuals respond to disturbances, whether on land or at sea, will likely be determined by the ecological landscape, level of exposure to tourism activities, and individual differences in tolerance to disturbances (Bejder et al. 2009, Bennett et al. 2013, Christiansen et al. 2013, 2015).

Grey seals *Halichoerus grypus* are a species of phocid that occupies a wide geographic range, breeds across a variety of substrates, and demonstrates variability in behaviours in response to topography and weather, across and within sites (Boness 1984, Anderson & Fedak 1985, Twiss 1991, Lawson 1993). Many of the studies investigating the ecology and behaviour of this species have been conducted on populations breeding on offshore islands in remote places such as northern Scotland (e.g. North Rona and the Monach Islands) or eastern Canada (Sable Island) (Fig. 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

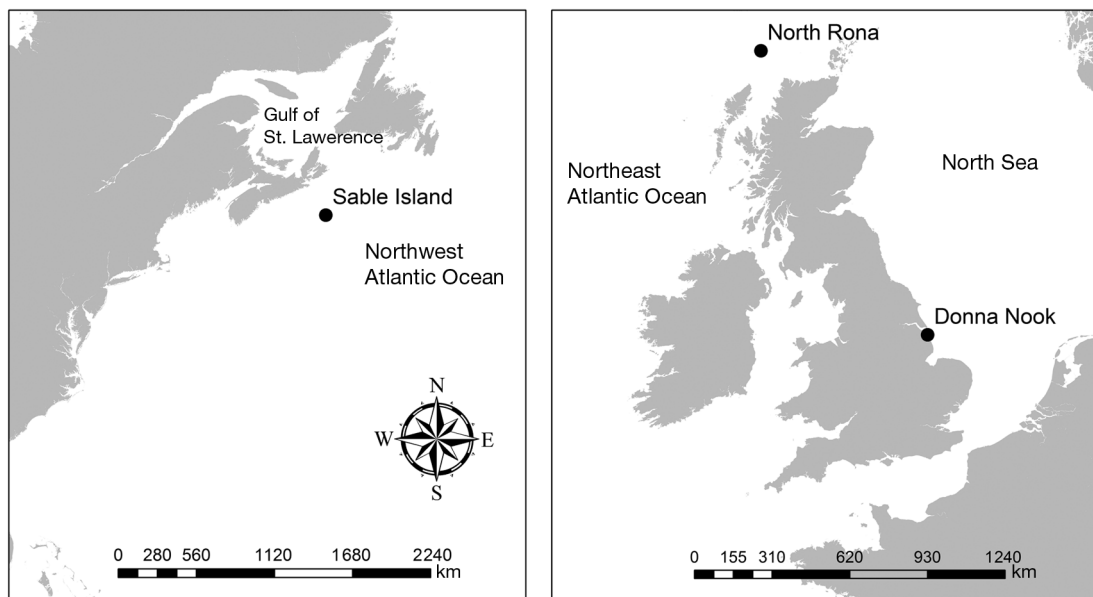


Fig. 1. Locations of grey seal *Halichoerus grypus* breeding colonies in the North Atlantic with published datasets available for male activity budgets. Data from Sable Island (Canada) and North Rona (Scotland) were collected by Twiss (1991). Data from Donna Nook were collected for the present study

coast (Duck & Morris 2010, NEFSC 2010). As such, haul-out sites and breeding colonies now persist 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, located on the mainland coast of England just south of the Humber Estuary (53.47° N, 0.15° E; Fig. 1). The site is managed as a part of the Lincolnshire Wildlife Trust's wildlife refuge system and the Defence Infrastructure Organisation air force training range. Since the mid-1990s, the colony has experienced rapid population growth with pup production increasing at rates of 5–40% between 1990 and 2014 (Duck & Morris 2010). As a mainland colony, Donna Nook is exposed to various levels of anthropogenic activity. The northern section of the colony is open to public viewing access. Visitors gather during the breeding season to view and photograph the seals, but physical contact with and proximity to the seals is restricted by a wooden double fence and by Wildlife Trust wardens. Due to the presence of the Defence Infrastructure Organisation base, the southern extent of the colony is off limits to visitor access, and human presence is limited to operational necessities. Throughout the breeding season, on weekdays, the colony as a whole is exposed to anthropogenic noise from military training exercises, usually consisting of periodic jet or helicopter flyovers.

Humans and human activities are often a part of the ecological system in which grey seal foraging and breeding occurs. Studying the behaviours of animals can reveal how this aspect of the environment influences behavioural choices and ultimately impacts fitness. Previous studies investigating the effects of human activities on grey seal behaviours have focused on non-terrestrial forms of disturbance, either noise pollution (Perry et al. 2002) or vessel-based viewing platforms (Curtin et al. 2009, Strong & 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 exhibited greater rates of alert behaviours. In contrast, Perry et al. (2002) found no evidence that adult male or female grey seals were responding behaviourally to sonic booms during the breeding season. These differences could represent changes in behavioural patterns across life history stages (breeding versus non-breeding) (Pavez et al. 2014); however, both of these studies focused on a single breeding or haul-out location and tested for acute response/no-response effects of anthropogenic activities. Our aim was to extend the scope of such

questions by utilizing data from across the geographic range of the grey seal to encompass as much of the natural variation in the behavioural ecology of this species as possible.

To do this, we compared activity budgets of males breeding on a mainland colony to those of males at colonies with historically little to no human presence and examined whether there appeared to be any cross-sectional behavioural indication of disturbance from terrestrial-based anthropogenic activities. 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 & Dill 2002, Holcomb et al. 2009, Côté et al. 2013). Bottlenose dolphins *Tursiops truncatus* 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 (Pirodda et al. 2014), and caribou *Rangifer tarandus caribou* herds 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 chronic anti-predator disturbance behaviours, we might assume individuals to be more active or vigilant across a breeding season than individuals from the more remotely located colonies. To test our hypothesis, we compared activity budgets for males at Donna Nook to those of males at North Rona, Scotland, and Sable Island, Canada (Twiss 1991), both of which are offshore colonies where the only human presence during the breeding season is associated with research. Specifically, we predict that time males spend in non-active behaviours will be lowest and time spent alert will be greatest at Donna Nook in comparison to males at North Rona and Sable Island.

METHODS

Description of breeding colonies

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. The entire colony is bordered

on the landward side by high dunes and thick vegetation. During the breeding season, 2 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. Seals often use tidal channels to move from the sea to locations across the sand flats. Sable Island (Canada) is topographically most similar to Donna Nook in some places. It is characterized by relatively unrestricted access and broad expanses of uniform flat sand around the periphery. Intricate dune assemblages occur centrally along some parts of the island (Boness & James 1979, Twiss 1991, Twiss et al. 1994). In contrast, North Rona (Scotland) has variable elevation up to 108 m (Twiss 1991). On the western coast, the high cliffs offer no access points and seals must access the breeding colony from 4 main gullies located on the eastern side. Once on the main breeding grounds, the vegetation is predominantly grassland interspersed with permanent and ephemeral freshwater pools, erratic stones and remnants of dry stone walls (Anderson et al. 1975, Twiss 1991, Pomeroy et al. 1994, Twiss et al. 1994).

Donna Nook general data collection

Field observations were conducted during all daylight hours (mean = 8 h 48 min daily) across 2 autumn breeding seasons from 3 November to 12 December in 2011, and from 27 October to 12 December in 2012. The breeding colony was split into 2 study sites to cover the range of topography: the PUB site with grassy dunes and mud wallows (53.476° N, 0.155° E), and the RAF site, which primarily comprised sand flats (53.474° N, 0.155° E). Males in the study area were identified daily via unique pelage markings or *post hoc* from high-resolution pictures taken with a Canon EOS 30D or 40D with a 100–400 mm lens (Twiss et al. 1994, Bishop et al. 2014) at distances ranging from 10 to 180 m, yielding a total of 183 males identified in 2011 and 140 males in 2012.

Estimated visitation numbers for Donna Nook were provided by the Lincolnshire Wildlife Trust (R. Lidstone-Scott pers. comm.). This included the number of visitors per day on the weekend and a total for visitors over the 5 consecutive weekdays in 2011 and 2012, and the total number of visitors each year since 1993. Differences in weekend visitor attendance between the 2 years of the present study were tested for using a *t*-test and differences in total weekday visitors per week across years were compared using a Mann-Whitney *U*-test due to small sample sizes.

Male activity budgets

An ethogram was generated to allow comparisons between this study and previously conducted behavioural assessments of male grey seals (Table A1 in the Appendix; Boness & James 1979, Anderson & Fedak 1985, Twiss 1991, Lawson 1993, Twiss et al. 1998). The primary observer conducted instantaneous scan sampling of all identified males at 5 min intervals while in the field (Altmann 1974, Twiss 1991). The order in which males had their behaviours recorded was consistent between scans. Although throughout the season a range of 5–20 males could be sampled at a time, even when peak numbers were scanned, the process of recording all males' behaviours took less than 1 min (mean = 50 s). Both of these considerations ensured that the interval between any given male's samples was consistent at 5 min. Activity budgets were then calculated from the scan samples to quantify the proportion of time each male spent in the distinct behavioural categories; in particular, time spent alert (Table A1). Some specific behaviours, such as attempted copulation, comprise a small percentage of the total activity budget and are not as informative for discerning potential effects of disturbance. Therefore, for this study, some behaviours were combined in order to investigate the percentage of time spent in the broad behavioural categories of non-active (rest + alert) and active (all other behaviours). The time spent in aggressive and reproductive activities was also calculated as the combined time spent in specific behaviours (as noted in Table A1).

Many males were only scanned for brief periods or for a single day, and over the course of the season there was considerable turnover of males in the study area. To restrict the potential for these records to skew overall averages, previous studies have calculated activity budgets only for individuals that exceed a threshold number of scans; Twiss (1991) used a minimum of 180 scans while Culloch (2012) used a minimum of 200 scans. We chose to calculate the activity budgets for males that had ≥ 200 scan records as this represented approximately 2 d of observations. Within the spectrum of male attendance behaviour on breeding colonies, these males would be classified as 'tenured' (Boness 1984, Twiss 1991). Raw values for Sable Island and North Rona activity budgets were provided by S.D.T. from the 1988–1989 seasons on North Rona and 1990 season on Sable Island (Twiss 1991). Due to a geographically isolated 'yodel' behaviour at Sable Island (Boness & James 1979), 'non-active' behaviours at this colony comprised rest, alert,

yodel, drink, and eat snow (Twiss 1991). All other behavioural categories were similar to those used at Donna Nook. We acknowledge that the use of these datasets might introduce observer biases between the North Rona/Sable Island data and the Donna Nook data. However, differences should be negligible since the observer at Donna Nook was trained by the observer from Twiss (1991), and all data were analysed at a relatively coarse behavioural scale.

The arcsine transformation for proportional data has been criticized for ecological data (Warton & Hui 2011). Therefore, we tested for differences in average activity budgets for behaviours between years within Donna Nook (total N = 118, male ID N = 95 [2011 N = 61 males; 2012 N = 57 males]) using generalized linear mixed-effects models with logit-transformed data (Warton & Hui 2011). Male ID was included as a random effect to account for pseudoreplication of some individuals across both years. The response variables were the proportion of time males spent in the broad behavioural categories of non-active, alert, rest, aggression, and locomotion, while the predictor variable was year. Since some males spent 0% of their time in aggression, to allow for logit transformation, male activity budgets for this behavioural category were shifted by adding the minimum, non-zero value for time spent in aggression to all data points prior to transformation (Warton & Hui 2011). This was also done for locomotion for the same reasons.

A similar analysis was then conducted to test for differences in activity budgets between breeding colonies (total N = 211, male ID N = 171 [Donna Nook N = 95 males, North Rona N = 56 males, Sable Island N = 20 males]) with models run to compare each of the above behavioural categories against the predictor variable of colony. Male ID was again included as a random factor. Best models were selected based on Akaike's information criterion (AIC) minimization following Richards' (2008) criteria, in which the model with the lowest ΔAIC is the best model, and all models that are not more complex versions of better models and have $\Delta\text{AIC} < 6$ are also retained. All analyses were carried out in R 2.13.1 (R Core Development Team 2011) with the lme4 package (Bates et al. 2011).

RESULTS

Anthropogenic presence at Donna Nook

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 stabilization and some yearly fluctuations in the subsequent years (Fig. 2). For the 2 years of the present study, the tourist visitation patterns exhibited variability within and between seasons, with the

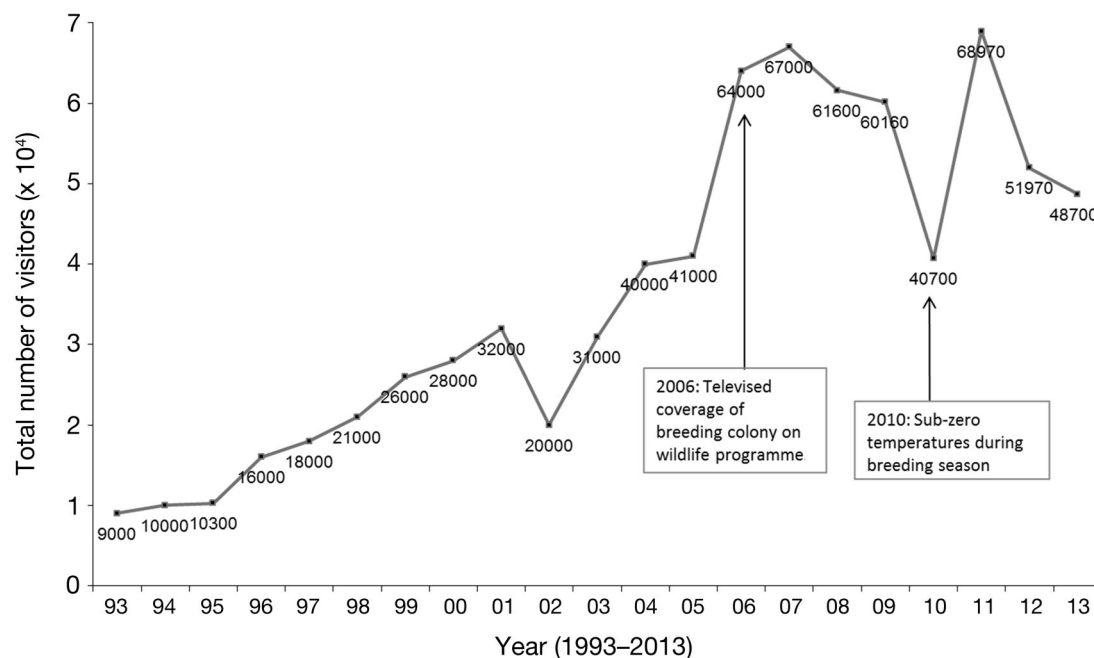


Fig. 2. Total visitors at Donna Nook during the breeding season (November and December) each year. Annotations indicate timing of events that correlate with dramatic increases or decreases in visitation numbers (data and annotations are from Lincolnshire Wildlife Trust, R. Lidstone-Scott)

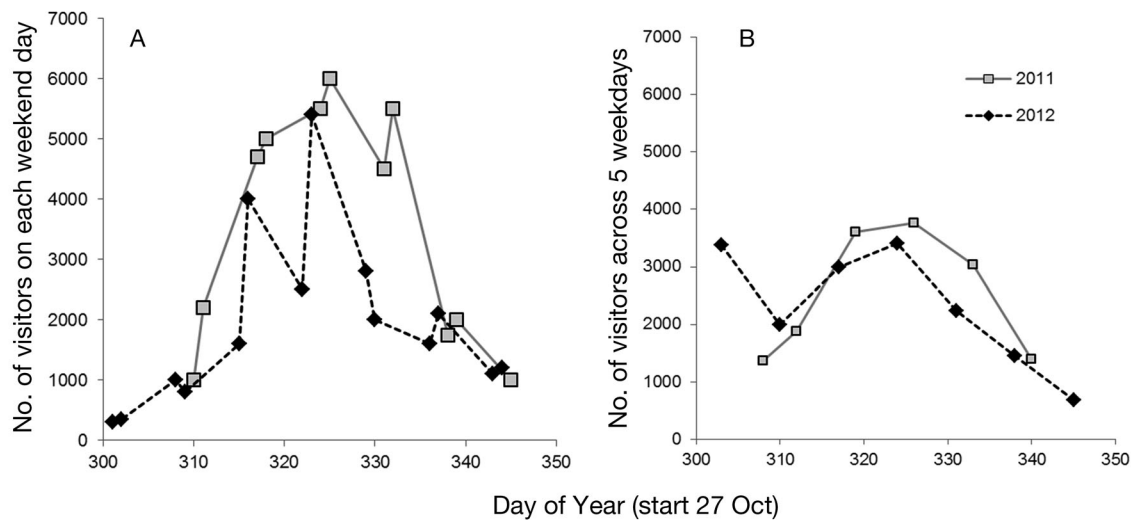


Fig. 3. Number of visitors at Donna Nook (A) on individual weekend days only for 2011 and 2012 at the PUB site and (B) week-day totals (total number of visitors across 5 weekdays)

Table 1. Activity budgets for males at Donna Nook in 2011 and 2012 and combined (DN). Activity budgets for comparison colonies are from North Rona colony 1988 and 1989 combined (NR), and Sable Island 1990 (SI) (Twiss 1991). Percentage of time spent in each activity is the mean (\pm SE) across all males with ≥ 200 scans (or ≥ 180 scans for NR and SI). Aggression to females consisted of any 'aggressive' behaviour directed at a female

Behaviour	2011 (N = 61)	2012 (N = 57)	DN (N = 118)	NR (N = 73)	SI (N = 20)
Rest	86.48 (0.62)	85.63 (0.76)	86.07 (0.45)	81.55 (0.63)	79.76 (2.02)
Alert	7.54 (0.45)	7.88 (0.47)	7.70 (0.33)	11.77 (0.42)	11.76 (1.27)
Yodel	—	—	—	—	0.72 (0.33)
Locomotion	1.47 (0.13)	1.33 (0.12)	1.40 (0.09)	1.70 (0.12)	1.83 (0.26)
Reproductive	1.39 (0.19)	1.81 (0.27)	1.59 (0.16)	2.48 (0.20)	1.68 (0.45)
Approach female	0.09 (0.02)	0.40 (0.15)	0.09 (0.02)	0.28 (0.04)	0.26 (0.08)
Attempted copulation	0.53 (0.07)	0.49 (0.07)	0.52 (0.05)	0.89 (0.10)	0.51 (0.14)
Copulation	0.77 (0.13)	0.91 (0.12)	0.84 (0.08)	1.32 (0.14)	0.90 (0.31)
Non-aggressive flipping	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.003)	0.01 (0.005)
Aggressive	3.11 (0.21)	3.34 (0.17)	3.21 (0.14)	2.27 (0.17)	3.55 (0.40)
Aggression to females	0.08 (0.02)	0.65 (0.08)	0.35 (0.05)	—	—
Non-contact aggression ^a	2.87 (0.27)	2.58 (0.18)	2.73 (0.13)	2.09 (0.16)	3.31 (0.37)
Contact aggression ^b	0.16 (0.03)	0.12 (0.06)	0.14 (0.02)	0.17 (0.06)	0.24 (0.10)
Non-active ^c	94.02 (0.33)	93.51 (0.39)	93.78 (0.25)	93.55 (0.36)	92.91 (0.72)
Active ^d	5.98 (0.33)	6.48 (0.39)	6.22 (0.25)	6.44 (0.36)	7.05 (0.72)

^aNon-contact aggression = Approach, Open mouth threat, Aggressive flipping, Roll, Body slap; ^bcontact aggression = Lunge, Bite, Fight; ^cnon-active = Rest + Alert + Yodel (SI only); ^dactive = Locomotion + Reproductive + Aggressive

highest weekend visitation numbers in 2011 ($t = 1.95$, $df = 17.64$, $p = 0.03$). Weekend visitation in 2011 averaged 3559 (± 591 SE) visitors per day during peak season (November 3–December 10), while attendance averaged 2175 (± 392 SE) visitors per day during the same period in 2012 (Fig. 3A). The average total number of weekday visitors (summed across 5 weekdays) did not differ between years ($U = 23$, $p = 0.42$; Fig. 3B). Aerial military training activities occurred during 50% of weekdays in 2011 and 83% of weekdays in 2012.

Activity budgets

Activity budgets for males at Donna Nook were generally consistent between seasons and demonstrated considerable similarities in comparison to other colonies (Table 1). At Donna Nook, activity budgets across years seemed relatively stable, and year was not retained as a significant predictor in the models examining differences in activity budgets for time spent in locomotion, aggression, alert, rest or non-active behaviours ($\Delta AIC_{\text{null}} = 0$ for all models,

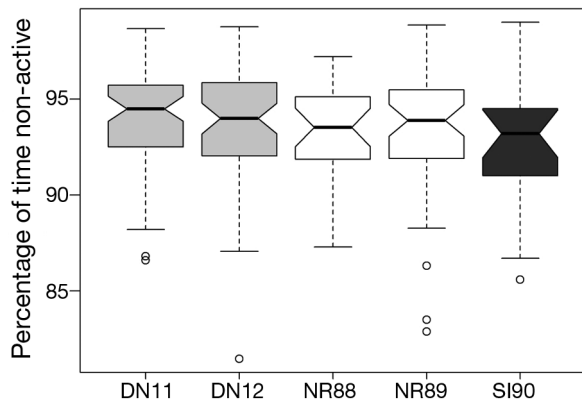


Fig. 4. *Halichoerus grypus*. Median percentage of time spent in non-active behaviours at each of the 3 colonies (Donna Nook = DN11 & DN12 [in 2011 and 2012]; North Rona = NR88 & NR89 [in 1988 and 1989]; Sable Island = SI90 [in 1990]). Boxes represent the interquartile range around the median (dark line), with notches displaying the 95% confidence intervals around the median. Whiskers represent the 75th and 25th percentiles. Circles outside of whiskers represent possible outliers

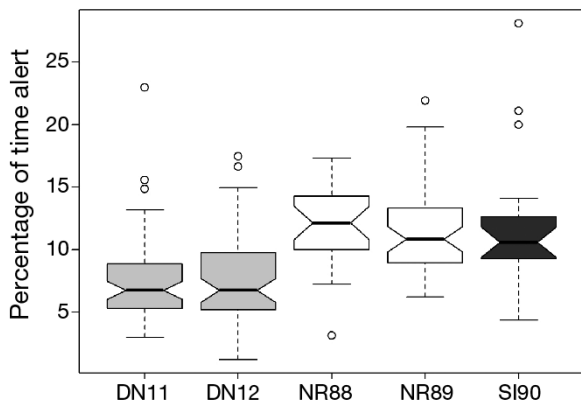


Fig. 5. *Halichoerus grypus*. Median percentage of time spent alert at each of the 3 colonies (Donna Nook = DN11 & DN12 [in 2011 and 2012]; North Rona = NR88 & NR89 [in 1988 and 1989]; Sable Island = SI90 [in 1990]). Boxes represent the interquartile range around the median (dark line), with notches displaying the 95% confidence interval around the median. Whiskers represent the 75th and 25th percentiles. Circles outside of whiskers represent possible outliers

Table 1). Across colonies, when examining the overall non-active (rest + alert) activity budgets, colony was not retained as a predictor variable ($\Delta\text{AIC}_{\text{colony}} = 9.1$, $\Delta\text{AIC}_{\text{null}} = 0$), although males from Sable Island spent a slightly reduced amount of time in non-active behaviours (Table 1, Fig. 4). Donna Nook males had higher percentages of time spent in aggression than

those at North Rona, but spent a similar amount of time in aggression compared to males on Sable Island (Table 1), and in the model, colony was retained as a significant variable for explaining the differences in the time spent in aggression ($\Delta\text{AIC}_{\text{colony}} = 0$, $\Delta\text{AIC}_{\text{null}} = 10.33$). There was no difference in time spent in locomotion between colonies ($\Delta\text{AIC}_{\text{colony}} = 3.11$, $\Delta\text{AIC}_{\text{null}} = 0$). Lastly, males spent more time resting at Donna Nook than at either of the other 2 colonies (Table 1), and males at Donna Nook spent the least amount of time alert of the 3 colonies (Table 1, Fig. 5). Both of these patterns were supported by the retention of colony in the best models for rest ($\Delta\text{AIC}_{\text{colony}} = 0$, $\Delta\text{AIC}_{\text{null}} = 27.04$) and alert ($\Delta\text{AIC}_{\text{colony}} = 0$, $\Delta\text{AIC}_{\text{null}} = 43.0$).

DISCUSSION

Across 3 breeding colonies, we found no behavioural evidence of increases in anti-predator, vigilance or movement behaviours by breeding male grey seals exposed to human activities relative to males at non-disturbed colonies, and overall, males exhibited similar time budgets for non-active behaviours. Rates of active behaviours such as aggression, attempted copulations and locomotion can reflect trade-offs between fitness and conservation of energy for capital breeders. For grey seals, these behaviours have been shown to vary across environmental gradients such as topography (Anderson & Harwood 1985, Twiss 1991), sex ratio (Twiss et al. 1998) and weather patterns (Twiss et al. 2006). However, the consistency across colonies we found for the time males spent in non-active behaviours suggests 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. Males in other highly polygynous species such as the South American sea lion *Otaria byronia* (Pavez et al. 2014) and the California sea lion *Zalophus californianus* (Holcomb et al. 2009) have also shown reduced responses to disturbance relative to females. Selection for this lack of a behavioural response 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, 2004).

Previous studies have found little evidence of military activities or helicopters disturbing grey seal behaviour (Perry et al. 2002, Southwell 2005), but

there is a lack of consensus on whether tourism activities, either on land or sea, negatively impact pinniped behaviours (Engelhard et al. 2002, Curtin et al. 2009, Holcomb et al. 2009, Pavez et al. 2011, 2014, Hoover-Miller et al. 2013, Le Boeuf & Campagna 2013, Cowling et al. 2014, Granquist & Sigurjonsdottir 2014). Studies that note negative effects at specific locations (Curtin et al. 2009, Pavez et al. 2011, 2014, Granquist & Sigurjonsdottir 2014) are often isolated or may not consider acute responses in relation to the broader behavioural ecology and evolution of the species. For example, Christiansen et al. (2013) found that the presence of whale-watching vessels did reduce the amount of time minke whales *Balaenoptera acutorostrata* spent foraging. However, when considering the temporal and spatial rates of individuals' exposure over an entire season, there appeared to be no potential for a population-level effect of these acute disturbances (Christiansen et al. 2015). By examining activity budgets of male grey seals across breeding colonies at a coarse, seasonal scale, our results also suggest that while acute responses to tourism disturbances might be occurring, there appear to be no differences in average time spent in non-active behaviours for males across breeding colonies.

Although the intensity of human activities differed between years for wildlife tourism and military actions at Donna Nook, there were no corresponding between-year differences in any behavioural categories and the time males spent alert in both years was lower than at the undisturbed colonies. In comparison, for harbour seals, increases in alert behaviours were positively correlated with the number of wildlife viewers during the breeding season (Granquist & Sigurjonsdottir 2014) and males both increased vigilance behaviours and showed some indication of increased heart rate following sonic booms during the non-breeding season (Perry et al. 2002). Harbour seals do not hold terrestrial territories during the breeding season (van Parijs et al. 2000), and are not sexually size-dimorphic (González-Suárez & Cassini 2014), suggesting that the selection pressures for conservation of energy in this species are potentially not as strong as those for male grey seals both during and outside of breeding seasons. These comparisons suggest that specific selection pressures, life histories, and ecological constraints should be considered if attempting to infer management strategies for disturbance, even across closely related species.

While we have demonstrated that male grey seals, like other male pinnipeds, appear to have strong se-

lection pressures driving their activity budgets during the temporally discrete breeding season, the present study was not able to discern the mechanism driving this pattern directly. 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 respect to human activities (Cobley & Shears 1999, Holcomb et al. 2009, Pavez et al. 2014), (2) differences in tolerance thresholds resulting in intolerant individuals being displaced (Bejder et al. 2009), or (3) individuals exhibiting initial acute responses to anthropogenic presence but subsequently habituating (Bright et al. 2003, Villanueva et al. 2012, Côté et al. 2013, Le Boeuf & Campagna 2013). None of these mechanisms are mutually exclusive, and we will consider each scenario in terms of the species' behavioural ecology and potential management implications.

Many of the species that exhibit increases in vigilance are social species, with considerable selection for anti-predator behaviours (Roberts 1996, Duchesne et al. 2000, Lusseau 2003, Côté et al. 2013). The last potential 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 (www.legislation.gov.uk/ukpga/1970/30), human culling of grey seals in England can only occur under licence, further reducing any potential for males to experience perceived risks while hauled out. The Donna Nook colony formed in the 1980s and did not begin to grow rapidly until 1992 (Duck & Morris 2010, R. Lidstone-Scott pers. comm.). Tourist visitation and the population of seals both gradually increased through 2006, but direct access to the colony has been limited by a fence since 1997 and further limited by a second fence layer in 2007 (R. Lidstone-Scott pers. comm.). Therefore, it is possible that current, reproductively active adult male seals (typically aged 8–20 yr; Twiss 1991) at Donna Nook have not experienced negative exposure that would have led individuals to associate human presence with a threat. Gentoo penguin *Pygoscelis papua* colonies in Antarctica have little to no history of land predators and do not exhibit behavioural changes in response to human activities (Cobley & Shears 1999). Similarly, a lack of terrestrial predators has also been suggested as a reason that male California sea lions do not respond to tourism disturbances (Holcomb et al. 2009). Thus, focusing on the historical evolutionary selection pressures could identify candidate species for future wildlife viewing opportunities, or help avoid species that have been selected for greater anti-predator responses.

A wide range of animals has demonstrated individual differences, but behavioural consistency, in responses to stimuli (Bell et al. 2009). Male grey seals exhibit individual behavioural consistencies in the amount of time they spend alert (Twiss & Franklin 2010). Female grey seals vary in their response to disturbance and either display proactive or reactive behavioural types (Twiss et al. 2012). The extent of variation in behavioural types in a population could influence responses to disturbance; for example, colonies might be selecting for individuals with specific behavioural types, such as high tolerance to disturbance, and displacing individuals spatially or temporally with lower thresholds (Bejder et al. 2009, Higham & Shelton 2011). The ease with which individuals with lower tolerance thresholds can be temporally or spatially displaced is likely dependent on the topography, available habitat (Bennett et al. 2013) and temporal constraints of key life-history periods. Therefore, population-level effects could be masked depending on the spatial or temporal scale of the sample. In the present study, male seals at Donna Nook are not space-limited and large portions of the beach are still available for breeding seals (A. B. pers. obs.). If males differed in their tolerance to disturbance, displacement might not result in being driven off the colony altogether, as it might at colonies with limited breeding substrate. Instead, less tolerant males might select to occupy more peripheral locations. While we cannot rule out spatial displacement within Donna Nook, it is unlikely to have influenced our results. Male distance from the fence ranged from 10 to 350 m, and all seals were exposed to the military training exercises.

Temporal displacement is quite different. Unlike hauling-out behaviours, which can be temporally and spatially displaced due to wildlife viewing (Granquist & Sigurjonsdottir 2014), breeding seasons are temporally keyed by females' reproductive cycles, involving the interplay of hormone and environmental cues controlling fertilization, implantation, gestation, parturition and oestrus (Pomeroy et al. 2000). This restricts the effectiveness of any plasticity males can demonstrate in their responses. Therefore, as capital breeders, the temporal constraints of the breeding season, along with the selection pressures for maintaining access to females and for conservation of energy, might be overriding any between-individual differences in tolerance, resulting in the observed lack of differences across colonies during this life-history stage.

Finally, habituation to tourism activities has been demonstrated in species such as the dabchick *Polio-*

cephalus rufopectus (Bright et al. 2003) and Magellanic penguins *Spheniscus magellanicus* (Villanueva et al. 2012). The lack of an observed increase in alert responses at Donna Nook could be due to males responding to protracted exposure by returning to pre-exposure levels. Due to the importance of 'not losing' for male grey seals (Anderson & 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 that males increased the frequency of alert behaviours. However, visitor presence has increased over the years simultaneously with the number of seals, potentially leading to a gradual habituation. At an even finer temporal scale, within a breeding season, the number of visitors also gradually increases over time, potentially leading to within-season habituation over the course of a few days (Villanueva et al. 2012).

In the present study, only adult, tenured males were included in our selection criteria for observation as these males experience the highest rates of mating success (Twiss 1991, Lidgard et al. 2001, 2004). Donna Nook is an expanding colony (Duck & Morris 2010), so it is likely that population growth is a product of both immigration as well as internal growth (with the observed 40% increases, the maximum intrinsic rate is ~12%; P.P. pers. comm.). If immigration is occurring, some males sampled could potentially be non-habituated, but if these newcomer males are younger, or males exhibiting the alternative, transient mating strategy (Boness & 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 for primates or small mammals is considered acceptable

(Higham & Shelton 2011). The present study cannot ascertain whether males have habituated to tourism 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 on individual fitness or on population growth.

Management implications and future work

Legislation such as the Marine Mammal Protection Act of 1972 in the USA (www.nmfs.noaa.gov/pr/laws/mmpa/text.htm) prohibits disturbance of marine mammals through clauses that define ‘harassment’ as any act that ‘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.’ (16 U.S.C. 1362, Section 3, para. 18) In Scotland, similar laws prohibit intentional harassment or disturbance of pinnipeds at significant haul-out sites (Marine Scotland Act 2010; www.legislation.gov.uk/asp/2010/5/pdfs/asp_20100005_en.pdf), 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. Ecotourism is often argued to be beneficial to wildlife through public education and establishment of wildlife reserves, but it is also criticized as being prone to the tragedy of the commons (Heenehan et al. 2014) and is an economy that can result in disturbance and reduced fitness for populations of animals (Shackley 1996). Likewise, military training grounds can often provide refuge or habitat for animals (Warren & Büttner 2008), but with potential costs of increased wildlife disturbance (DeRuiter 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 energy limited and have often been considered critical times (Hoover-Miller et al. 2013), strong natural or sexual selection pressures during this discrete period can potentially mitigate the pressures to change behaviours across a gradient of anthropogenic exposure in the form of wildlife tourism.

We recognize the specific conditions of our study (e.g. we only considered breeding males and not females, pups or subordinate males), but within this framework, we 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 paramount for effective management. Thus, future work in the field of human–wildlife interactions and management will benefit from studies that: (1) are targeted to specific sexes and life-history stages to examine potential differences in how selection pressures and responses vary (Cowling et al. 2014), (2) are spatially and temporally explicit across a wide range of exposure levels within and between populations to examine differences in responses to disturbance (Christiansen et al. 2015), (3) incorporate both behavioural and physiological metrics such as heart rate (Lydersen & Kovacs 1995) and stress hormones to examine ‘hidden’ effects and individual variation in responses (Villanueva et al. 2012), and (4) use interdisciplinary methods to investigate the efficacy of specific management practices (Le Boeuf & Campaigna 2013). Further consideration of these questions will work towards improving our knowledge of how human presence functions as part of the ecological and selection pressures driving marine mammal behaviours.

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Appendix. Table A1. Ethogram of behaviours used during scan-sampling and for calculating activity budgets of males at Donna Nook. For additional behaviours, see Twiss (1991) and Lawson (1993)

Aggressive behaviours	
Approach male	Focal male moves directly towards another male (Bishop et al. 2014).
Open mouth threat	A threat display that consists of a male opening his mouth to a wide gape directed at opponent with no vocalization or contact with a conspecific (Twiss 1991, Lawson 1993, Bishop et al. 2014).
Aggressive flippering	A male vigorously waving his fore-flippers and/or slapping his own sides in a clearly aggressive manner.
Lunge	An attempt to bite without making contact.
Bite	A singular bite or contact made through a lunge. This behaviour is sometimes associated with a vigorous shaking of the head laterally while maintaining a grasp on the opponent. A subcategory of this behaviour is bite hind-flippers (BHF), where the male grasps the opponent's hind-flippers or tail with his mouth.
Fight or contact AI	The segment of an aggressive interaction (AI) during which repeated contact is made by one or both males. This is usually preceded by a threat period during which males exchange non-contact threats (for further details, see Twiss 1991).
Roll	Usually seen after a fight or chase, male turns on his dorsal-ventral axis. Suggested as a form of locomotion or a 'victory roll' (Twiss 1991, Lawson 1993).
Body slap	A male pushing his body off the ground and slamming his ventral surface back down onto the substrate. Usually performed in multiple repetitions per bout (Bishop et al. 2014).
Reproductive behaviours	
Approach female	A subgroup of general locomotion; approach refers to direct movement of a male towards a female.
Non-aggressive flippering	Male slowly strokes the flank of the intended mate with his flipper. Usually seen prior to mounting or during male positioning.
Attempted copulation	Attempted copulations begin when a male attempts to get his fore-flippers on the female's back and grabs the scruff of her neck with his jaws (Twiss 1991). This behaviour has also been called a 'mount' (Boness 1984).
Copulation	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'. From Twiss (1991), 'successful' copulations last on average 15–20 min and we assume that if shorter than 10 min, it is unlikely that insemination will occur.
Unsuccessful copulation	Copulations that do not last for longer than 10 min post-intromission are considered unsuccessful. '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.
Other	
Rest	Non-active state. Head down, eyes may be open or closed.
Comfort move	General repositioning, scratching or flipper movements while stationary. Eyes may be open or closed and head may be off the ground.
Alert	Cases where a male is clearly observant, with the head raised or gaze directed.
Locomotion	Movement around the colony without directed approach towards a female or male. Change in geographic location.
Out of sight	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.