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ScienceDirect
Hormones and Behavior 53 (2008) 241 – 248
Hormones and Behavior
www.elsevier.com/locate/yhbeh

# The implications of stress on male mating behavior and success in a sexually dimorphic polygynous mammal, the grey seal

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Received 20 July 2007; revised 1 October 2007; accepted 3 October 2007
Available online 12 October 2007

**Abstract**

Studies on primates and other taxa have shown that the physiological response of an individual to stress reflects their social status. We combined behavioral observations with measures of stress to test the hypothesis that stress is an important physiological determinant of mating behavior and success in the male grey seal. Known-age males ($N=19$) were studied during the breeding seasons of 2004 and 2005 at Sable Island, Canada. The stressor was a capture and restraint period of 35 min and serial samples of cortisol and testosterone were taken as measures of stress. The mean baseline concentrations of cortisol and testosterone were $9.7 \pm 0.5$ ug/dl and $6.2 \pm 0.6$ ng/mL, respectively. The baseline cortisol concentration was negatively correlated with the duration of time a male spent at a site ($r=-0.507$, $P=0.027$), which was a strong correlate of mating success ($r=0.659$, $P=0.002$). All males experienced an increase in the concentration of cortisol during the restraint period ($79.1 \pm 8.4\%$; CV$=46.1\%$). The percentage rise in cortisol during restraint was correlated with the mean duration of time spent at a site ($r=0.544$, $P=0.016$) and thus success. The concentration of testosterone also increased during the restraint period ($32.8 \pm 9.7\%$). This might be an adaptive response to maintaining the ability to reproduce while under stress. Our study indicates that stress is an important determinant of success in male grey seals. More successful males might exhibit an adaptive response to stress by maintaining low concentrations of cortisol during breeding.


*Keywords:* Cortisol; Breeding behavior; Breeding success; Glucocorticoids; Pinniped; Seal; Stress; Testosterone

## Introduction

Animals are faced with a diverse array of stressors during their lifetime. These may originate from the environment (e.g., population density, Rogovin et al., 2003) or from aspects of life history (e.g., breeding events, Abbott et al., 2003). Stressors can upset the physiological balance, or homeostasis of the individual and consequently affect growth, reproductive behavior, energetics, the immune system and survival (Bartsh et al., 1992; Boonstra et al., 1998; Creel, 2001; Jessop et al., 2002; Rogovin et al., 2003; Sapolsky, 2002).

In vertebrates, the typical response to a stressor is a complicated cascade of physiological events that results in the release of glucocorticoids (e.g., cortisol) to ready the animal for a 'fight or flight' response (Sapolsky et al., 2000). Glucocorticoids are also involved in suppressing reproductive behavior which, in the case of males, occurs through several mechanisms that lead to a decrease in the concentration of testosterone (Sapolsky, 2002; Wingfield and Sapolsky, 2003). Several studies have shown that in some species the actions of glucocorticoids on reproductive function are suppressed during the breeding season as an adaptive response to allow individuals to reproduce in stressful environments (e.g., Silverin et al., 1997) or to maximize their success during a short breeding season (e.g., Astheimer et al., 2000). However, studies on primates and other taxa have shown that the magnitude of this suppression differs according to the individual's social status in the breeding group (Sapolsky, 1982; Creel, 2001; Abbott et al., 2003). In olive baboons (*Papio anubis*), males that have high copulatory success experience an increase in testosterone concentration during a stressful event

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doi:10.1016/j.yhbeh.2007.10.003

despite concurrent increases in cortisol concentration, while individuals with low copulatory success (i.e., subdominants) experience a decrease (Sapolsky, 1982). Thus, dominant individuals are able to maintain reproductive function while exposed to stress, whereas subdominants experience a temporary inhibition. The study also found that subdominant individuals that were subjected to high and unpredictable rates of aggression from dominant individuals had higher baseline concentrations of glucocorticoid secretion compared with dominants. Alexander and Irvine (1998) found a similar result in horses. These results are in accord with the 'stress of subordination hypothesis' which predicts that in social systems where it is more costly for subdominants to acquire and maintain access to females for mating opportunities, subdominants will have higher basal glucocorticoid concentrations than dominants (Sapolsky, 1982; Sapolsky and Share, 1994; Creel, 2001; Abbott et al., 2003). Thus, subdominants may not only suffer from low copulatory success, but also from the deleterious effects of chronic stress (Boonstra et al., 1998; Sapolsky, 2002; Rogovin et al., 2003).

The grey seal (*Halichoerus grypus*) is a sexually dimorphic tournament species in that males do not invest in parental care, but compete aggressively for access to females and opportunities to mate. Males reach sexual maturity at the age of 7 years (Hammill and Gosselin, 1995) and may continue to breed through to their mid-thirties (this study). In the North-west Atlantic, the breeding season starts in mid-December and continues through to early February. However, given that males rely heavily on stored energy reserves during the breeding period, the average duration of breeding for an adult male is only 29 days (Lidgard et al., 2005). The breeding season therefore represents a short and very stressful period where males lose an average of 2.4 kg per day and frequently engage in male–male conflict and risk injury (Lidgard et al., 2005). To achieve success males may form stable relationships with females in the form of a consortship and defend more than one consort at a time (Anderson et al., 1975; Boness and James, 1979; Anderson and Fedak, 1985; Twiss et al., 1998; Lidgard et al., 2001). There may be a number of sequential periods of female defense at more than one site and several studies have shown that the duration of stay at a site is correlated with success (Anderson et al., 1975; Boness and James, 1979; Twiss et al., 1994; Tinker et al., 1995; Lidgard et al., 2001, 2005). Males that are unable to defend females due to their lower competitive ability or smaller body size (Lidgard et al., 2005) may act promiscuously and mate with females after they have weaned their pup and are leaving the breeding colony. Lidgard et al. (2004) have shown that males that exhibit the tactic of defending females have a greater chance of siring offspring than those that exhibit the tactic of mating with departing females. Other mating tactics may occur although their nature and success are less understood (Ambs et al., 1999; Worthington Wilmer et al., 1999). Males may exhibit one or more tactics during a single breeding season (Lidgard, 2003).

Given the short length of the breeding period, we might expect male grey seals to suppress the effects of stress on reproductive behavior to maximize their success. However, this might vary according to the ability of the male to defend females. Males that are successful at defending females might be those that are able to maintain reproductive function after a stressful event, such as a fight with a competitor, whereas less successful males might be those that exhibit the typical response to stress and suffer from temporary inhibitions of reproductive function. Boness (1979) has shown that consort males engaged less frequently in threats and fights with their neighboring consort males compared with competing males and had their mating attempts interrupted less frequently than non-consort males (i.e., those not in defense of females). So, males that are less successful at defending females will likely receive more social stress and have higher baseline cortisol concentrations due to engaging in more aggressive interactions and having their mating attempts frequently interrupted. This would support the 'stress of subordination hypothesis'.

The aim of this study was to address three hypotheses: (1) breeding male grey seals are able to suppress the effects of stress on reproductive function during a stress event, (2) the magnitude of this suppression is greatest in those males that achieve a high success by defending females, and (3) the baseline level of cortisol is lowest in those males that achieve a high success by defending females.

## Methods

### *Study site and study animals*

The study was conducted during the breeding seasons of 2004 to 2005 at Sable Island (43°55′N, 60°00′W), situated approximately 300 km ESE of Halifax, Nova Scotia, Canada. The Island is approximately 50 km long and 1.2 km wide, with vegetated sand dunes along its length and both wide and narrow beaches around its perimeter. The breeding season extends from mid-December to early February and the estimated pup production in 1997 was 25,400 with an estimated annual rate of increase of 13% (Bowen et al., 2003). Between 1969 and 1989, a proportion of males were branded at weaning providing a pool of identifiable known-age adults.

We studied 19 known-age branded males representing a wide range of body masses and lengths. Males were selected according to whether they were part of an ongoing long-term study on male behavior. The study design was cross-sectional such that each male was studied in only 1 year. Males were captured as close to their first sighting on the island as possible (median = 2; 25–75% quartiles = 0–4; Table 1) and toward the end of the season before males departed the breeding colony. At each capture, males were weighed using tandem 300 kg (± 1 kg) Salter spring balances. At the initial capture, each male was fitted with a radio transmitter (164–165 MHz, Advanced Telemetry Systems, http://www.atstrack.com) to determine locations on land. Details of how the transmitter was attached and how length measurements were taken are given in Lidgard et al. (2003). Males wore the radio transmitter until they terminated breeding and were re-captured. However, in some cases the male unexpectedly departed the island before it could be re-captured in which case the radio transmitter will fall off at the annual molt.

### *Blood sampling and hormone analysis*

It was not possible to collect blood samples remotely so we used a capture followed by a restraint period of 35 min as a stressor to examine changes in circulating cortisol and testosterone concentrations in response to a stressor. Several studies on different taxa have demonstrated the successful use of a capture and restraint period to examine the effects of stress on hormonal concentrations (Sapolsky, 1982; Kenagy and Place, 2000; Jessop et al., 2002; Klose et al., 2006). A restraint period of 35 min was chosen to minimize the length of time a male was restrained in the net under stress, but of sufficient duration to observe significant increases in cortisol. Sapolsky (1982) and Kenagy and Place (2000) observed significant increases in glucocorticoid concentration

Table 1
Number of days captured post arrival, physical characteristics and study period for breeding grey seal males on Sable Island, NS, 2004 to 2005 ($N=19$)

| Male Id | Number of days captured post arrival | Age, years | Mass, kg | Length, m | Study period, days |
|---|---|---|---|---|---|
| 1 | 0 | 30 | 358 | 2.20 | 17.0 |
| 7 | 3 | 19 | 316 | 2.25 | 25.0 |
| 8 | 4 | 18 | 276 | 2.07 | 12.1 |
| 9 | 0 | 18 | 295 | 2.16 | 15.9 |
| 12 | 2 | 15 | 294 | 2.06 | 24.1 |
| 15 | 6 | 19 | 325 | 2.07 | 19.1 |
| 16 | 5 | 18 | 255 | 2.00 | 20.9 |
| 21 | 1 | 34 | 249 | 1.99 | 9.3 |
| 117 | 6 | 17 | 326 | 2.22 | 25.0 |
| 118 | 0 | 17 | 320 | 2.20 | 14.2 |
| 119 | 4 | 18 | 353 | 2.17 | 24.0 |
| 122 | 3 | 30 | 282 | 2.10 | 14.2 |
| 131 | 6 | 18 | 330 | 2.13 | 22.1 |
| 191 | 0 | 18 | 314 | 2.17 | 21.2 |
| 192 | 4 | 34 | 328 | 2.15 | 25.9 |
| 206 | 0 | 34 | 321 | 2.29 | 16.2 |
| 13 | 0 | 18 | 253 | 2.05 | 12.0 |
| 120 | 0 | 31 | 330 | 2.25 | 19.0 |
| 124 | 0 | 32 | 241 | 2.09 | 20.2 |

in olive baboons and yellow-pine chipmunks after 25 and 30 min of restraint, respectively. The duration of the capture process (i.e., the time between the male responding to the presence of the capture team and the time the first blood sample was taken) was between 1 and 4 min (2.0±0.20 min). The response of the male to the capture team involved behaviors that are typical of male–male encounters, e.g., fleeing and aggressive threats, such as open mouth threats, growling and lunging. The capture process involved two to four people distracting the male while another person carried a hinged pole net and approached the male from behind. Once the male was caught in the net, the open end was drawn closed and secured using a rope. As soon as the male was secure a blood sample was taken. Our aim was to take a blood sample (approximately 10 mL) within 3 min from the time the male was first made aware of the capture team's presence to obtain baseline concentrations of circulating cortisol and testosterone. Romero and Reed (2005) showed that samples collected within 3 min of capture in six avian and reptilian species were still considered to be close to baseline and significantly less than titers after 30 min of stress. Of the 19 males in this study, 17 males were sampled within 3 min of the approach of the capture team. The remaining two males were sampled at 3.1 and 4.0 min due to the difficulty of capturing males. The baseline cortisol concentration and the percentage change in cortisol concentration for the male sampled at 4.0 min was intermediate among the data for males sampled at less than 3 min, so we included this data point in our analyses.

To examine changes in the concentrations of cortisol and testosterone during capture and restraint, but to limit the amount of handling to minimize stress, a second blood sample was taken at approximately 20 min after the first sample and another at approximately 30 min. During the restraint period, other than sampling blood, males were not handled to ensure all males were treated equally. Telemetry instruments were attached after the 35-min restraint period. Oki and Atkinson (2004) have demonstrated a diurnal rhythm in cortisol concentration in the harbor seal (*Phoca vitulina*), although this pattern was only observed during the summer months. Due to logistics we were unable to confine the capture of males to either the morning (9:00 to 12:00) or afternoon (12:00 to 16:00) periods. However, we found no significant difference in the baseline concentration of cortisol or testosterone between samples collected in the morning ($N=7$) and those collected in the afternoon ($N=12$) for either cortisol (ANCOVA controlling for male traits of age, body mass and length: $F_{1,14}=2.70$, $P=0.123$) or testosterone ($F_{1,14}=1.22$, $P=0.287$). Samples were collected in 10 mL Serum Separation tubes (Fisher Scientific, http://www.fishersci.ca) and centrifuged for 15 to 20 min. Approximately 2 mL of serum were removed and stored frozen at −20 °C in cryovials. Frozen sera were sent to the Atlantic Veterinary College, P.E.I., Canada (http://www.upei.ca/diagserv) for analysis within 3 months of collection. Both cortisol and testosterone concentration were measured with standard commercial kits (Inter Medico, http://www.inter-medico.com) using a competitive chemiluminescent immunoassay method (Immulite®; Diagnostic Products Corporation, CA, USA; http://www.dpcweb.com). The analytical sensitivity for cortisol and testosterone was 0.20 ug/dl and 0.15 ng/mL, respectively. The intra-assay variability for cortisol as given by the manufacturer is between 5.8% and 8.8% and the inter-assay variability between 6.3% and 10.0% ($N=6$). The intra-assay variability for testosterone as given by the manufacturer is between 6.8% and 13.0% and the inter-assay variability is between 7.7% and 16.4% ($N=6$).

### *Behavioral data collection*

The behavior of each male was recorded throughout the breeding period according to the protocol outlined in Lidgard et al. (2001). Briefly, each male was located twice daily using a R2000 radio receiver (164–165 MHz, Advanced Telemetry Systems). For each sighting, a GPS reading (Garmin 76, http://www.garmin.com) was recorded. To minimize the influence of capture on subsequent male behavior, the first location used in the analysis was the first land location the day after capture.

The operational sex ratio (OSR = number of males prepared to mate/(number of males + females prepared to mate) Kvarnemo and Ahnesjo, 1996) was used as a measure of male competition for estrous females. The OSR has a range of 0 to 1.0 as the number of males, relative to receptive females, increases. The number of males and females in estrous within a 10 m radius of the male was recorded at each location. We chose a radius of 10 m because this would include immediate competitors and consort females (Boness and James, 1979). We assumed that females came into estrus when their pup was at least 14 days of age (Boness and James, 1979; *see* Kovacs et al., 1996 for the age-classification scheme).

### *Mating tactics and success*

The primary mating tactic of the male grey seal is female defense. From the inspection of a histogram of duration of time spent at a site in defense of estrous females, we defined the minimum duration of a consortship as a period ≥2 days. This definition agrees with the earlier studies of Lidgard et al. (2001, 2004, 2005) and Boness and James (1979). Males that spent <2 days defending a female were assumed to be exhibiting alternative tactics as previously described.

During the period of data collection, the authors adhered to the appropriate guidelines for the use of animals in research ASAB (2006) and to the appropriate legal requirements of Canada.

### *Data analysis*

Male grey seals change location often during the breeding season (Lidgard et al., 2001). To determine the scale for analyzing movements, the number of sites visited and the mean and maximum duration of stay at a site were calculated for each male at five spatial scales (where a move was defined as <20 m, <40 m, <60 m, <80 m and <100 m). Paired *t*-tests were used to determine the scale at which there was no significant difference in the behavioral measures at higher scales. The scale chosen for analyses was 60 m. Due to the timing of the branding programs, there were no known-aged males available for study between the ages of 20 to 29 years. Thus, males were categorized as either young (15 to 19 years; $N=12$) or old (30 to 34 years; $N=7$). The variable mass/length has a strong positive relationship with the amount of body fat (ANOVA, $F_{1,40}=76.9$, $P<0.001$; Damian C. Lidgard, Daryl J. Boness & W. Don Bowen, unpublished data), thus mass/length was used as a measure of male condition. The median value for male condition (138 kg/m) was used to define two categories. Given our small sample in each year the effects of year were not addressed in this study. Data were checked for normality prior to analysis and transformed as necessary to meet the assumptions of parametric tests. Outliers, defined as >mean + 2 standard deviations, were removed from analyses. All analyses were performed using SPSS (v.11.5) for Windows. The probability level for significance was $\alpha=0.05$. The standard error (S.E.) is given as a measure of variability about means.

## Results

The mean study period was 18.8±1.1 days (CV=26.5%). The first blood sample was taken at 2.0±0.20 min (1–4 min;

CV=43.7%) after the male first responded to the approach of the capture team. The last sample was taken 32.6±0.5 min (30–37 min; CV=6.5%) after the initial response of the male to the capture team.

*Change in cortisol and testosterone concentration during capture and restraint*

The mean baseline concentration of cortisol was 9.7±0.5 ug/dl (CV=21.1%). All males experienced an increase in the concentration of cortisol during the restraint period indicating that capture induced a stress response (Fig. 1). The mean percentage increase in cortisol concentration was 79.1±8.4%, but there was considerable variation among males in the magnitude of this increase (19.3% to 147.4%; CV=46.1%). During the first interval of restraint (2.0±0.2 to 22.6±0.4 min), all males exhibited an increase in cortisol concentration with a mean percentage increase of 67.3±6.8% (CV=44.0%). However, during the second interval of restraint (22.6±0.4 to 32.6±0.5 min), eight males showed no change (i.e., the percentage change in cortisol concentration was within the range of variability expected from the assay) and three males showed a decrease in cortisol concentration. The mean percentage change in cortisol concentration during the second interval was significantly less (7.1±2.7%; paired *t*-test: $t_{18}=8.148$, $P<0.001$) and more variable (−12.4 to 23.8%; CV=166.9%) than during the first interval, and fell within the range of variability expected from the assay. The baseline concentration of cortisol was negatively correlated with the percentage increase in cortisol during the first capture and restraint interval (Pearson correlation: $r=-0.618$, $N=19$, $P=0.005$) and across the whole restraint period ($r=-0.517$, $N=19$, $P=0.023$).

The mean baseline concentration of testosterone was 6.2±0.6 ng/mL (CV=38.6%). The change in the concentration of testosterone during the restraint period was more variable compared with the change in cortisol concentration (Fig. 1). In general, the concentration of testosterone increased across the restraint period (mean percentage increase=25.0±6.2%; $N=18$) but there was substantial variation among males in the magnitude of this increase (−18.3% to 71.4.1%; CV=105.3%). During the first interval of restraint, one male showed a decrease in testosterone concentration and seven males showed no change. The mean percentage change in testosterone concentration during this period was 18.3±5.5% (CV=128.0%). During the second interval of restraint, four males showed an increase in testosterone concentration while the remaining 14 males showed no change. The mean percentage change in testosterone concentration during this period was 6.0±2.8% (CV=200.0%) and fell within the range of variability expected from the assay. In contrast to the change in cortisol concentration, the magnitude of change in testosterone concentration did not differ between the two intervals (paired *t*-test: $t_{17}=1.892$, $P=0.076$).

The baseline cortisol level was not correlated with the baseline testosterone level (Pearson correlation: $r=-0.129$, $N=19$, $P=0.598$). Similarly, the percentage change in cortisol concentration during capture and restraint was not correlated with the percentage change in testosterone concentration (Pearson correlation: $r=0.174$, $N=18$, $P=0.489$).

*Male traits, behavior and stress*

The age span of males was 15 to 19 years and 30 to 34 years ($N=19$; Table 1). The mean body mass on arrival was 303.4±8.1 kg ($N=19$), mean length was 2.1±2.0 m and the condition (mass/length) of males was 141.7±3.0 kg/m. There was no significant difference in the body mass or length of young and old males (MANOVA, $F_{2,16}=0.547$, $P=0.589$) and therefore no significant difference in the condition of young and old males (MANOVA, $F_{1,17}=0.285$, $P=0.600$). The baseline concentration of cortisol or testosterone, or the percentage increase in cortisol or testosterone concentration during the restraint period was not significantly influenced by the age (MANOVA, $F_{4,11}=0.318$, $P=0.860$) or condition ($F_{4,11}=0.903$, $P=0.495$) of the male.

Mating behavior varied considerably among males. The mean number of sites visited during the season was 7.9±1.1

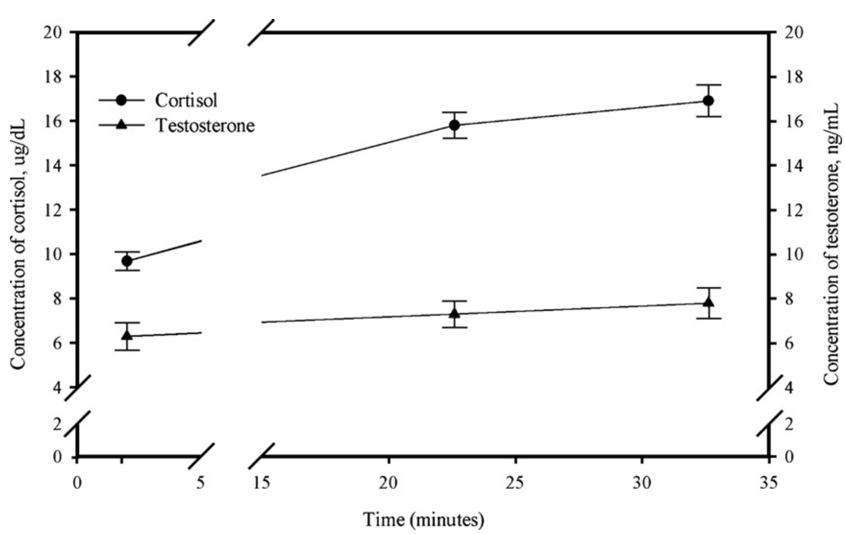


Fig. 1. Profiles of the concentration of cortisol ($N=19$) and testosterone ($N=18$) during capture and restraint in breeding male grey seals on Sable Island, NS.

(CV = 58.0%) and the mean and maximum duration of time spent at a site was 2.4 ± 0.4 days (CV = 64.3%) and 7.1 ± 1.1 days (CV = 65.7%), respectively. Males that had low baseline concentrations of cortisol during the stress event had a greater maximum duration of stay at a site (Pearson correlation: $r = -0.507$, $N = 19$, $P = 0.027$; Fig. 2a). Further, males that experienced a large percentage increase in cortisol concentration during capture and restraint also had a greater maximum duration of stay at a site (Pearson correlation: $r = 0.501$, $N = 19$, $P = 0.029$) and spent, on average, more time at a site ($r = 0.544$, $P = 0.016$; Fig. 2b). Neither the basal concentration of testosterone nor the percentage change in the concentration of testosterone was correlated with measures of the duration of stay ($P > 0.358$).

Sixteen males achieved success through defending females, however most males achieved a low success (median consort success = 1.0). As shown in other studies, the mean and maximum duration of stay at a site was strongly correlated with consort success (Spearman correlation: $r = 0.640$, $N = 19$, $P = 0.003$; $r = 0.659$, $P = 0.002$, respectively). As expected, consort success was strongly correlated with the basal concentration of cortisol (Spearman correlation: $r = -0.561$, $N = 19$, $P = 0.013$) although not correlated with the percentage change in the concentration of cortisol (Spearman correlation: $r = 0.419$, $N = 19$, $P = 0.074$). The basal concentration of testosterone or the percentage change in the concentration of testosterone during the stress event was not correlated with consort success ($P > 0.311$).

The mean number of estrous females that were defended by the focal male was 0.67 ± 0.12 (CV = 79.1%), and the mean OSR within a 10-m radius of the focal male was 0.77 ± 0.02 (CV = 11.7%). The baseline concentration of, or the percentage change in cortisol or testosterone concentration during the restraint period was not correlated with either the number of estrous females in defense or the OSR (Pearson correlation: all $P$ values > 0.087).

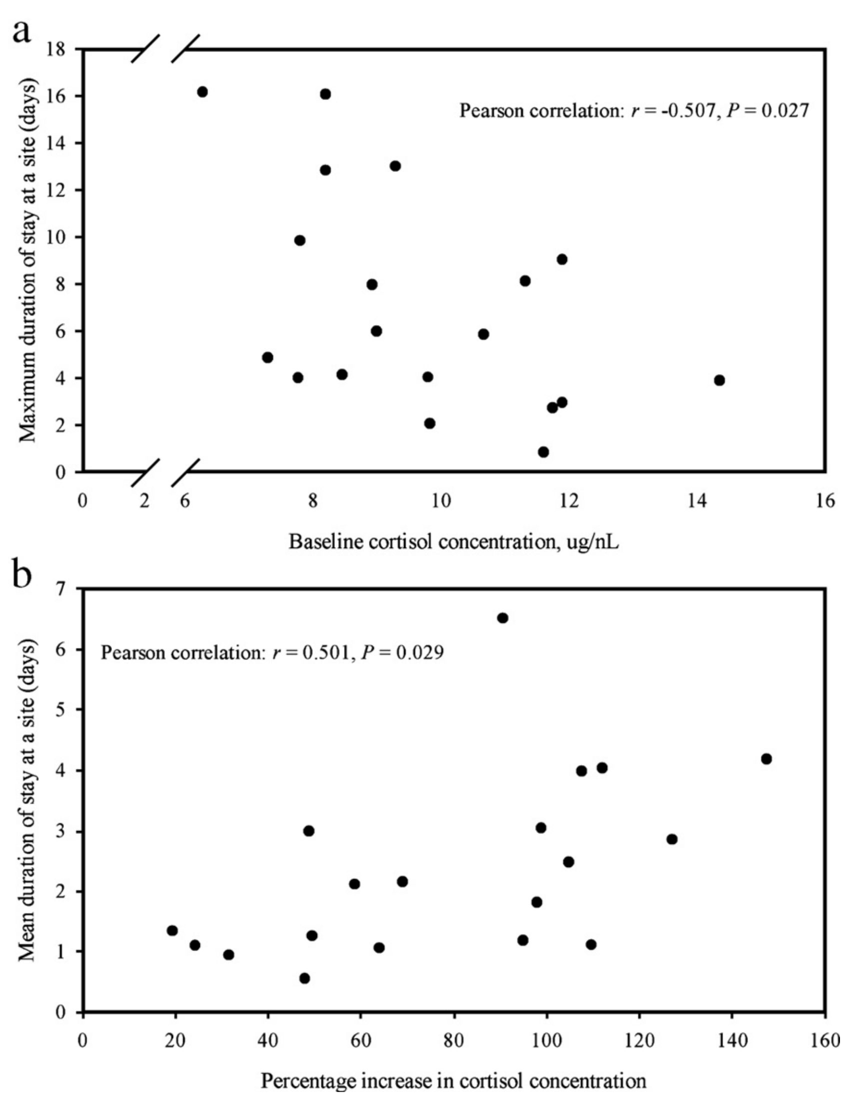


Fig. 2. (a) The maximum duration of time spent at a site and the baseline concentration of cortisol for breeding male grey seals ($N = 19$) on Sable Island, NS. (b) The mean duration of time spent at a site and the percentage increase in the concentration of cortisol during capture and restraint for breeding male grey seals ($N = 19$) on Sable Island, NS.

## Discussion

The baseline level of cortisol in this study was within the range reported for the harbor seal (4.14 ug/dL; Oki and Atkinson, 2004) and Steller sea lion (*Eumtopias jubatus*) (9.41 ug/dL; Mashburn and Atkinson, 2004) although lower than that reported in other taxa (olive baboon, 20.2 ug/dL, Sapolsky, 1982; Arctic ground squirrel (*Spermohilus parryii*), 23.1 ug/dL, Boonstra et al., 2001a). In this study, the baseline level of cortisol and its response to stress and subsequent effects on reproductive behavior differed among individuals according to their ability to remain at a site and defend females. Males that achieved long periods of female defense had lower baseline concentrations of cortisol at capture and exhibited a greater increase in cortisol concentration during restraint. In this and other studies (Anderson et al., 1975; Boness and James, 1979; Twiss et al., 1994; Tinker et al., 1995), the duration of stay at a site was correlated with consort success. These males are also more likely to sire offspring than those that adopt the alternative tactic of mating with departing females (Lidgard et al., 2004). In summary, males that had low basal concentrations of cortisol achieved a greater consort success and were more likely to achieve a greater reproductive success.

This pattern supports the ‘stress of subordination hypothesis’ wherein subdominant males are predicted to have higher basal glucocorticoid concentrations relative to dominant males due to their greater costs of acquiring and maintaining access to females for mating (Creel et al., 1997; Boonstra and McColl, 2000; Creel, 2001; Muller and Wrangham, 2004; Sands and Creel, 2004). Given that chronic high concentrations of cortisol can lead to numerous deleterious effects such as reduced growth, osteoporosis, suppressed immune function and shortened life-span (Boonstra et al., 1998; Sapolsky, 2002; Rogovin et al., 2003), maintaining low concentrations of cortisol during the breeding season while still able to respond adequately to a stress event may be viewed as adaptive. Males that achieved a high success by defending females will not only gain reproductive advantages but physiological advantages too.

Much of the work on the relationship between cortisol profiles and breeding status in mammals comes from the primate literature (e.g., Abbott et al., 2003), the majority of which are based on the olive baboon (Sapolsky, 1982, 1985, 1986, 1992). The male olive baboon is a good candidate for comparing the effects of stress on glucocorticoids with breeding male grey seals since it is also a tournament species with a high degree of sexual dimorphism, little male parental care and high male–male competition for access to females. However, unlike the grey seal, male olive baboons establish a linear dominance hierarchy with dominant individuals achieving a higher copulatory success than subdominants. Sapolsky (1982) has shown that dominant male baboons have the lowest baseline concentrations of cortisol and show the greatest increase in the concentration of cortisol while subjected to capture stress compared with subdominants.

The higher cortisol concentrations in less successful grey seal males suggests that these males may be subjected to greater psychological stressors compared with successful males such as higher rates of social stress from frequent aggressive interactions and interruptions of copulations, and greater social instability and lack of control due to their poor ability at defending females. Lidgard et al. (2005) have shown that males that are unable to defend females are smaller in body size and consequently have smaller energy reserves. Less successful males may also be subjected to greater physiological stressors such as those arising from endurance rivalry (Sapolsky, 2002; Muller and Wrangham, 2004; Mooring et al., 2006). Differences in energy expenditure may also increase cortisol concentrations (Kotrschal et al., 1998), however Lidgard et al. (2005) did not find differences in energy expenditure between males that were successful in defending females and those that were not.

The baseline level of testosterone in this study was within the range reported for the Weddell seal (*Leptonychotes weddelli*) (6.8 ng/mL; Bartsh et al., 1992) and the harbor seal (4–5 ng/mL; Coltman et al., 1999; 5.2 ng/mL; Oki and Atkinson, 2004) and other mammalian taxa (olive baboon, 6–21.6 ng/mL, Sapolsky, 1982; Arctic ground squirrel, 9.65 ng/mL, Boonstra et al., 2001a). On average, the concentration of testosterone increased during the capture and restraint period despite the concurrent increase in cortisol concentration. The typical response to a stressor is an increase in cortisol concentration and a subsequent decrease in testosterone concentration and hence inhibition of reproductive behavior. Thus, breeding grey seal males on Sable Island do not exhibit the typical response to stress. On Sable Island, the grey seal breeding season extends from mid-December to early February, a period of approximately 7 weeks. However, male grey seals are unable to sustain breeding for this length of time since they gain very little energy from foraging and mostly rely on stored energy reserves (Lidgard et al., 2003, 2005). The average duration of the breeding period for a male grey seal is 29 days (Lidgard et al., 2005). Further, in this study the operational sex ratio was skewed toward males, suggesting that competition for gaining access to females is high. Given that grey seals breed only once a year, and that males likely receive frequent threats, and therefore bouts of stress, from competitors for access to females, the ability to suppress the stress response during the breeding season would be an adaptive response to maximizing their breeding potential. Several other iteroparous vertebrates have been found to suppress the response to stress during the breeding season (Sapolsky, 1982; Creel et al., 1997; Silverin et al., 1997; Astheimer et al., 2000; Boonstra et al., 2001b).

However, the response of testosterone to stress varied substantially among individuals thus we would like to advise caution when interpreting these results. Although one male showed a decrease in the concentration of testosterone during the capture and restraint period and thus exhibited the typical response to stress, six males showed no change. However, this adds further support to our hypothesis that grey seal males can suppress the effects of cortisol on testosterone concentration during a stress event. Several behavioral and physiological mechanisms have been proposed to explain why some breeding individuals exhibit an increase in testosterone during stress while others exhibit a decrease or no change (Sapolsky, 1985, 1986, 2002; Sapolsky and Share, 1994).

Sapolsky (1982) showed that the relative change in testosterone concentration during a capture and restraint event was related to copulatory success and therefore rank; males with the highest copulatory success showed the greatest increase in testosterone concentration while those with the lowest success showed the greatest decline. In this study neither the baseline concentration of testosterone nor the percentage change in testosterone concentration during the capture event was related to any of the behavioral measures or to consort success. This may be an artifact of a low sample size or short sampling period. Due to field logistics it was not possible to restrain males for more than 35 min so it may be possible that a longer restraint time is required to observe the full response of stress on testosterone concentration. On Sable Island there is no structured dominance hierarchy among males, rather males adopt a position among a group of females that may temporally shift in size and composition (Anderson et al., 1975; Boness and James, 1979; Twiss et al., 1998). The absence of a structured dominance hierarchy is likely to complicate the relationship between reproductive behavior, success and testosterone concentration. Regardless, the relationship between testosterone and behavior has been a difficult one to establish (e.g., Wingfield, 2005).

In the grey seal it appears that males that have a poor ability at defending females may suffer from greater physiological stress as a result. If males experience heightened cortisol concentrations throughout the breeding period, then these males may also be exposed to the deleterious effects of chronic stress. In contrast, successful males may have an adaptive response to stress. If successful males are able to maintain low cortisol concentrations throughout the breeding season, they will minimize the physiological costs of stress but still be able to fully respond to stressful events. For the grey seal male, being reproductively successful may not only provide reproductive benefits but also physiological benefits as well.

## Acknowledgments

We are very grateful to Debbie Austin, Greg Breed, Suzanne Budge, Sara Iverson, Shelley Lang, Strahan Tucker and Jennifer van Dommelen for assistance in the field. We are also grateful for infrastructure support provided on Sable Island by Gerry Forbes. The study was supported by funds from the Friends of the National Zoo, the Smithsonian Institution, the Christensen Fund, the Canadian Department of Fisheries and Oceans and the National Science and Engineering Research Council of Canada.

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