

1 TITLE: The difference between night and day: the nocturnal and diurnal activity
2 budget of gray seals (*Halichoerus grypus*) during the breeding season

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25 All pinniped species are constrained to give birth and raise their pups on land
26 or ice (Bartholomew 1970). This constraint has allowed for detailed behavioral
27 observations on several species of pinniped during the breeding season (*e.g.*, Redman
28 *et al.* 2001; Dobson and Jouventin 2003; Maniscalco *et al.* 2006; Young and Gerber
29 2008). From these observations, activity budgets (also referred to as time budgets) can
30 be calculated; typically to provide information on how individuals, or groups of
31 individuals, partition their time across defined behavioral categories (*e.g.*, Boness
32 1984; Anderson and Harwood 1985; Arnold and Trillmich 1985; Trillmich 1986;
33 Lydersen *et al.* 1994; Twiss and Franklin 2010). However, observational studies are
34 usually constrained to daylight periods and, as a result, there is little information from
35 behavioral observations on any pinniped species during the breeding season (or whilst
36 hauled-out) at nighttime (gray seals (*Halichoerus grypus*), Anderson 1978, southern
37 elephant seals (*Mirounga leonina*), Galimberti *et al.* unpublished data cited in
38 Galimberti *et al.* 2002). Yet, for some species, such as the gray seal, which breed in
39 temperate regions during autumn and winter, daylight periods can be as little as one
40 third of the circadian cycle.

41

42 The paucity of studies investigating nighttime activity budgets of pinnipeds on
43 land (breeding colonies or haul-out sites) has previously been attributed to
44 technological limitations in commercially available night-vision equipment (Shipley
45 and Strecker 1986, Acevedo-Gutiérrez and Cendejas-Zarelli 2011). Where recent
46 technological advances in telemetry devices, for example, have given ecologically
47 important insights into the circadian behavior of pinnipeds at sea (*e.g.*, Jessopp *et al.*
48 2013) and on their haul-out patterns (*e.g.*, Cronin *et al.* 2009), there still remains only
49 one study to date that has successfully undertaken behavioral observations of a

50 pinniped species on land during the nighttime (Anderson 1978). In the
51 aforementioned study, Anderson (1978) investigated the variation in the daytime and
52 nighttime activity budget of one male gray seal during two consecutive breeding
53 seasons and found the ‘Look’ behavior, defined as “head up or turned, gaze directed”,
54 occurred significantly more during the daytime. Subsequently, a plethora of studies on
55 gray seals have used Anderson’s, arguably limited, study to justify using daytime
56 observations as representative of the entire 24 h cycle of activity, either explicitly or
57 implicitly (*e.g.*, Amos *et al.* 1993; Worthington Wilmer *et al.* 1999; Redman *et al.*
58 2001; Twiss and Franklin 2010). This has potentially far-reaching implications on
59 studies of energetics, maternal investment and mating behavior, for example, which
60 do not consider the possibility of variation in circadian behavior. If a significant
61 difference between daytime and nighttime activity budgets exist, then such studies
62 may need to re-interpret their findings.

63

64 Given the progressive technological advances in night-vision devices, the
65 present preliminary study uses commercially available equipment to investigate the
66 circadian activity budget of gray seals whilst on the breeding colony. As gray seals
67 are capital breeders (Bartholomew 1970), we hypothesize that nighttime (*i.e.*, an
68 extended period of darkness) gives individuals’ an important opportunity to increase
69 time spent resting and thus limit energy expenditure. The study site was at Donna
70 Nook on the North Lincolnshire coast, eastern England, U.K. (53.47°N, 0.15°E),
71 which is a National Nature Reserve (NNR) that consists of approximately 1,150
72 hectares of salt marsh, sand dune systems and large inter-tidal sand and mud flats.
73 During November and December the NNR is host to a large breeding colony of gray
74 seals that gathers on the sand flats far inshore close to publicly accessible areas. The

75 seals also use adjacent areas where public access is restricted; therefore, seals within
76 this region of the Donna Nook breeding colony are not exposed to the high levels of
77 tourists experienced elsewhere within the NNR. It was within the restricted area that
78 the preliminary study took place.

79

80 Gray seals are polygynous, colonial, and annual breeders with a discrete,
81 predictable reproductive season (Boyd *et al.* 1962). In the U.K., adult female gray
82 seals come ashore in the autumn, each giving birth to one pup. Movement of
83 postpartum females on the colony is over short distances, and they tend to remain
84 close to their pupping site, rarely moving further than 10 m from their pup (Redman *et*
85 *al.* 2001). Once females have given birth they become aggressive towards one another
86 (Bonner 1981). Consequently, mothers tend to maintain a minimum distance of 2.5 m
87 from their nearest female neighbor (median distance = 4.36 m, Pomeroy *et al.* 1994).
88 A female will spend 18 d, on average, nursing her pup (Bonner 1972) and on
89 approximately day 16 of lactation she will enter estrus (Pomeroy *et al.* 1999), during
90 which time she will mate with one or more males before returning to sea (Twiss *et al.*
91 2006). As such, movement on the colony is relatively infrequent and is typically over
92 short distances, which makes this an ideal study system for obtaining data on
93 circadian activity budgets.

94

95 The nighttime video footage was recorded using a custom-made weatherproof
96 camera constructed by Astra Communications Ltd (<http://www.astrasec.com/>). The
97 specifications of the camera were: 540TV color/monochrome, 9-22 mm auto-iris lens
98 with a minimum illumination of 0 Lux. A weatherproof Infrared lamp was also used
99 to increase the area of illumination, the lamp had an output of 850 nanometers IR with

100 a range of up to 40 m and an IR spread of 30°. The camera and the lamp were
101 powered using two 12v batteries and the footage was recorded on to a 32GB SD
102 memory card. The size of the area under observation was limited to approximately 10
103 m x 8 m by the field-of-view of the camera and the area illuminated by the infrared
104 lighting. Given this limitation, coupled with the fact that breeding adult male gray
105 seals show a considerably greater degree of mobility over the colony than females and
106 pups (Twiss *et al.* 1994), the present study investigated the variation between daytime
107 and nighttime behavior of postpartum females and their pups, only.

108

109 In-field behavioral observations were collected using a five min scan sampling
110 approach (Altmann 1974) between 0800-1600 during the 26 November; 7, 8, and 9
111 December 2010. Observations were conducted at the periphery of the breeding colony
112 from the cabin of a 4x4 vehicle that was parked approximately 10 m from a fence that
113 prevented the seals coming further ashore. The video footage was collected between
114 1600-0800 over three nights: 25 November and 7 and 8 December 2010. Video
115 footage was played back in real-time and the same sampling approach was used (five
116 min scan sampling). To avoid observer bias all data were collected by a single
117 observer. For each of the days in which observations were undertaken, to allow for the
118 transition between nighttime and daytime, data 30 min either side of morning and
119 evening civil twilight was omitted; these times were taken at Grimsby, U.K.
120 (approximately 10 km north of Donna Nook; <http://www.sunrisesunset.com>).

121

122 Using photo-identification, the unique pelage of the females' allowed for
123 identification of individuals (Hiby and Lovell 1990) during the daytime observations
124 and from the nighttime video footage. Where individuals were further from the

125 camera (> 8 m), it was not always possible to observe the pelage in the video footage
126 during nighttime; in these instances individuals were identified in the video footage
127 prior to the onset of darkness. Individual pups were identified where possible by their
128 association with their mothers. The ethogram comprised of nine behavioral categories
129 for females and four for pups (Table 1). With the exception of social interactions and
130 energy transfer behaviors associated with the mother, the active behaviors of gray seal
131 pups are often ambiguous to interpret. For this reason these behaviors were grouped
132 into the ‘Active’ behavioral category.

133

134 Behavioral data for both daytime and nighttime were obtained for five
135 postpartum females and three pups. The other two pups had too few scan samples at
136 night ($n \leq 20$) (typically due to mothers obstructing the field-of-view of the camera);
137 therefore they were excluded from the analysis. The number of daytime scan samples
138 per individual ranged between 98 – 279 for females, and 98 – 276 for pups. Nighttime
139 observations yielded 68 – 276 and 132 – 324 for females and pups, respectively. If an
140 individual was recorded as out-of-sight during daytime or nighttime observations or
141 out-of-frame during nighttime observations, then these data were not included in the
142 calculation for the activity budgets. As expected, based on previous studies (Anderson
143 and Harwood 1985, Kovacs 1987), the gross activity budget showed that both females
144 (Fig. 1) and pups (Fig. 2) spent the vast majority of their time resting.

145

146 To control for repeated observations on the same individuals and to avoid
147 pseudoreplication we employed binomial Generalized Estimating Equations (GEEs)
148 (Hardin and Hilbe 2013) using the *geepack* package (Højsgaard *et al.* 2006) in R (R
149 Core Team 2013). The difference between resting during daytime and nighttime was

150 compared for females and pups separately. The response variable was whether or not
151 the individual was recorded as resting during each five min scan sample. As residual
152 autocorrelation was an issue, an auto-regressive (AR1) correlation structure was
153 included in the GEEs (Hardin and Hilbe 2013). The sole explanatory variable,
154 whether the observation took place during daytime or nighttime, was included as a
155 factor.

156

157 For females and pups the time of day was highly significant, with both females (P
158 <0.001 , Estimate = 0.635, SE = 0.048, Wald $\chi^2= 173.9$) and pups ($P <0.001$, Estimate
159 = 0.756, SE = 0.133, Wald $\chi^2= 32.5$) resting more during the nighttime. As females
160 have finite energy reserves and a discrete and limited time period to maximize energy
161 transfer to the pup to enhance pup survival (Hall *et al.* 2001), the significant increase
162 in the time spent resting at nighttime, for both female and pup, could be an example of
163 adaptive behavioral plasticity, where both mother and pup are maximizing the
164 opportunity to conserve energy. Furthermore, the females' activity budget suggested
165 that vigilance behavior decreased during nighttime, which is similar to Anderson's
166 (1978) findings for male gray seals. As discussed by Anderson (1978), this makes
167 biological sense, as in-air visual acuity is likely to be reduced during darkness, which
168 has been shown in other species of pinniped (Schusterman and Balliet 1971,
169 Schusterman 1974). Therefore, it is highly likely that individuals are responding to
170 olfactory and auditory, rather than visual cues at nighttime. In addition, the percentage
171 of time pups spent active during nighttime decreased (which may also be attributed to
172 visual acuity), and given that females respond to their pup's behavior (Fogdon 1971;
173 Kovacs 1987; Smiseth and Lorentsen 1995*a, b*; 2001) this is also likely to reduce the
174 need for maternal vigilance behavior at nighttime, and thus allow more time for rest.

175

176 The findings presented here show that there is a significant difference in how
177 females and pups partition aspects of their activity budgets between daytime and
178 nighttime. As such, caution should be exercised when daytime activity budgets are
179 used to represent nocturnal behavior or are used to draw general conclusions on the
180 energetics, maternal investment or mating behavior of gray seals during the breeding
181 season (*e.g.*, assuming uniformity across the circadian cycle). Although the sample
182 size is small, given the highly significant results, the pattern appears evident; females
183 and pups do spend more time resting during the nighttime. To investigate variation in
184 circadian patterns of the more rarely recorded behaviors (in order to quantify energy
185 budgets, maternal investment or mating patterns, for example) then more extensive
186 data on individuals (including adult males) for their entire duration on the breeding
187 colony would be required, and perhaps a different sampling regime (*e.g.*, *ad libitum* or
188 focal sampling) depending on the behavior of interest (Altmann 1974).

189

190 This preliminary study has provided information that has been previously
191 unavailable, adding to our knowledge of gray seal activity whilst on the breeding
192 colony and provides a good example of what can be achieved with current,
193 commercially available night-vision technology.

194

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343 *Table 1.* The names, abbreviations (in parentheses) and definitions of each of the nine behavioral categories, * indicates the behavior is
 344 applicable to females, ^ indicates the behavior is applicable to pups. The activity budget was based on the behavioral categories and definitions
 345 presented in Anderson (1978), Anderson and Harwood (1985) and Kovacs (1987).

346

Behavior	Definition
Resting (R) *^	Non-active state lying with head on the ground, eyes may be open or closed.
Vigilance (VIG)*	Looking generally around or in the direction of an event, typically the head is up and neck extended. This includes a definite, distinct and directed look to their pup.
Comfort Move (CM)*	Makes adjustments to position and/or shuffles body on the spot but remains in the same geographical location. May also scratch themselves with their flippers.
Locomotion (L)*	Changes geographic location. This behavior may involve the use of the fore-flippers (for forward or backwards motion), 'barrel' rolling or shuffling (for sideways motion; note the distinction between shuffling on the spot (see 'Comfort Move'), and shuffling to change geographic location). This behavioral category excludes chasing behaviors (see 'Aggression').
Active (ACT)^	All active behaviors (<i>i.e.</i> , when the pup is not 'Resting'), with the exceptions of 'Energy Transfer' and 'Social Interactions'.

Energy Transfer (ET)*^	The female lies on her flank exposing her nipples to the pup, at which point the pup will typically bring its nose to its mother's nipples. The mother is considered to be nursing when the pup makes oral contact with a nipple. This behavioral category represents time spent in behaviors that are associated with energy transfer to the pup.
Social Interactions (SINT)*^	The female physically interacts with her pup and/or vice versa, this includes (but is not limited to) nosing (touching the pup/mother with their nose) and flippering (using their flipper to 'stroke' their pup/mother). This behavioral category represents time spent in behaviors that are associated with social interactions between the mother and her pup.
Aggression (AGG)*	Includes but is not limited to; wailing (a vocal threat); aggressive flippering (the female vigorously 'waves' her flipper towards the perceived threat, and may make contact); slapping (the female will lie on her side and continuously slap her flipper against her flank); open mouth threats (the female will open her mouth baring her teeth at the perceived threat); lunging (the female extends her neck, lunging towards the perceived threat); biting (if the female makes contact they attempt to bite) and chasing (the female chases the perceived threat, this is the same as 'Locomotion' but with the clear intent of chasing the perceived threat).
Sex (SEX)*	A male mounts or attempts to mount the female. The male uses his jaws to grip the female by the neck and uses his fore-flippers to grip her body. Copulation attempts may be unsuccessful; this can occur if the female is unreceptive (typically

resulting in aggressive behaviors on the female's part). A successful copulation occurs when intromission is clearly achieved and the copulation proceeded, uninterrupted, to completion.

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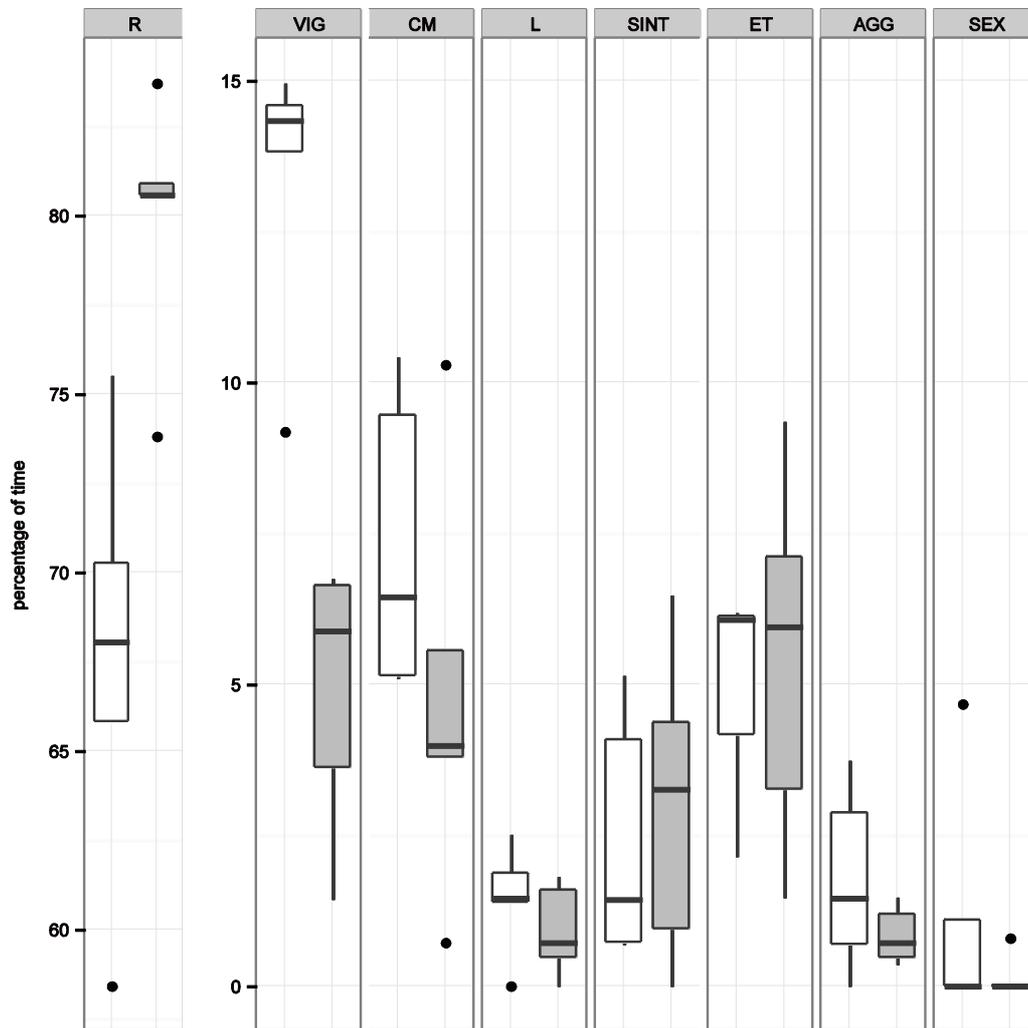
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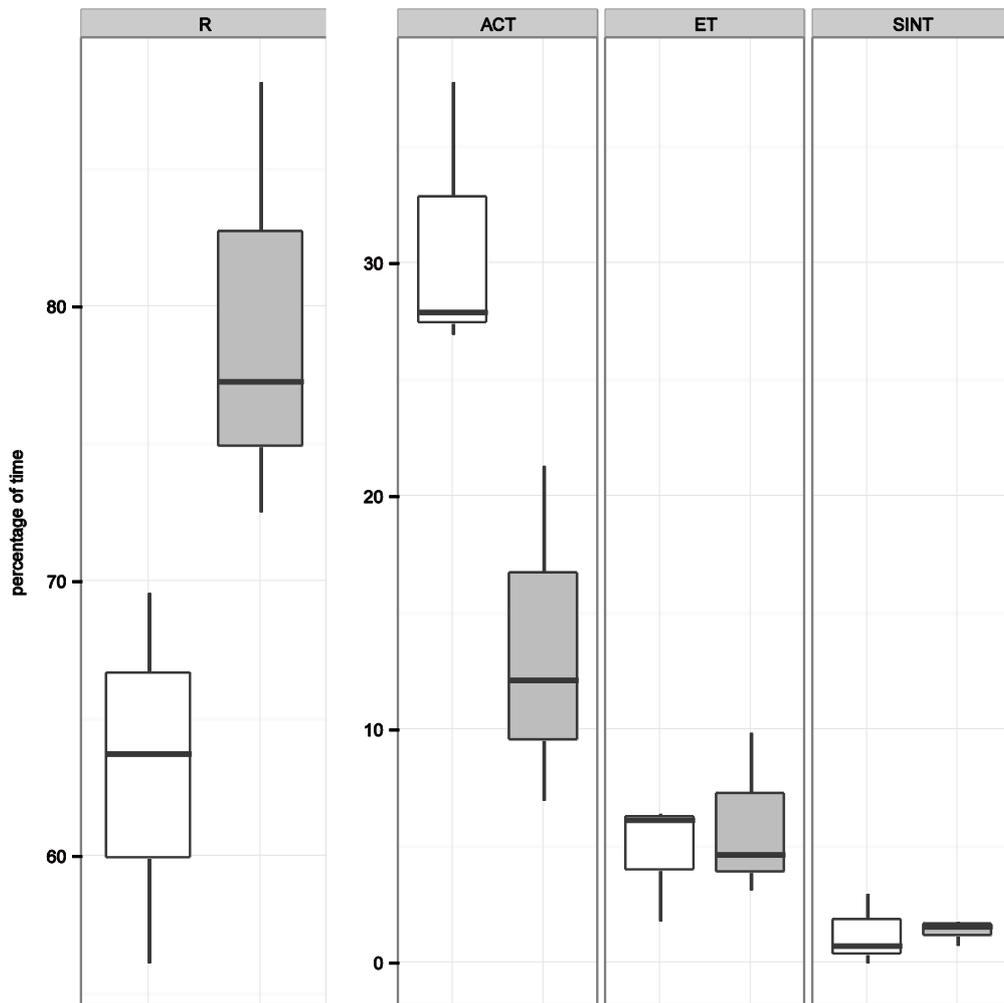
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361

362 *Figure 1.* The percentage of time females ($n = 5$) spent in each of the eight behavioral
 363 categories (see Table 1 for definitions of behavioral categories) during daytime (white
 364 boxplots) and nighttime (gray boxplots) observations. ‘Resting’ (R) is presented in a
 365 separate plot, as it constitutes a considerably larger percentage of time spent than the
 366 other behavioral categories. The boxplots show the lower quartile, the median, the
 367 upper quartile and the whiskers, which extend to the most extreme data point that is
 368 no more than 1.5 times the inter-quartile range from the box.

369



371

372 *Figure 2.* The percentage of time pups ($n = 3$) spent in each of the four behavioral
 373 categories (see Table 1 for definitions of behavioral categories) during daytime (white
 374 boxplots) and nighttime (gray boxplots) observations. ‘Resting’ (R) is presented in a
 375 separate plot, as it constitutes a considerably larger percentage of time spent than the
 376 other behavioral categories. The boxplots show the lower quartile, the median, the
 377 upper quartile and the whiskers, which extend to the most extreme data point that is
 378 no more than 1.5 times the inter-quartile range from the box.