

1           **Comparative influence of intrinsic and extrinsic drivers on activity budgets in**  
2                                   **sympatric grey and harbour seals**

3

4 Running title: Grey and harbour seal activity budgets.

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## 20 **Abstract**

21 Investigating activity budgets requires a continuum of behaviours to be categorised into  
22 distinct states using direct or remote observations. Furthermore, one type of movement or  
23 behaviour (e.g. diving) may encompass multiple states (e.g. travelling and foraging). We  
24 addressed this by combining behavioural and location data from telemetry tags deployed on  
25 63 grey seals (*Halichoerus grypus*) and 126 harbour seals (*Phoca vitulina*) within a state-  
26 space model to define population-level activity budgets in the UK. The large sample size  
27 allowed us to investigate how time spent in four states (resting on land (hauled out), resting at  
28 sea, foraging and travelling) was influenced by seasonal, intrinsic (age, sex) and extrinsic  
29 covariates (time of day, region, tag parameter settings). We demonstrate that resting at sea  
30 (prolonged surface activity) was prevalent in both species and occurred both inshore near  
31 haul-outs and offshore between foraging intervals, potentially serving differing functions.  
32 The activity budgets of both species were similar and in both species were influenced by all  
33 considered covariates demonstrating the importance of both intrinsic and extrinsic factors in  
34 determining activity budgets. However, the influence of covariates on aspects of the  
35 allocation of activity budget varied markedly between the species. We found no link between  
36 significant regional patterns in activity budgets and regional population trajectories and thus  
37 we caution against using activity budgets as indicators of population health. More generally  
38 we have demonstrated a framework for using both behavioural and movement data to  
39 categorise activity budgets and identifying the factors that drive them.

40

41 **Keywords:** area-restricted search, Bayesian, energetic requirements, energy budget, hidden  
42 process models, pinnipeds, time budget.

43

44

## 45 **Introduction**

46 Animals divide their time into various activities (e.g. resting, foraging, travelling, breeding,  
47 socialising, predator avoidance and provisioning of young) at a variety of temporal scales  
48 (hours to lifespans). These activity budgets are likely to be influenced by both intrinsic (e.g.  
49 sex and age) and extrinsic factors (e.g. food availability and density of predators; (Mooring  
50 and Rominger 2004). Investigation of activity budgets throughout annual cycles provides a  
51 unique opportunity to understand the relative importance of intrinsic and extrinsic factors on  
52 behavioural strategies (McNamara and Houston 1986). However, such studies are rare, in  
53 part due to the difficulties in categorising animal behaviour into distinct activity classes. This  
54 is especially difficult if many behaviours are hidden, for example those species using marine  
55 and subterranean habitats. Consequently, it is often only during periods for which animals  
56 are visible (e.g. breeding season) that activity budgets that can be successfully defined using  
57 direct field observations (Neumann 2001). Alternatively, activity budgets may be defined  
58 using behavioural (Härkönen et al. 2008) or movement data (Breed et al. 2009) derived from  
59 animal-borne instruments. However, activity budgets cannot always be clearly defined from  
60 these data because one behaviour (e.g. diving or flying) may be characteristic of multiple  
61 activities (or states) such as foraging and travelling. Similarly one type of movement (e.g.  
62 tracks which exhibit slow speed and high turning angles) may occur during multiple activity  
63 states (such as foraging and resting). Previously, the expense and effort required to deploy  
64 such instruments has also meant that sample sizes were often too small to thoroughly  
65 investigate intrinsic and extrinsic drivers of activity budgets. However, analytical  
66 developments (McClintock et al. 2013) and increasing sample sizes now offer the potential to  
67 make inferences about population-level activity budgets from both behavioural and  
68 movement data.

69

70 Such data exist in the UK for two sympatric species of seal: harbour (*Phoca vitulina*) and  
71 grey seals (*Halichoerus grypus*). Investigation of comparative activity patterns is of particular  
72 interest due to marked differences in the recent population dynamics of these two species in  
73 the UK. In the last decade, overall the number of grey seals has increased (Lonergan et al.  
74 2011) whereas the number of harbour seals has decreased (Lonergan et al. 2007). However,  
75 trends vary regionally, especially in harbour seals for which there are stable populations and  
76 those showing decreases and increases; the causes of these differing regional trajectories are  
77 not known. Both species are central place foragers that alternate trips to sea with hauling out  
78 on land, and have similar diets (Brown et al. 2012) but there are stark differences in other  
79 aspects of their ecology and morphology. Grey seals are larger and more sexually dimorphic  
80 and the annual breeding and moulting cycles of the two species are asynchronous (Bonner  
81 1972). In the UK, grey seals show a clockwise geographic cline in pupping date between  
82 September (in south-west England) and December (south-east England), followed by  
83 moulting between December and April. In contrast, UK harbour seals pup in June and July  
84 and then moult in August. There are also differences in their lactation strategies; while  
85 harbour seal females forage during lactation (Bowen et al. 2001), grey seals rarely if ever do  
86 (Boyd 1998). Finally, their foraging ecology also appears to differ; harbour seals exhibit  
87 shorter trip durations and have a more inshore distribution than grey seals (McConnell et al.  
88 1999, Sharples et al. 2012)

89

90 Detailed studies on aspects of activity budgets have previously been carried out in various  
91 populations of both species. For harbour seals, studies have focussed on factors influencing  
92 the proportion of time that individual seals spent hauled out on land. In particular, extensive  
93 work on harbour seal haul-out patterns has been conducted to allow counts to be scaled to  
94 estimates of abundance. Such studies have highlighted the effect of a variety of intrinsic

95 factors such as age and sex (Thompson 1989) and extrinsic factors such as weather (e.g.  
96 Watts 1992), time of day (e.g. Cunningham et al. 2009), tidal cycle (e.g. Thompson et al.  
97 1989) and marine predation risk (London et al. 2012). However, such influences vary  
98 geographically (Hamilton et al. 2014) and no comparative analysis has been conducted on the  
99 factors driving haul-out patterns in grey seals. Other studies of these species have focused on  
100 at-sea activities using metrics such as foraging trip duration and distance (Thompson et al.  
101 1998) or proportion of time spent diving (Beck et al. 2003). More recently, studies have  
102 endeavoured to apportion time at sea into foraging and travelling using dive shape (Baechler  
103 et al. 2002) or movement data within state space models (Breed et al. 2009). Seals may  
104 spend time on the surface (hereafter resting at sea) in inshore waters when inter-tidal haul-out  
105 sites are unavailable (Thompson et al. 1991) and some species have been reported to rest at  
106 sea during longer foraging trips (Gentry and Kooyman 1986), possibly to allow food  
107 digestion (Sparling et al. 2007). However studies are only beginning to incorporate resting at  
108 sea in species which alternate relatively short foraging trips with periods of haul-out (i.e.  
109 harbour seals; Ramasco et al. in press, McClintock et al. 2013).

110

111 Here we use both activity and location telemetry data from 63 grey seals and 126 harbour  
112 seals to compare the factors influencing the activity budgets of these two species in UK  
113 waters. We define mutually exclusive hierarchical states: (1) resting or (2) diving and then  
114 within each of these categories as (1a) resting on land (haul-out), (1b) resting at sea (non-  
115 diving), (2a) area-restricted search behaviour which we define as foraging and (2b) faster  
116 movements with lower turning angles defined as travelling. Note that the label *resting* refers  
117 to the fact the animal is on land or at sea but not diving; it does not necessarily mean the  
118 animal is inactive. Our main aims are to (1) define population-level activity budget for these  
119 sympatric seal species; (2) investigate the seasonal trends in their activity budgets and how

120 these varied with age and sex (3) investigate extrinsic factors shown to affect activity budgets  
121 (time of day, spatial region).

122

## 123 **Methods**

### 124 Telemetry Data

125 We used data from telemetry transmitters deployed on grey and harbour seals in the UK  
126 between 1991 and 2008 (McConnell et al. 1999), and between 2001 and 2011 (Sharples et al.  
127 2012), respectively. We excluded data from tags deployed in areas of high tidal currents (e.g.  
128 Pentland Firth) because they may lead to unreliable movement-based estimates of the  
129 proportion of time spent foraging and travelling (Gaspar et al. 2006). The tags used included  
130 both Sea Mammal Research Unit ARGOS SRDL (Satellite Relay Data Logger) tags and  
131 GPS/GSM phone tags that used Fastloc GPS (Wildtrack Telemetry Systems Ltd). Both tag  
132 types transmitted locational data at irregular intervals. Positions from ARGOS tags were less  
133 frequent and had greater distance error, ranging from 50m to > 2.5km (Vincent et al. 2002).  
134 To correct for positional error in ARGOS data, locations were filtered by an algorithm that  
135 used a 'maximum speed parameter' of  $2\text{ms}^{-1}$  (McConnell et al. 1992), and the remaining  
136 locations were processed through a Kalman filter (Royer and Lutcavage 2008). Kalman filter  
137 observation model parameters were derived from (Vincent et al. 2002) and process model  
138 parameters were derived from average speeds of 142 grey seal GPS tracks. Occasional  
139 erroneous GPS locations were removed using thresholds of residual error and number of  
140 satellites; tests on land showed 95% of the remaining locations had a distance error of < 50m.

141

142 The tags also transmitted both detailed and summarised behavioural data based on patterns of  
143 submergence as determined by wet/dry and pressure sensors. We used two and six-hour  
144 summary records of the proportion of time spent engaged in one of three mutually exclusive

145 behaviours. These categories were determined on-board the tag using sensor information and  
146 were classified as "hauled out", "diving", and "at-surface". A haul-out event occurred when  
147 the tag had been dry for 10 minutes and ended when the tag had been wet for 40 seconds (the  
148 start and end times were then adjusted accordingly). Dives started when the animal was  
149 below a specified depth (1.5, 2, 4 or 6m) threshold for a specified period (6-16 seconds)  
150 which both depended on tag settings. Dives ended when the animal moved shallower than  
151 the depth threshold. The remaining time (not hauled out or diving) was categorised as at-  
152 surface. For comparison between tags summarising data at different resolutions, we  
153 aggregated all summary data into 6-hour intervals, resulting in four intervals in each day,  
154 beginning at midnight (GMT).

155

156 Some individual haul-out events (start and end time) were also transmitted, and it was  
157 assumed that the mean of any observed locations during this period represented the seal's  
158 position at both the start and end of the haul-out event. These and all observed locations were  
159 then synchronised with the 6 hour summary data using linear interpolation. Intervals were  
160 flagged as inestimable if there was a gap of  $> 12$  hours between the observed locations  
161 surrounding the interpolated location, or if there were no summary data for the 6 hour  
162 interval. Tag deployments were excluded from the study if  $>50\%$  of intervals were  
163 inestimable or if there were  $<10$  days of data. Following these procedures, data remained for  
164 65 grey seals and 126 harbour seals; tag durations were between 17 and 256 days (median  
165 178) for grey seals, and between 26 and 245 days (median 115) for harbour seals.

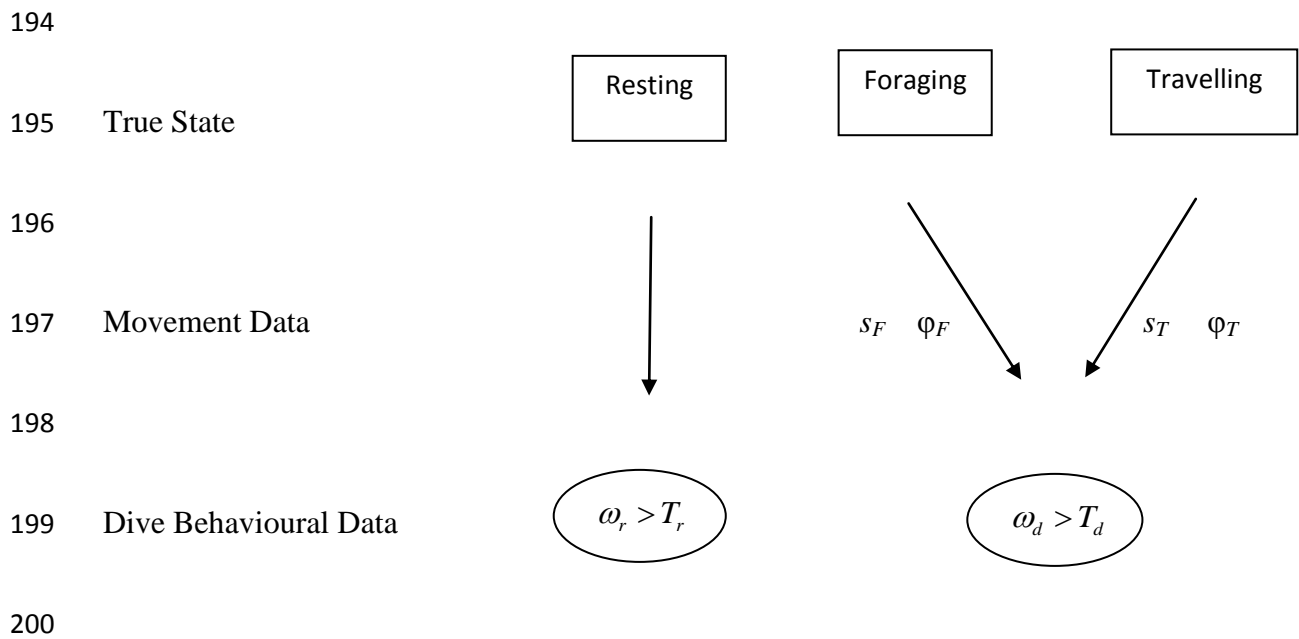
166

167 State assignment

168 Grey and harbour seals make foraging trips that are typically characterised by travel to, from  
169 and between localised areas in which area restricted search, and presumably foraging, takes

170 place (Thompson et al. 1991, 1998). While at sea, animals dive regularly when foraging and  
 171 travelling, but may also spend extended periods of time above the tag depth threshold, which  
 172 we define as resting at sea. Firstly, we defined resting and diving using behavioural (pressure  
 173 and wet/dry sensor) data and then assigned diving as foraging and travelling using a state  
 174 space model (McClintock et al. 2013) to obtain three latent states ( $z_t$ ) for time intervals  $t =$   
 175  $1, \dots, N$ : resting ( $z_t = R$ ), foraging ( $z_t = F$ ), and travelling ( $z_t = T$ ). The behavioural data used  
 176 to classify resting vs diving were the combined proportion of a time interval  $t$  spent hauled  
 177 out and at the surface ( $\omega_{r,t}$ ), vs diving ( $\omega_{d,t}$ ), respectively. We assume  $z_t = R$  when  $\omega_{r,t} > T_r$ ,  
 178 where  $T_r$  is a pre-defined proportion of an interval spent engaged in combined haul-out and  
 179 at-surface behaviour for a time step to be assigned to resting. In other words we assume  
 180  $z_t \in \{F, T\}$  when  $\omega_{d,t} > T_d$ , where  $T_d$  is  $1 - T_r$ . Intervals could not be assigned to resting or  
 181 diving simply based on the majority behaviour because all diving behaviour must include a  
 182 surface breathing overhead which is apportioned to at-surface behaviour in the summary data.  
 183 To obtain a threshold which included the surface overhead value we extracted data on the  
 184 proportion of time spent diving in summary intervals from GPS tags from which most  
 185 summary intervals are transmitted. There was little individual variation in the maximum  
 186 proportion of time spent diving with medians of 88.8% for both grey and harbour seals thus  
 187 the surface overhead was estimated as 11.2%. Based on a majority rule, the threshold for an  
 188 interval to be assigned to diving was half of the maximum that could be spent diving ( $T_d =$   
 189  $0.444$ ) thus  $T_r = 0.556$ . Diving states were assigned to foraging or travelling based on step  
 190 distance (the distance travelled during the interval;  $s_t$ ) and bearing ( $\phi$ ). We also defined the  
 191 distribution of step length and bearing for resting states. The movement and behavioural data  
 192 therefore relate to the latent states as in Fig 1.





201 Figure 1. Structure of the state-space model to estimate whether an interval is resting,  
 202 foraging or travelling.

203

204 Following McClintock et al. (2013), we assumed step distance ( $s$ ) would be longest when  
 205 travelling and used a Weibull distribution where the state-specific scale parameter was  
 206 constrained  $a_{i,T} > a_{i,F}$ . For the bearing ( $\phi$ ) we assumed a wrapped Cauchy distribution. Time  
 207 steps with  $\omega_{d,t} > T_d$  were assumed to be equally likely to have been travelling or foraging  
 208 states, and we incorporated memory into the state transition probabilities ( $\psi$ ) as a first-order  
 209 Markov process. For any flagged intervals, due to missing activity data or unreliable location  
 210 data, state assignments were based entirely on the Markov property of the state transition  
 211 probabilities and were excluded from further analysis. Appendix 1 provides details of the  
 212 Bayesian state-space model.

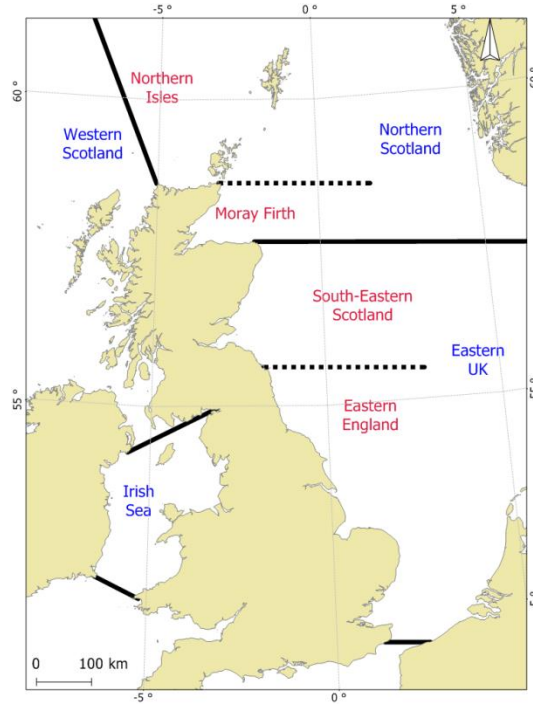
213

214 Adopting a Bayesian perspective, we fitted the state-space model using a Markov chain  
215 Monte Carlo (MCMC) algorithm written in C (adapted from McClintock et al. 2013). Data  
216 from each seal were run individually with two chains starting at different initial values with a  
217 burn in of 50,000 iterations. Convergence was judged by visual inspection of the chains and  
218 using the Gelman-Rubin (gbr) statistic. Usually 50,000 iterations were used for the posterior  
219 distributions but 50,000 more iterations were run if the gbr statistic was not 1.0.

220

221 After running this model, resting intervals were assigned to haul-out or resting at sea if more  
222 than 50% of an interval was spent hauled out or at-surface, respectively. Occasionally neither  
223 state was assigned to the majority of the interval (as only combining both resting on land and  
224 at sea, resting had the majority), the interval was designated as undefined resting. We used all  
225 harbour seals deployments (n=126) to assign haul-out (1a), resting at sea (1b) and diving (2)  
226 but we found that only one diving state was identified in 20% of animals (see Discussion).  
227 Excluding this 20% when examining travelling and foraging in harbour seals may result in  
228 bias finding such behaviour (and covariates thereof) in harbour seals. Thus we only  
229 considered foraging and travelling separately in South-Eastern Scotland (Fig. 2), where there  
230 are defined foraging patches (Fig. 3) and 28 of 30 individuals demonstrated both foraging and  
231 travelling states. Two diving states were identified in 63 of 65 grey seals. Given that  
232 exclusion of two individuals should result in minimal bias, we examined full activity budgets  
233 for 63 grey seals.

234

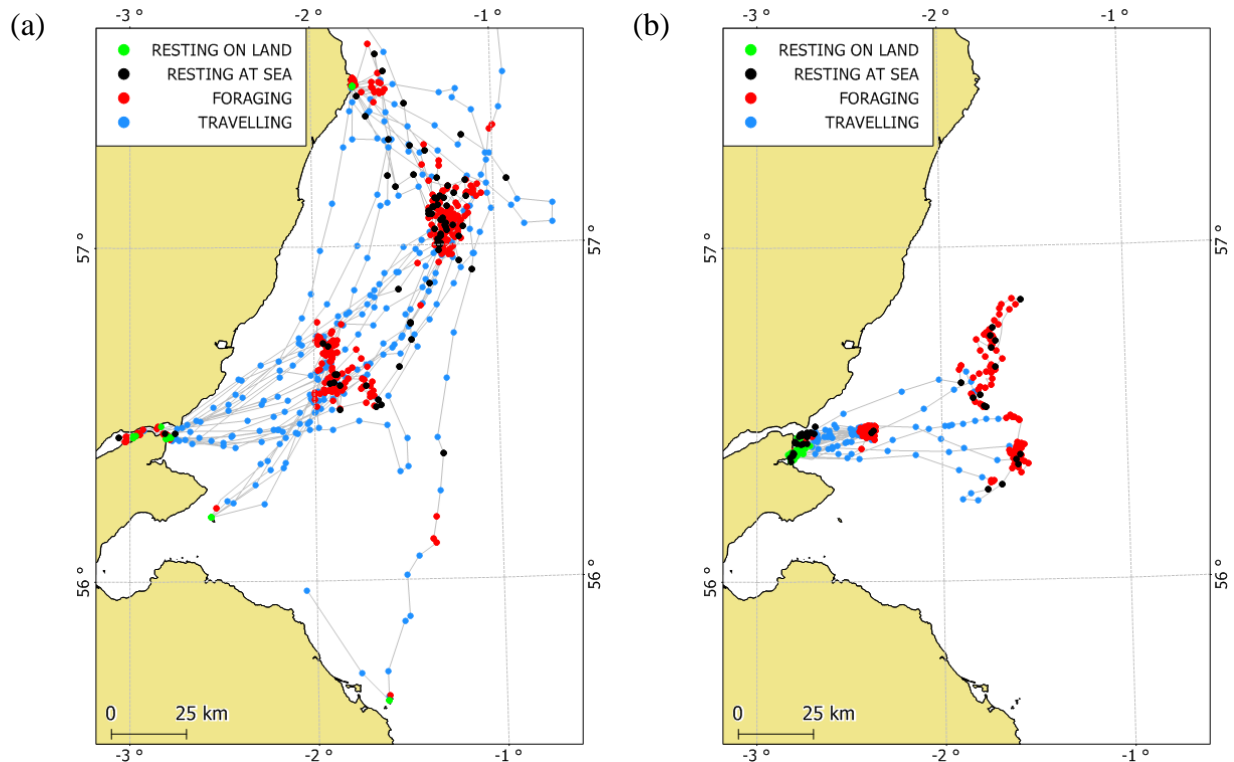


235

236 Figure 2. Regions considered for grey seals are shown in blue divided by solid black lines.

237 Regions for harbour seals are Western Scotland and regions shown in red and divided by both

238 solid and dotted lines.



239 Figure 3. An example of a track characterised into foraging, travelling, resting on land and at  
 240 sea for a grey (a) and harbour seal (b).

241

#### 242 Activity budgets

243 Average activity budgets were calculated for both species, using individuals for which there  
 244 were  $> 100$  valid intervals of data. For a comparison between grey and harbour seals, we  
 245 excluded data from their respective pupping and moult periods. Data from mid-April to  
 246 August were used for grey seals, and data from October to May were used for harbour seals  
 247 (inclusive). The mean proportion of time spent in each state was calculated for each  
 248 individual and the activity budget defined as the median of these values (grey seals:  $n=53$ ,  
 249 harbour seals,  $n=121$ ). For the proportion of time spent foraging and travelling in harbour  
 250 seals we only considered South-East Scotland ( $n=28$ ).

251

252

253 We found that both species spent a substantial proportion of time resting at sea, and that for  
254 the most part this state occurred in two distinct locations: inshore and offshore (e.g. Fig. 3).

255 We estimated the minimum proportion of time that each individual spent resting offshore  
256 using location data. Conservatively, resting at sea was only classified as offshore if the  
257 distance between an interpolated location and coast was greater than a tag-specific threshold  
258 distance. Intervals defined (from behavioural data) as haul-out intervals occasionally  
259 appeared to occur at sea due to location and interpolation error. Location error varies with  
260 tag and seal behaviour so the maximum distance between locations of haul-out intervals and  
261 land, or 5 km, whichever was larger, was used as the tag threshold distance. By default, if  
262 animals never ventured far from the coast, resting at sea within foraging areas would not be  
263 classified as offshore. Furthermore, all undefined resting intervals were assumed to be  
264 resting inshore.

265

## 266 Covariate Analysis

267

268 Activity budget data were analysed using a nested binomial approach within a generalised  
269 estimating equation (GEE) framework using package `geepack` (Højsgaard et al. 2006) within  
270 R (R Development Core Team 2012). By using robust sandwich-based estimates of variance  
271 (Pirodda et al. 2011) the uncertainty about the parameter estimates returned were robust to the  
272 presence of serial autocorrelation within individuals whilst not explicitly modelling this  
273 correlation using a specified working correlation structure. Using a nested binomial approach  
274 we investigated how the proportion of time spent (1) resting and (2) diving; (1a) hauled out  
275 and (1b) resting at sea; and (2a) foraging and (2b) travelling was related to model covariates.  
276 For the first two models, the response was binary because the states were assigned using a

277 threshold but for foraging and travelling the response term was a probability: the estimated  
278 posterior probability that the interval belonged to the foraging state. Backwards hypothesis  
279 testing using GEE-based  $p$ -values was used for model selection. Confidence intervals around  
280 predictions were based on a parametric bootstrapping approach using GEE-based measures of  
281 uncertainty. In addition to predicting the time spent resting and diving, predictions were  
282 combined to predict the non-conditional probability of haul-out, resting at sea, foraging and  
283 travelling. All results are displayed based on default values of covariates if they were selected  
284 in the model (Table S3).

285

286 We considered the following explanatory variables for all three response terms: day of year  
287 (DOY), sex, age, time of day (TOD: four 6 hour intervals), region, and tag dive depth  
288 threshold. These were all input as factors with the exception of DOY which was included as a  
289 continuous covariate. As the effect of DOY may depend on whether an animal is male or  
290 female and whether or not it is breeding, we included a three way interaction between age,  
291 sex and DOY. Year was not included in the analysis because it was confounded with depth  
292 threshold and region.

293

294 Using these covariates we were able to control for intrinsic factors such as DOY, age and sex,  
295 allowing the use of all data, including those from the pupping seasons. Only a few individuals  
296 were of known age (aged using tooth growth rings), so we assigned animals to two age  
297 classes; juveniles and adults (see Table S1 in Appendix 2) using a length threshold based  
298 upon age/length curves. Thresholds were based upon asymptotic length (lower 95<sup>th</sup>  
299 percentile): grey seals: 166 cm for females, 190 cm for males (Fedak and Hiby 1985) and  
300 harbour seals: 128.9cm for females and 134.5 for males (Hall et al. 2012, SMRU unpublished  
301 data). Although animals may breed before they reach full size, this threshold reflected

302 reported estimates of age of first breeding for grey (Harwood and Prime 1978) and harbour  
303 seals (Härkönen and Heide-Jørgensen 1990).

304

305 For both species, there was a gap in the data because tags were lost during the moult. This  
306 meant that DOY was not required to be cyclic and was thus modelled as a cubic *B*-spline with  
307 the median DOY as the single interior knot. Data were selected so that seasonal coverage was  
308 the same for all four pairwise age and sex classes. This resulted in data from between October  
309 (DOY 279) and July (192) for harbour seals and between April (104) and November (333)  
310 for grey seals. When examining covariates of the proportion of time harbour seals spent  
311 foraging and travelling in South-Eastern Scotland, only data from adults (n=20) between  
312 January (DOY 17) and July (DOY 190), the minimal data range for both sexes, were  
313 considered; the sample size for juveniles was too small to enable inferences to be made.

314

315 Four geographical regions were defined for grey seals (Fig. 2) which minimised the  
316 movement between regions within the foraging season (Russell et al. 2013). For harbour  
317 seals, Northern Scotland was split into Northern Isles and Moray Firth and Eastern UK into  
318 South-Eastern Scotland and Eastern England. This reflected the largely separate harbour seal  
319 populations in these areas (Sharples et al. 2012). For both species, seals were assigned to a  
320 region (Table S2) on the basis of where they spent the majority of their time while tagged.

321

## 322 **Results**

323

### 324 Activity budgets (Table 1)

325 Activity budgets were estimated for each individual of both species (see Fig. 3 for illustrative  
326 examples). Although the median of these activity budgets gives an indication of population-

327 level activity budgets, it should be noted the data encompass different age and sex structures,  
 328 regions and seasons. In both species, approximately a third of time was spent resting (as  
 329 opposed to diving) but this varied markedly among individuals with 95% confidence intervals  
 330 ranging from 0.15 to >0.5. Two thirds of time spent diving was apportioned to foraging in  
 331 grey seals; harbour seals spent a similar proportion of time foraging (in South-Eastern  
 332 Scotland). The proportion of time spent resting was split approximately equally into land and  
 333 sea for grey seals whereas in harbour seals two thirds of the time resting was on land. The  
 334 median minimum time spent resting offshore was 0% for harbour seals and 0.01% for grey  
 335 seals. However, for both species the upper 95<sup>th</sup> percentile extended to about 10%. In fact,  
 336 25% and 8% of grey and harbour seals, respectively, spent over 5% of their time resting  
 337 offshore.

338

339 Table 1. The median proportion (and 95% confidence intervals) of time spent by individual  
 340 seals in each activity during the non-breeding season.

species	resting		diving	
	on land	at sea	foraging	travelling
grey seal	0.36		0.64	
	(0.21-0.54)		(0.46-0.79)	
	0.17	0.17	0.40	0.21
	(0.07-0.31)	(0.07-0.33)	(0.22-0.63)	(0.09-0.41)
harbour seal	0.32		0.68	
	(0.15-0.53)		(0.47-0.85)	
	0.20	0.11	0.47*	0.20*
	(0.10-0.36)	(0.01-0.30)	(0.28-0.62)*	(0.06-0.29)*

341 \* These values are for the South-Eastern Scotland region only.



342 Influence of intrinsic & extrinsic drivers

343 The activity budgets of both species were influenced by all intrinsic and extrinsic covariates.  
344 The relationships between activity and all retained covariates (Table 2) are shown graphically  
345 in Appendix 3. The deviance explained by the models was low overall, especially for models  
346 delineating resting/diving and foraging/travelling (pseudo  $R^2 < 5\%$ , Table 2). For both species,  
347 the retained covariates explained about 7% of the deviance in the proportion of time resting  
348 that was allocated to land and sea.

349

- 1 Table 2. The significant covariates ( $P < 0.05$ ) in the activity budgets of grey and harbour seals using  $p$ -values based on Generalised Estimating Equations. Although included, the significance of the main effects are not shown if the interaction was significant.

covariates	resting/diving		given resting: land/sea		given diving: foraging/travelling	
	grey seal ( $R^2 = 0.02$ )	harbour seal ( $R^2 = 0.02$ )	grey seal ( $R^2 = 0.07$ )	harbour seal ( $R^2 = 0.07$ )	grey seal ( $R^2 = 0.02$ )	harbour seal* ( $R^2 = 0.03$ )
TOD	$X^2_3 = 27.95, P < 0.0001$	$X^2_3 = 24.60, P < 0.0001$	$X^2_3 = 11.15, P = 0.011$	$X^2_3 = 92.70, P < 0.0001$	$X^2_3 = 10.12, P = 0.018$	
region		$X^2_4 = 12.37, P = 0.015$	$X^2_3 = 49.81, P < 0.0001$	$X^2_4 = 48.2, P < 0.0001$		NA
depth threshold	$X^2_2 = 82.17, P < 0.0001$	$X^2_2 = 10.93, P = 0.0042$		$X^2_2 = 6.72, P = 0.035$		$X^2_1 = 6.28, P = 0.012$
DOY				$X^2_4 = 15.10, P = 0.0045$		
age						NA
sex						NA
DOY:age						NA
DOY:sex		$X^2_4 = 42.39, P < 0.0001$	$X^2_4 = 10.62, P = 0.031$			$X^2_3 = 7.88, P = 0.048$
age:sex		$X^2_1 = 4.65, P = 0.031$	$X^2_1 = 7.19, P = 0.0073$			
DOY:age:sex					$X^2_4 = 19.22, P = 0.00071$	

- 3 \* These results are for the South-Eastern Scotland region only.

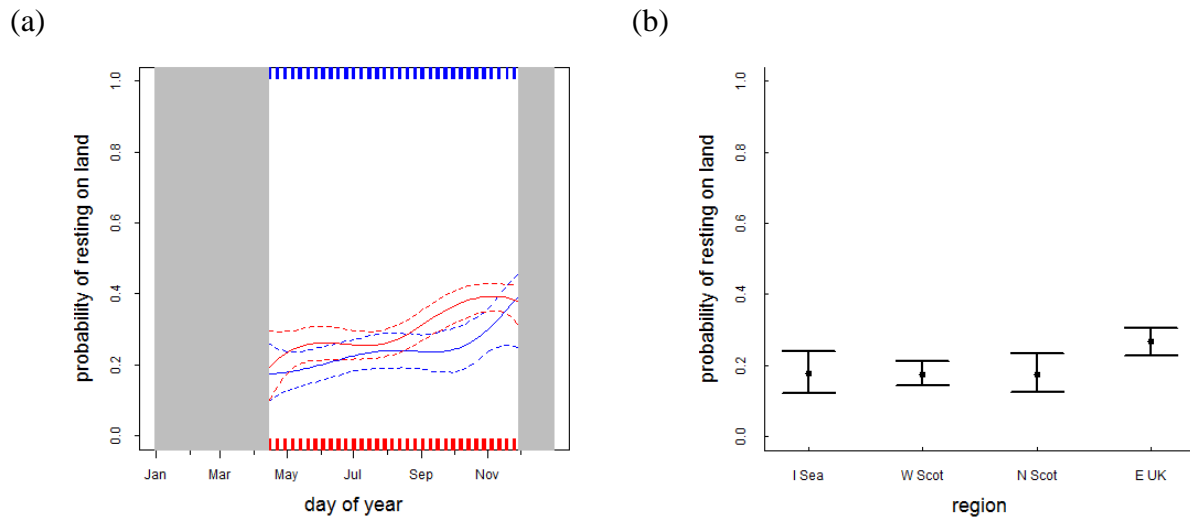
1 *Grey seals*

2 There was a significant effect of TOD and depth threshold on the probability of resting versus  
3 diving. The probability of resting was lowest in the last quarter of the day (Q1: 0.46, 95% CI:  
4 0.43-0.49; Q4: 0.37, 0.34-0.39). There was a decreased probability of resting at the  
5 shallowest dive threshold (e.g. 6m: 0.46, 0.43-0.49; 1.5m: 0.31, 0.28-0.35).

6

7 Given that an animal was resting, the probability of haul-out or resting at sea was  
8 significantly affected by a DOY/sex interaction a sex/age interaction, region and TOD. The  
9 unconditional probability of haul-out in females (Fig. 4a) increased from 0.26 (95% CI: 0.21-  
10 0.31) in spring and summer to 0.39 (0.35-0.43) in autumn. The probability of haul-out in  
11 males (Fig. 4a) was relatively constant (e.g. June: 0.20, 0.15-0.25) increasing only in  
12 November (0.39, 0.25-0.45). The probability of haul-out was highest in Eastern UK (0.27,  
13 0.23-0.30) in comparison to other regions (e.g. Western Scotland: 0.17, 0.14-0.21; Fig. 4b).  
14 Because there was no DOY, sex, age or region effect on the probability of resting, the  
15 probability of resting at sea showed opposite trends to the probability of haul-out for these  
16 variables.

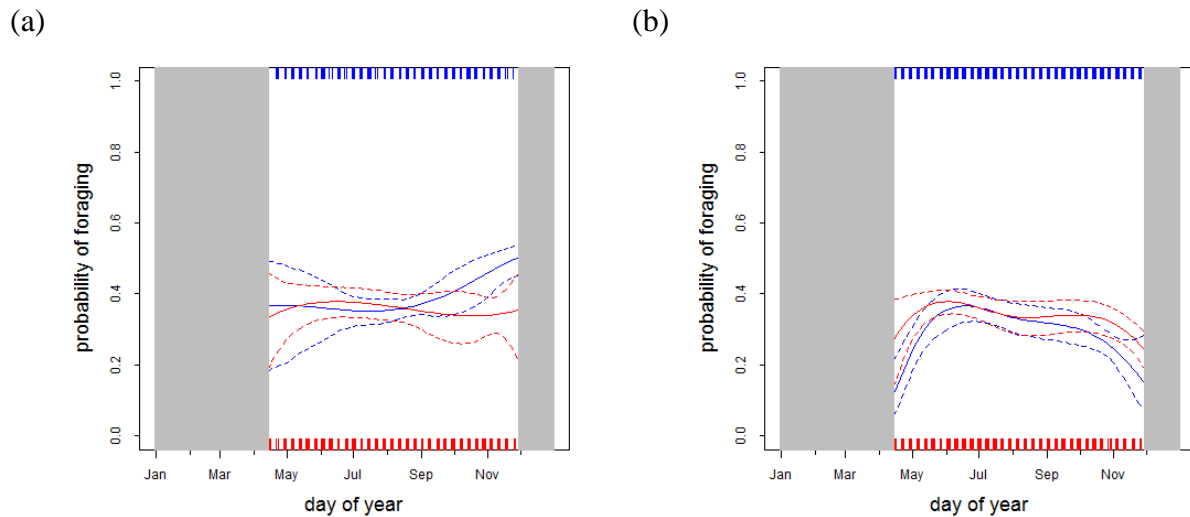
17



1 Figure 4: The unconditional probability of resting on land (hauling out) in grey seals (with  
 2 95% confidence intervals) given DOY with the relationship and data rug plots shown in blue  
 3 for males and red for females (a) and region (Eastern UK, Northern Scotland, Western  
 4 Scotland, Irish Sea; b).

5  
 6 Given that an animal was diving, the probability of foraging or travelling was significantly  
 7 affected by a DOY/sex/age interaction and TOD. The unconditional probability of foraging  
 8 was constant throughout the year for adult females (mid DOY: 0.36, 0.32-0.40); males  
 9 showed a similar trend but probability of foraging increased in the pupping season (95% CI:  
 10 0.45-0.54; Fig. 5a). The relationship between DOY and the proportion of time foraging was  
 11 more marked in juveniles (Fig. 5b). In juvenile females foraging probability dropped slightly  
 12 at the end of the year from its highest in the May and June (0.38, 0.34-0.41) to 0.24 (0.19-  
 13 0.30) by the end of November. In contrast, the probability of foraging in juvenile males was  
 14 lowest at the start (April/May: 0.12, 0.06-0.21) and end (November: 0.15, 0.07-0.28) of the  
 15 study period and highest in June (0.37, 0.32-0.41). The probability of foraging was highest in  
 16 the last quarter of the day (Q1: 0.36, 0.32-0.40; Q4: 0.44, 0.39-0.48). In contrast, the

1 probability of travelling did not show a marked pattern with TOD. Because there was no  
 2 effect of DOY, age or sex on the probability of diving, the probability of travelling showed  
 3 opposite trends to the probability of foraging for these variables.



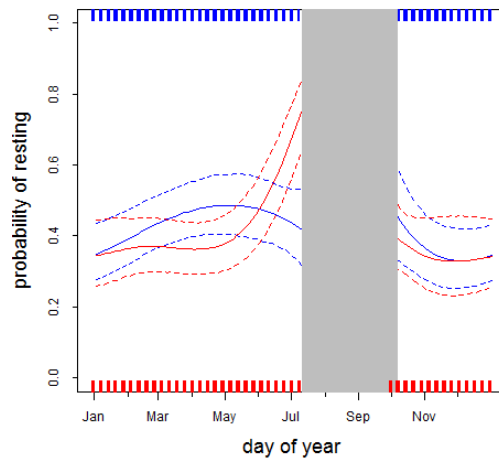
4 Figure 5: The unconditional probability of foraging in grey seals (with 95% confidence  
 5 intervals) given: day of year for adult seals (a) and juvenile seals (b). The relationships and  
 6 data rug plots are shown in blue for males and red for females.

7

### 8 *Harbour seals*

9 The probability of resting was affected by a DOY/sex interaction (Fig. 6), a sex/age  
 10 interaction, TOD, region and depth threshold. In males, there was a slight seasonal pattern  
 11 with the probability of resting being lowest in January (0.35, 95% CI: 0.28-0.44) and highest  
 12 in May (0.49, 95% CI: 0.40-0.57). In females, the probability of resting was constant with  
 13 DOY (January: 0.34, 0.26-0.45) until the end of April when it increased rapidly during the  
 14 pupping season (0.76, 0.64-0.84). Large confidence intervals surround the predictions for the  
 15 probability of resting by region but it was lowest in Western Scotland (0.31, 0.26-0.36) in  
 16 comparison to other regions (e.g. Eastern England: 0.39, 0.31-0.47). The probability of

1 resting increased slightly with the depth threshold (1.5m: 0.29, 0.24-0.34; 6m: 0.37, 0.30-  
 2 0.45).



3

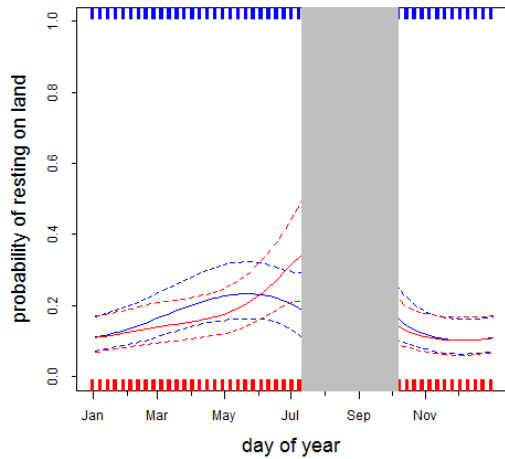
4 Figure 6: The probability of resting in harbour seals (with 95% confidence intervals) given  
 5 day of year with relationships and data rug plots shown in blue for males and red for females.

6

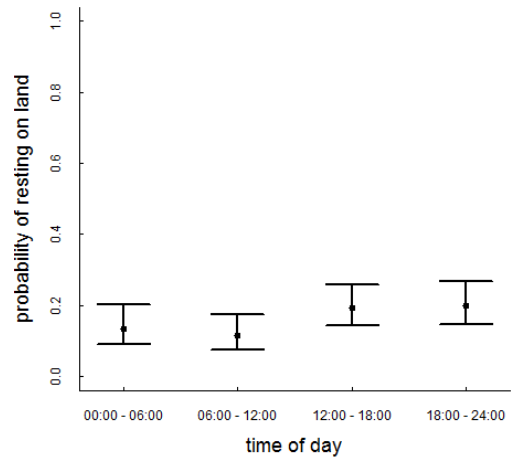
7 Given an animal was resting, there was a significant effect of DOY, region, TOD and depth  
 8 threshold on the probability of haul-out. The unconditional probability of haul-out in females  
 9 (Fig. 7a) increased by about 15% between the end of April (0.18; 0.12-0.25) and mid-July  
 10 (0.34; 0.21-0.49), with probability of resting at sea also increasing from 0.20 (0.14-0.27) at  
 11 the start of May to 0.42 (0.27-0.55) by mid-July (Fig. 8a). The probability of being hauled out  
 12 was similar between males and females in winter but in males it peaked in May (0.23, 0.16-  
 13 0.32; Fig. 7a). The probability of being hauled out was lowest in the Moray Firth and Eastern  
 14 England (both 0.11; 0.7-0.17), with resting at sea being favoured. Animals in Western  
 15 Scotland had a relatively low probability of resting at sea (0.13, 0.10-0.17; Eastern England:  
 16 0.28, 0.21-0.35; Fig. 8b). The probability of haul-out was highest in the second half of the  
 17 day (Q2:0.11, 0.08-0.17; Q4: 0.20; 0.15-0.27; Fig. 7b), with the opposite being the case for

1 resting at sea (Fig. 8c). There was little effect of depth threshold on the probability of haul-  
 2 out but the probability of resting at sea was slightly higher at a 6m depth threshold compared  
 3 to the 2m and even more so, 1.5m threshold.

(a)



(b)

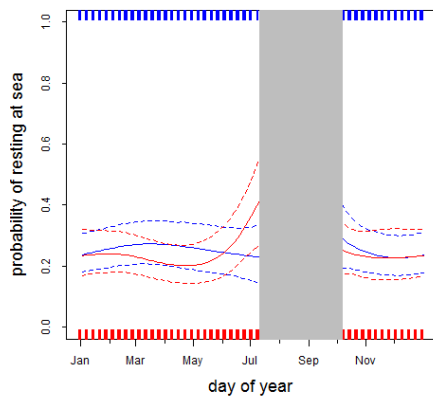


(c)

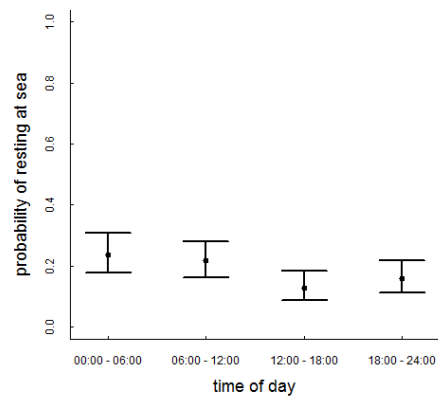
4 Figure 7: The unconditional probability of resting on land in harbour seals (with 95%  
 5 confidence intervals) given day of year with the relationship and rug plots shown in blue for  
 6 males and red for females (a) and time of day (b).

7

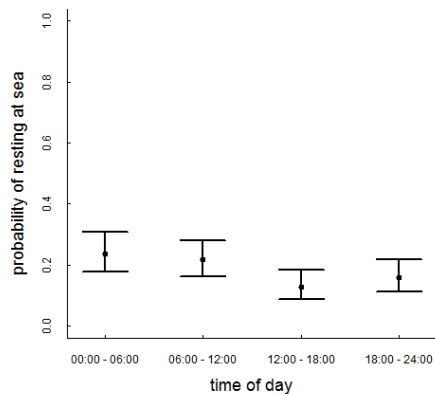
(a)



(b)



(c)



1 Figure 8: The unconditional probability of resting at sea in harbour seals (with 95%  
 2 confidence intervals) given day of year with the relationship and rug plots shown in blue for  
 3 males and red for females (a), region (South-Eastern Scotland, Northern Isles, Moray Firth,  
 4 Western Scotland, Eastern England; b), time of day (c).

5

6 In South-Eastern Scotland, given diving, the probability of foraging was affected by a  
 7 DOY/sex interaction and depth threshold. There was little evidence for a strong seasonal  
 8 trend in the proportion of time diving that males spent travelling (median 0.18) or foraging  
 9 (median 0.44). In females the probability of foraging peaked in March (0.47; 0.42-0.52) and  
 10 then decreased to a minimum towards the pupping season (0.24; 0.16-0.32). Similarly, the  
 11 probability of travelling was also lowest towards the pupping season (0.05, 0.02-0.10) but  
 12 was highest at the start of the year (0.30; 0.21-0.40). A deeper tag depth threshold was  
 13 associated with a lower proportion of diving spent foraging (1.5m: 0.83; 0.73-0.89; 2m: 0.69,  
 14 0.64-0.74).

15

16

17



## 1 **Discussion**

2 We used behavioural and movement data from telemetry tags to define population-level  
3 activity budgets for UK grey and harbour seals (aim 1). Both species spent approximately  
4 one third of their time resting and two thirds diving. Given that harbour seal trips are shorter  
5 in duration than those of grey seals (McConnell et al. 1999, Sharples et al. 2012) this indicates  
6 that harbour seals trips occur at a higher frequency. Thus our findings caution against using  
7 trip duration or extent (Thompson et al. 1989) as comparative indices of foraging effort in  
8 these species. In both species, time spent diving could be divided into two thirds foraging  
9 and one third travelling. It should be noted though that, for harbour seals, allocation of  
10 foraging and travelling was only considered in South-Eastern Scotland. Both species spent a  
11 substantial proportion (median of 0.19 and 0.11 for grey and harbour seals respectively) of  
12 their time resting at sea. Despite the low overall deviance explained (2 - 7%) the significance  
13 and shapes of covariates considered here provide an indication of the intrinsic and extrinsic  
14 influences on activity budgets. Addressing aim two, we found that although there was no  
15 effect of seasonal or intrinsic factors on the allocation of time to resting and diving in grey  
16 seals, these factors did affect the allocation to hauling out, resting at sea, foraging and  
17 travelling. In fact, seasonal trends in the proportion of time spent foraging and travelling  
18 were specific to each four-pairwise combination of age and sex. In harbour seals there were  
19 sex-specific seasonal trends in the allocation of all aspects of the activity budget. In both  
20 species, extrinsic factors (aim three), affected all aspects of activity budgets; TOD affected all  
21 but the allocation of diving into foraging and travelling in harbour seals. In harbour seals,  
22 region influenced the both allocations considered (resting/diving and resting on land/at sex)  
23 whereas in grey seals only the allocation of resting to land and sea differed with region.

24

1 The drivers of inter-trip haul-outs in pinnipeds are not fully understood (Brasseur et al. 1996)  
2 but since it is observed in all individuals of both study species it must serve a function that is  
3 less well satisfied at sea. We found that resting at sea could be divided into two sub-states in  
4 both species (Fig 3): resting at or near to tidal haul-outs, presumably waiting for them to  
5 become exposed (inshore resting), and resting during trips (offshore resting) which mainly  
6 occurred between foraging intervals. Due to the dive depth threshold on the tags, inshore  
7 resting is likely to include diving at shallow depths near haul-outs; such behaviour is  
8 associated with resting and socialising (Thompson et al. 1991). At the temporal resolution of  
9 this study (6 hours) it was not possible to fully separate resting inshore and offshore, and  
10 investigate their allocation with regard to covariates. However, we did find that some  
11 individuals of both species spent a substantial percentage of their time (>5%) resting  
12 offshore. Previous studies have demonstrated large variation in the proportion of time  
13 harbour seal populations haul-out, associated with spatial and temporal variation in drivers  
14 such as predation pressure (London et al. 2012). Such variation may be feasible because  
15 hauling out can be traded off against resting offshore to a degree to fulfil a function such as  
16 digestion which can occur in prolonged surface intervals in grey seals (Sparling et al. 2007).  
17 Offshore resting may be more favoured in populations which have low marine predation  
18 pressure and exhibit relatively long trips (Thompson et al. 1998). In this study we found  
19 regional variation in both the proportion of time spent resting overall (harbour seals) and also  
20 the how this was allocated to land and sea (both species). For harbour seals, the lowest  
21 proportion of time spent resting at sea and overall was in Western Scotland where haul-outs  
22 are largely non-tidal (Cunningham et al. 2009). The low proportion of time spent resting  
23 suggests relatively high foraging effort but the population does not show signs of being  
24 nutritionally stressed; the population is not declining and does not exhibit particularly long  
25 duration or distance trips (Sharples et al. 2012). Inshore resting intervals are more common in

1 tidal areas (South-Eastern Scotland) where animals spend time on the surface or exhibit  
2 shallow dives between haul-outs being exposed (SMRU, unpublished data). If inshore resting  
3 does not offset the need to rest on land then in areas, such as Western Scotland, where haul-  
4 outs are largely non-tidal, inter haul-out surface activity between low tides is not necessary  
5 and so overall time spent resting can be reduced.

6

7 This study also revealed intrinsic and temporal patterns in harbour seal activity budgets.  
8 Although there was no evidence that sex specific trends in the allocation of time spent resting  
9 and diving varied with age this does not preclude such sex-specific patterns being driven by  
10 reproduction because the sample size of juveniles was relatively small (n=26 compared to  
11 adults; n=100) and the age threshold was not based on reproductive status. Indeed our results  
12 are in keeping with previous studies on breeding individuals showing that females increase  
13 the proportion of time spent hauled out during pupping while males defend territories at sea  
14 (Van Parijs et al. 1997). Although diurnal patterns in haul-out are not temporally or spatially  
15 consistent even within the UK (Thompson et al. 1989, Cunningham et al. 2010), in this broad  
16 study we found that haul-out probability was highest in the second half of the day. The  
17 seasonal trends in haul-out found in this study were also reflected in time spent resting at sea  
18 suggesting an overall change in preference to rest or dive, rather than an increased preference  
19 to haul-out *per se*. Thus seasonal changes in time spent hauled out may be driven by changes  
20 in metabolism (Rosen and Renouf 1998) or prey availability.

21

22 In grey seals, both intrinsic and temporal covariates influenced aspects of their activity  
23 budgets. Intrinsic drivers considered did not significantly influence the overall proportion of  
24 time spent resting and diving despite the varying energetic requirements of different ages and  
25 sexes, and observed age and sex specific seasonal trends in condition (Fedak and Hiby 1985).

1 However, the allocation of hauling out, resting at sea, foraging and travelling were in part  
2 driven by intrinsic factors. The proportion of time females spent hauled-out was highest  
3 during the pupping season. For males, time spent hauled out increased towards the end of the  
4 pupping season when males may come on shore to mate with females that have reached  
5 oestrus (Anderson et al. 1975). The sex-specific seasonal trends in the division of diving  
6 activity in juveniles differed from adults and were more marked. Juveniles, particularly  
7 males, spent a higher proportion of time travelling in winter, possibly because they found it  
8 harder to fulfil their energetic requirements. Indeed juveniles are more likely to be  
9 energetically stressed with starvation being reported as a main cause of death in juveniles but  
10 not in adults (Baker et al. 1998). The fact that seasonal trends in activity budget vary with sex  
11 in a different way to adults demonstrates sexual differences aside from those driven by  
12 differences in reproductive costs. Such differences may be driven by innate differences or  
13 size dimorphism (Ruckstuhl and Neuhaus 2005). Juvenile grey seals show size dimorphism  
14 (SMRU unpublished data) so males require more energy and thus may need to travel more  
15 when food availability is low. However, some sex-specific differences in behaviour (Breed et  
16 al. 2011) and lower male survival (Hall et al. 2001) occur in young of the year when there is  
17 little size dimorphism (Anderson and Fedak 1987) suggesting that innate factors play a role.

18

19 When interpreting our results, the assumptions made and how they differ from those in other  
20 studies should be considered, particularly the temporal resolution of the data and the use of  
21 both behavioural and movement data to define full activity budgets encompassing four states.  
22 In order to include historical ARGOS data, which comprised the majority of telemetry data,  
23 we investigated activity budgets at a 6-hour resolution, similar to the resolution used in  
24 previous studies (Breed et al. 2009, 2011). Because we effectively use a majority rule for  
25 categorising resting versus diving and to allocate the components of resting, the effective

1 resolution for attributing an interval to these activities is 3 hours. This is unlikely to have led  
2 to inaccurate estimates of grey seal activity budgets as they have often forage far from their  
3 haul-out. Although, such an interval is also likely to be appropriate for defining harbour seal  
4 haul-out events which average over 3 hours (Cunningham et al. 2009), allocating diving  
5 intervals to foraging or travelling at a 6 hour resolution was problematic for harbour seals in  
6 most regions and thus could only be estimated in South-Eastern Scotland. This is likely to be  
7 because harbour seals stay closer to their haul-outs than grey seals and thus at the temporal  
8 resolution considered here there were very few travelling intervals. Indeed, investigation of  
9 harbour seal activity budgets on a finer temporal resolution using data solely from GPS tags  
10 allowed diving to be apportioned to foraging and travelling (McClintock et al. 2013).  
11 However, it is possible that in some environments where there are not discrete foraging  
12 patches there may only be one diving state which constitutes exploratory, meandering  
13 foraging.

14

15 Using both behavioural and movement data we were able to define activity budget comprised  
16 of four states. As well as identifying resting at sea this allowed us to include all at sea  
17 behaviour whereas in previous studies using movement data alone, 2-5 km buffers  
18 surrounded land or haul-outs to exclude all inshore behaviour (Breed et al. 2009, 2011). Such  
19 boundaries may result in an underestimate of inshore foraging (Thompson et al. 1991). Such  
20 inshore foraging is especially important for harbour seals that have a coastal distribution with  
21 some individuals staying exclusively within 10km of the coast (Sharples et al. 2012).  
22 Although some of the inshore activity classed as foraging in our study may have represented  
23 other activities, such as sleeping under water and socialising, these predominantly occur in  
24 shallow water near haul-outs (Thompson et al. 1991) and thus their influence would have

1 been excluded to a degree by considering parameter estimates based on the deeper depth  
2 threshold of 6m.

3

4 We have assumed movement characteristics could be used to assign a probability of foraging  
5 or travelling. Importantly, this enabled the use of data from historical ARGOS data for which  
6 there is intermittent dive data. Furthermore, although U-shaped dives appear to be related to  
7 foraging in harbour seals, the characteristics of dive shape differed by sex and age resulting in  
8 mixed success using dive parameters to categorise behaviour (Baechler et al. 2002).  
9 However, we note that diving will also encompass other activities that due to their low  
10 horizontal movement are likely to be classed as foraging including displaying in male  
11 harbour seals (Van Parijs et al. 1997). Recent evidence suggests that harbour seals do  
12 perform resting dives (Ramasco et al. in press). Although they may be a common occurrence  
13 in some individuals, their short duration means that at the resolution of this study it is  
14 unlikely that such dives would have resulted in overestimation of foraging states.

15

16 In this study we defined activity budgets and their intrinsic and extrinsic covariates for two  
17 sympatric species (aims 1 - 3). Although we found that the activity budgets of the harbour  
18 seal, whose overall UK population is declining, were slightly more sensitive to extrinsic  
19 factors than those of grey seals, regional patterns in activity budgets were not correlated to  
20 regional population trajectories. This suggests that the relationship between activity budgets  
21 and population trajectories are complex and we suggest caution in using activity budgets  
22 (Breton et al. 2008) as indicators of population trends or ecosystem health. Unlike a previous  
23 study of harbour seal activity budgets based on location and behavioural data (McClintock et  
24 al. 2013), we have explicitly distinguished resting on land from resting at sea. We found that  
25 a substantial proportion of time is spent resting at sea and that, at least in some individuals,

1 some of this is spent offshore. Previous studies that solely used movement data have assumed  
2 that time at sea outwith a buffer of land can be assigned to either foraging or travelling in  
3 grey seals (Breed et al. 2009, 2011). Resting at sea will, by definition, involve little horizontal  
4 movement and so previous studies may have overestimated the proportion of time spent  
5 foraging offshore whilst potentially underestimating foraging inshore, which could result in  
6 misleading conclusions about activity budgets and their drivers. The substantial proportion  
7 of time resting at sea, when presumably the underlying habitat is of little importance, also  
8 highlights the potential problem of using all location data within habitat preference analyses  
9 for seals.

10

11 Supplementary Information

12 Appendix 1. State assignment

13 Appendix 2. Details of telemetry data

14 Table S1. The age and sex of study animals.

15 Table S2. The regional allocation of study animals.

16 Appendix 3. Activity budget covariate figures

17 Table S3. The default covariates values used for all results.

18 Fig S1. The probability of resting in grey seals.

19 Fig S2. The probability of resting on land in grey seals.

20 Fig S3. The probability of resting at sea in grey seals.

21 Fig S4. The probability of foraging in grey seals.

22 Fig S5. The probability of travelling in grey seals.

- 1 Fig S6. The probability of resting in harbour seals.  
2 Fig S7. The probability of resting on land in harbour seals.  
3 Fig S8. The probability of resting at sea in harbour seals.  
4 Fig S9. The probability of foraging in harbour seals.  
5 Fig S10. The probability of travelling in harbour seals.

6

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17 Any use of trade, product or firm names does not imply an endorsement by the US  
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19

20

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