

Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals

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Investigation of activity budgets in relation to seasonal, intrinsic (age, sex) and extrinsic (time of day, spatial) covariates enables an understanding of how such covariates shape behavioural strategies. However, conducting such investigations in the wild is challenging, because of the required large sample size of individuals across the annual cycle, and difficulties in categorising behavioural states and analysing the resulting individual-referenced and serially correlated data. In this study, from telemetry tags deployed on 63 grey seals *Halichoerus grypus* and 126 harbour seals *Phoca vitulina* we used behavioural data, and movement data within a Bayesian state–space model (SSM), to define population-level activity budgets around Britain. Using generalised estimating equations (GEEs) we then examined how time spent in four states (resting on land (hauled out), resting at sea, foraging and travelling) was influenced by seasonal, intrinsic and extrinsic covariates. We present and discuss the following key findings. 1) We found no evidence that regional variation in foraging effort was linked to regional population trajectories in harbour seals. 2) Grey seals demonstrated sex-specific seasonal differences in their activity budgets, independent from those related to reproductive costs. 3) In these sympatric species there was evidence of temporal separation in time hauled out, but not in time foraging. 4) In both species, time spent resting at sea was separated into inshore (associated with tidal haul out availability) and offshore areas. Time spent resting at sea and on land was interchangeable to some extent, suggesting a degree of overlap in their functionality. This may result in a relaxation of the constraints associated with a central place foraging strategy. More generally, we demonstrate how a large dataset, incorporating differing tag parameters, can be analysed to define activity budgets and subsequently address important ecological questions.

Animals divide their time into various activities (e.g. resting, foraging, travelling, breeding, predator avoidance and provisioning of young) at a variety of temporal scales (minutes to lifespans). Investigation of activity budgets throughout annual cycles provides an opportunity to understand the relative importance of intrinsic and extrinsic factors on behavioural strategies (McNamara and Houston 1986). However, such studies on wild populations are rare, in part because of the difficulties in categorising animal behaviour into distinct activities. This is especially difficult in species for which some behaviours are not directly observable, for example wide-ranging species and animals using marine and subterranean habitats. Behavioural (Härkönen et al. 2008) or movement (Breed et al. 2009) data derived from animal-borne instruments are often used to classify activities (e.g. foraging and travelling) within a defined time period (e.g. a foraging trip). However, complete activity budgets cannot

always be clearly defined from these data because a particular type of behaviour (e.g. diving or flying) may be characteristic of multiple activities (or states) such as foraging and travelling. Similarly, one type of movement (e.g. tracks which exhibit slow speed and high turning angles) may occur during multiple activity states (such as foraging and resting). Until recently, the expense and effort required to deploy such instruments has also meant that sample sizes were often too small to thoroughly investigate intrinsic and extrinsic drivers of activity budgets. However, analytical developments (McClintock et al. 2013) and increasing sample sizes now offer the potential to make inferences about population-level activity budgets from a combination of behavioural and movement data.

Such data are available for two species of seal that coexist around Britain, harbour *Phoca vitulina* and grey seals *Halichoerus grypus*, making them ideal study species to

investigate the determinants of activity budgets and how these vary between sympatric species. This is of particular interest because of marked differences in recent population dynamics of these species. In the last decade, for Britain as a whole, the total number of grey seals has increased (Lonergan et al. 2011) whereas the number of harbour seals has decreased (Lonergan et al. 2007). Similar trends have also been observed in the northwest Atlantic population (Bowen et al. 2003). Both species are central place foragers that alternate trips to sea with hauling out at a limited number of terrestrial sites (haul out sites), and have similar generalist diets (Brown et al. 2012). However, there are differences in other aspects of their ecology and morphology; for example, grey seals are larger and more sexually dimorphic.

Studies on how activity metrics such as foraging trip duration differ between sexes, and among life history stages, regions and species have focussed on a single issue such as sensitivity to environmental stressors (Fort et al. 2013); behavioural strategies (e.g. foraging; McNamara and Houston 1986 and migration; Bailleul et al. 2005) or how animals coexist (Schwartz et al. 2014). In our study system, the data allow us to define complete activity budgets across the majority of the year for different species, sexes, ages and regions, providing the opportunity to investigate multiple issues simultaneously. Many central place foragers show a degree of flexibility in their time budgets which can buffer, to some extent, against decreased food availability (Cairns 1988, Burger and Piatt 1990). For example, in response to decreased prey availability, foraging effort has been reported to increase up to a threshold (Cairns 1988, Furness and Tasker 2000) after which decreased prey availability can result in decreased reproductive success (Wanless et al. 2005). Thus, an examination of foraging effort can be used to identify vulnerable components of the population that are under pressure from extrinsic drivers. For example, in New Zealand sea lions *Phocartos hookeri* differing population trajectories in two colonies were linked to differences in foraging trip duration and environmental conditions (Augé et al. 2011). Harbour seals in Britain show stark contrasting regional population trends. If declines are mediated through decreased prey availability, we expect the declining sub-populations to show some signal in their activity budgets.

Similarly, within species, foraging strategies may be related to seasonal changes in prey availability or quality but such relationships are complicated by the reproductive cycle (McNamara and Houston 1986, 2008). By investigating both immature and mature sections of populations, the effect of intrinsic factors such as reproductive status and sex can be disentangled, and the effects of the environment understood. A previous study on grey seals in the northwest Atlantic revealed pairwise age and sex-specific seasonal trends in the proportion of time spent foraging and travelling (Breed et al. 2011). These differing foraging strategies were likely driven by reproductive costs and seasonal prey availability, in mature and immature individuals respectively (Breed et al. 2011). However, it is not known to what extent this result can be generalised across geographical regions, and if it extends to the complete time budget (overall time spent diving).

Competition for prey, between grey and harbour seals, has been postulated as a reason for harbour seal declines both in Britain (Sharples et al. 2012) and elsewhere (Bowen et al. 2003). In order to coexist, sympatric species must segregate at least one aspect of their niches: spatial, temporal or resource segregation (Schoener 1974). The annual breeding and moulting cycles of the two species are asynchronous (Bonner 1972). In Britain, grey seals show a clockwise geographic cline in pupping period from September (in southwest England) to December (southeast England), followed by moulting between December and April. In contrast, British harbour seals pup in June and July and then moult in August. However, during the majority of the year, both species engage in foraging trips out to sea and although grey seals do exhibit longer distance trips than harbour seals, their at-sea distributions overlap (McConnell et al. 1999, Matthiopoulos et al. 2004, Sharples et al. 2012). Sympatric predators with overlapping spatial distributions may show temporal segregation; this can be a result of interference competition (Schoener 1974) or differing activity drivers (Monterroso et al. 2014). If grey and harbour seals are competing for prey, we expect that these species will show differing diurnal niches.

Between foraging trips, central place foragers return to a certain place to provision young or shelter (Orlans and Pearson 1979). Pinnipeds are central place foragers; they must return to land or ice to pup and moult. However, some species demonstrate central place foraging behaviour outwith the pupping and moulting seasons: hauling out on land between foraging trips. They do not always return to the same site and the reason for this central place foraging behaviour is not understood (Brasseur et al. 1996). Seals spend extended periods of time on the surface (hereafter referred to as resting at sea) in inshore waters when intertidal haul out sites are unavailable (Thompson et al. 1991) and some species show extended surface intervals offshore (Gentry and Kooyman 1986). Indeed recent studies have demonstrated this behaviour in harbour seals (McClintock et al. 2013, Ramasco et al. 2014). In a captive environment, grey seals have demonstrated extended surface intervals associated with food digestion (Sparling et al. 2007). If resting on land and offshore share some functionality (such as digestion), this may reduce the frequency with which animals have to return to land.

We use both behavioural and movement data from telemetry tags deployed on 63 grey seals and 126 harbour seals to define population level activity budgets. We build on a previous study by McClintock et al. (2013), where both behavioural and movement data from harbour seals were used to classify three states (resting, foraging and travelling). We define mutually exclusive hierarchical states: 1) resting or 2) diving and then within each of these categories as 1a) resting on land (haul out), 1b) resting at sea (non-diving), 2a) area-restricted search behaviour which we define as foraging and 2b) faster movements with lower turning angles defined as travelling. Note that the label 'resting' refers to the fact the animal is on land or at sea but not diving; it does not necessarily mean the animal is inactive but it is associated with little horizontal movement (McClintock et al. 2013, Ramasco et al. 2014). In contrast to McClintock et al.

(2013) we define the activity budget of each individual separately to avoid making any assumptions about the consistency of manifestations of behaviour among individuals. In this study, we present a framework within which the resulting activity classifications are analysed while taking into account individual variation and the serial correlation inherent in telemetry data. We do this to investigate four key questions: 1) Do harbour seals in regions of decreasing population size show relatively high foraging effort? 2) Do adult and juvenile grey seals demonstrate differing sex-specific seasonal activity budgets? 3) Is there diurnal segregation in activity budgets of grey and harbour seals? 4) Do these populations spend time resting offshore and is there any evidence of interchangeability between resting on land and at sea?

Methods

Telemetry data

We used data from telemetry transmitters deployed on grey and harbour seals in Britain between 1991 and 2008 (Matthiopoulos et al. 2004), and between 2001 and 2011 (Sharples et al. 2012), respectively. We excluded data from tags deployed in areas of high tidal currents because they may lead to unreliable movement-based estimates of the proportion of time spent foraging and travelling (Gaspar et al. 2006). The tags used included both Sea Mammal Research Unit Argos SRDL (Satellite Relay Data Logger) tags and GPS/GSM phone tags that used Fastloc GPS. Both tag types transmitted location data at irregular intervals. Positions from Argos tags were less frequent and had greater distance error, ranging from 50 m to > 2.5 km (Vincent et al. 2002). To correct for positional error in Argos data, locations were filtered by an algorithm that used a 'maximum speed parameter' of 2 ms^{-1} (McConnell et al. 1992), and the remaining locations were processed through a Kalman filter (Royer and Lutcavage 2008). Kalman filter observation model parameters were derived from Vincent et al. (2002) and process model parameters were derived from average speeds of 142 grey seal GPS tracks. Occasional erroneous GPS locations were removed using thresholds of residual error and number of satellites; tests on land showed 95% of the remaining locations had a distance error of < 50 m.

The tags also transmitted both detailed and summarised behavioural data based on patterns of submergence as determined by wet/dry and pressure sensors. Depending on the tag settings either 2 or 6 hour summary records were available which provided the proportion of time spent engaged in one of three mutually exclusive behaviours. These behaviours were determined on-board the tag using sensor information and were classified as 'hauled out', 'diving' and 'at-surface'. A haul out event occurred when the tag had been dry for 10 min and ended when the tag had been wet for 40 s (the start and end times were then adjusted accordingly). Dives started when the tag was below a specified depth (1.5, 2, 4 or 6 m) threshold for a specified period (6–16 s) that both depended on tag settings. Dives ended when the animal moved shallower than the depth threshold. The remaining time (not hauled out or diving) was categorised as at-surface. To allow inclusion of all tags, we aggregated all summary data into

6 hour intervals, resulting in four intervals in each day, beginning at midnight (GMT).

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

State assignment

Grey and harbour seals make foraging trips that are typically characterised by travel to, from and between localised areas in which area restricted search, and presumably foraging takes place (Thompson et al. 1991, 1998). Whilst at sea, animals dive regularly when foraging and travelling, but may also spend extended periods of time above the tag depth threshold, which we define as resting at sea. In contrast to McClintock et al. (2013), we first defined resting and diving based on behavioural thresholds. We then allocated time diving into foraging and travelling using movement data within a state space model (McClintock et al. 2013, Russell et al. 2014). Through this process we obtained three latent states (z_t) for time intervals $t = 1, \dots, N$: resting ($z_t = R$), foraging ($z_t = F$), and travelling ($z_t = T$).

The behavioural data used to classify resting were the combined proportion of a time interval t spent hauled out and at the surface ($\omega_{r,t}$) versus diving ($\omega_{d,t}$). We assume $z_t = R$ when $\omega_{r,t} > T_r$. In other words we assume $z_t \in \{F, T\}$ when $\omega_{d,t} > T_d$, where T_d is $1 - T_r$. A value of 50% could not be used as the threshold because the activity of diving must include a surface breathing overhead but in the summary data this overhead is included in at-surface behaviour. To obtain a threshold we extracted data on the proportion of time spent diving in summary intervals from GPS tags from which most summary intervals were transmitted. There was little individual variation in the maximum proportion of time spent diving with medians of 88.8% for both grey and harbour seals thus the surface overhead (minimum time above the depth threshold) associated with diving was estimated as 11.2%. Based on a majority rule, the threshold for an interval to be assigned to diving was half of the maximum that could be spent under the depth threshold and thus $T_d = 0.444$ and $T_r = 0.556$. Diving states were assigned to foraging or travelling based on step distance (the distance travelled during the six h interval; s_t) and bearing (ϕ). We also defined the distribution of step length and bearing for resting states. The movement and behavioural data therefore relate to the latent states as in Fig. 1.

Following McClintock et al. (2013), we assumed step distance (s) would be longest when travelling and used a

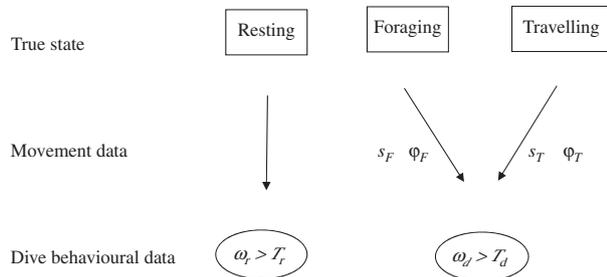


Figure 1. Structure of how the data is used to estimate whether an interval is resting, foraging or travelling.

Weibull distribution where the state-specific scale parameter was constrained $a_{i,T} > a_{i,F}$. For the bearing (ϕ) we assumed a wrapped Cauchy distribution. Time steps with $\omega_{d,t} > T_d$ were assumed to be equally likely to have been travelling or foraging states, and we incorporated ‘memory’ into the state transition probabilities (ψ) as a first-order Markov process. For any flagged intervals, due to missing activity data or unreliable location data, state assignments were based entirely on the Markov property of the state transition probabilities and were excluded from further analysis. The Supplementary material Appendix 1 provides details of the Bayesian state-space model.

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

After running this model, resting intervals were assigned to land or sea if more than 50% of the interval was spent hauled out or at-surface, respectively. Occasionally over 50% of the interval was spent in neither state (as only combining both resting on land and at sea $\omega_{r,t} > T_r$). In these cases the interval was designated as undefined resting. We used all harbour seals deployments ($n = 126$) to assign resting on land, resting at sea and diving but we found that only one diving state was identified in 20% of individuals. Excluding this 20% when examining travelling and foraging in harbour seals may have resulted in bias in describing the population level behaviour. Thus, we only considered foraging and travelling separately in southeastern Scotland (Fig. 2), where there are defined foraging patches (Fig. 6) and 28 of 30 individuals demonstrated both foraging and travelling states. Two diving states were identified in 63 of 65 grey seals. Given that exclusion of two individuals should result in minimal bias, we examined full activity budgets for 63 grey seals.

Covariate analysis

Activity budget data were analysed using a nested binomial approach within a generalised estimating equation (GEE) framework using package *geepack* (Højsgaard et al. 2006) within R (<www.r-project.org/>). By using robust sand-

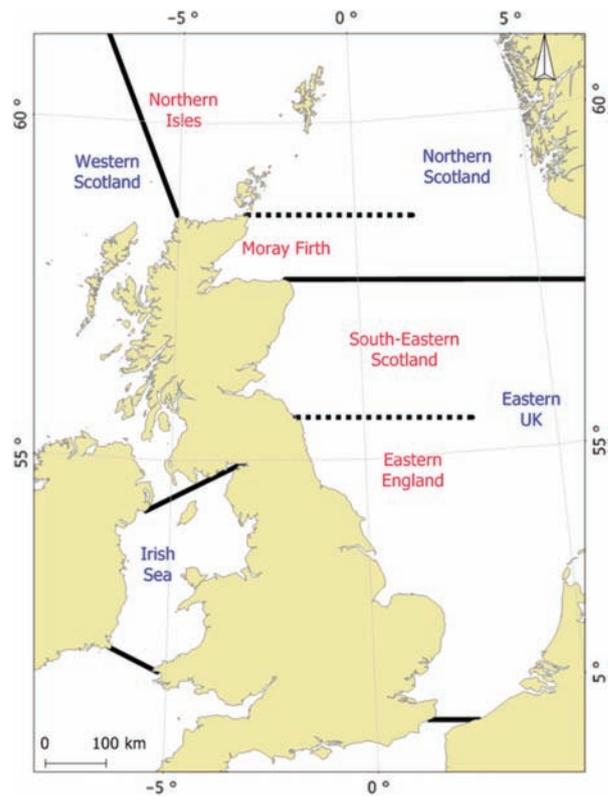


Figure 2. Regions considered for grey seals are shown in blue divided by solid black lines. Regions for harbour seals are western Scotland and regions shown in red and divided by both solid and dotted lines.

wich-based estimates of variance (Pirodda et al. 2011) the uncertainty about the parameter estimates returned were robust to the presence of serial autocorrelation within individuals whilst not explicitly modelling this correlation. We investigated how the proportion of time spent 1) resting and 2) diving; 1a) resting on land and 1b) resting at sea; and 2a) foraging and 2b) travelling was related to model covariates. For the first two models, the response was binary because the states were assigned using a threshold but for foraging and travelling the response term was a probability: the estimated posterior probability that the interval belonged to the foraging state. Backwards hypothesis testing using GEE-based p -values was used for model selection. Confidence intervals around predictions were based on a parametric bootstrapping approach using GEE-based measures of uncertainty.

We considered the following covariates for all models: day of year (DOY), sex, age, time of day (TOD: four 6 h intervals), region, and tag dive depth threshold. These were all input as factors with the exception of DOY which was included as a continuous covariate. As the effect of DOY may depend on whether an animal is male or female and whether or not it is breeding, we included a three way interaction between age, sex and DOY. Year was not included in the analysis because it was confounded with depth threshold and region. Only a few individuals were of known age, so we assigned animals to two age classes; juveniles and adults (Supplementary material Appendix 2 Table A1) using a length threshold based upon age/length curves. Thresholds were based upon asymp-

total lengths (lower 95th percentile); grey seals: 166 cm for females, 190 cm for males (Fedak and Hiby 1985) and harbour seals: 128.9 cm for females and 134.5 for males (Hall et al. 2012, SMRU unpubl.). Although individuals may breed before they reach full size, this threshold reflected estimates of age of first breeding for grey (Harwood and Prime 1978) and harbour seals (Härkönen and Heide-Jørgensen 1990).

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

Four geographical regions were defined for grey seals (Fig. 2) which minimised the movement between regions within the foraging season (Russell et al. 2013). For harbour seals, northern Scotland was split into northern isles and Moray Firth, and eastern UK into southeastern Scotland and eastern England. This reflected the largely separate harbour seal populations in these areas (Sharples et al. 2012). The population trajectories for harbour seals differ between the regions and in most cases these trends have been apparent throughout the duration of study (Duck et al. 2014). While the population in western Scotland has remained relatively constant, the populations in the northern isles and southeastern Scotland have declined rapidly. The population in eastern England has shown continuous rapid increase since the 1970s, punctuated by large declines resulting from epidemics of Phocine Distemper in 1988 and 2002 (Thompson et al. 2010, Duck et al. 2014). For both species, tagged individuals were assigned to a region (Supplementary material Appendix 2 Table A2) on the basis of where they spent the majority of their time while tagged.

Results

All considered covariates significantly influenced activity budgets of both species (Table 1). In addition to predicting the time spent resting and diving, predictions from multiple models were combined to predict the non-conditional probability of resting on land, resting at sea, foraging and travelling. All results are displayed based on default values of covariates if they were retained in the model (Supplementary material Appendix 3 Table A3). The relationships between activity and all retained covariates are shown graphically in Fig. 3–5, Supplementary material Appendix 3. The deviance explained by the models was low overall, especially for models delineating

Table 1. 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 effect is 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	$\chi^2_3 = 27.95, p < 0.0001$	$\chi^2_3 = 24.60, p < 0.0001$	$\chi^2_3 = 11.15, p = 0.011$	$\chi^2_3 = 92.70, p < 0.0001$	$\chi^2_3 = 10.12, p = 0.018$	NA
region		$\chi^2_4 = 12.37, p = 0.015$	$\chi^2_3 = 49.81, p < 0.0001$	$\chi^2_4 = 48.2, p < 0.0001$		NA
depth threshold	$\chi^2_2 = 82.17, p < 0.0001$	$\chi^2_2 = 10.93, p = 0.0042$		$\chi^2_2 = 6.72, p = 0.035$		$\chi^2_1 = 6.28, p = 0.012$
DOY				$\chi^2_4 = 15.10, p = 0.0045$		
DOY:sex		$\chi^2_4 = 42.39, p < 0.0001$	$\chi^2_4 = 10.62, p = 0.031$			$\chi^2_3 = 7.88, p = 0.048$
age:sex		$\chi^2_1 = 4.65, p = 0.031$	$\chi^2_1 = 7.19, p = 0.0073$			NA
DOY:age:sex					$\chi^2_4 = 19.22, p = 0.00071$	NA

*these results are for adults in the southeastern Scotland region only.

resting/diving and foraging/travelling (pseudo $R^2 < 5\%$, Table 1). However, in both species, about 7% of the deviance in the allocation of resting to land and sea was explained by the retained covariates.

Question 1

Do harbour seals in regions of decreasing population size show relatively high foraging effort?

There was significant regional variation in the activity budgets of harbour seals; less time was spent resting in western Scotland than in other regions. The regional pattern in the proportion of time resting overall or on land was not linked to population trajectory (Fig. 3b); the population in western Scotland is stable, whereas the populations are declining in northern isles and southeastern Scotland.

Question 2

Do adult and juvenile grey seals demonstrate differing sex-specific seasonal activity budgets?

The proportion of time grey seals spent diving did not vary by day of year, age or sex. However, seasonal trends in the time spent foraging and travelling did vary with the pairwise age and sex combinations. In adult females the proportion of time foraging and travelling was comparatively constant throughout the year, whereas in adult males the proportion of time travelling dropped from September onwards (Fig. 4a). In juveniles a higher proportion of time was spent travelling in the winter months and this was particularly evident in males (Fig. 4b).

Question 3

Is there diurnal segregation in activity budgets of grey and harbour seals?

Grey seals rested less in the last quarter (Fig. 5a) in favour of diving (particularly foraging; Supplementary material Appendix 3 Fig. A2). There was an indication that resting on land was lowest in the second half of the day. In harbour seals, the time spent resting and the apportionment of diving into foraging and travelling varied very little with time of day (Fig. 5b). However, the apportionment of resting to

land and sea did show a diurnal pattern; more time was spent resting on land in the second half of the day (Fig. 5b). These patterns did not lead to temporal segregation in time spent diving but it did result in a degree of temporal segregation in the time spent hauled out (Fig. 5).

Question 4

Do these populations spend time resting offshore and is there any evidence of interchangeability between resting on land and at sea?

Both species spent a substantial proportion of time resting at sea (Fig. 3), and for the most part this state occurred in two distinct locations: inshore and offshore (e.g. Fig. 6). We estimated the minimum proportion of time that each individual spent resting offshore using location data. Conservatively, resting at sea was only classified as offshore if the distance between an interpolated location and coast was greater than a tag-specific threshold distance. Intervals defined (from behavioural data) as haul out intervals occasionally appeared to occur at sea due to location and interpolation error. Location error varies with location and tag so the maximum distance between locations of haul out intervals and land, or 5 km, whichever was larger, was used as the tag threshold distance. By default, if animals never ventured far from the coast, resting at sea within foraging areas would not be classified as offshore. Furthermore, all undefined resting intervals were assumed to be resting inshore. The median minimum time spent resting offshore was 0% for harbour seals and 0.01% for grey seals. However, for both species the upper 95th percentile extended to about 10%. In fact, 25% and 8% of grey and harbour seals, respectively, spent over 5% of their time resting offshore.

There was no significant regional variation in time spent diving and resting in grey seals. However, the allocation of time spent resting to land and sea did vary significantly with region (Fig. 3a); eastern UK showed a relatively high proportion of time resting on land. In harbour seals, there was substantial regional variation in the allocation of resting to land and sea (Fig. 3b). In contrast, the time spent resting overall was only significantly different in one region compared to the others (western Scotland). These findings suggest that

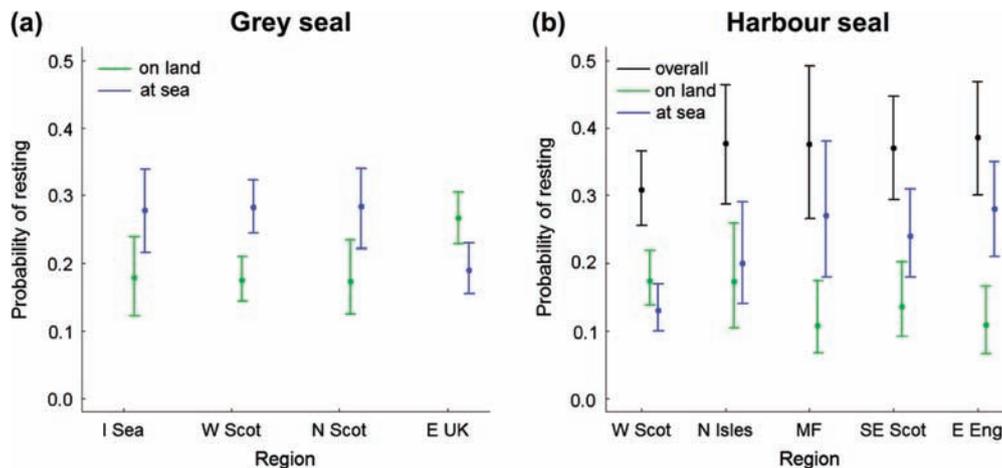


Figure 3. The predicted probability of resting in grey (a) and harbour seals (b). The points show the median estimate and the whiskers, the 95% confidence intervals.

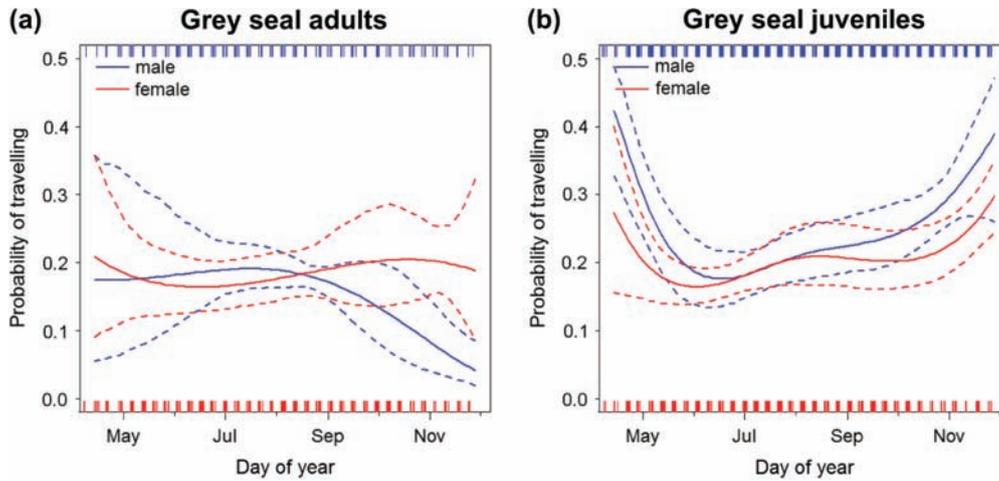


Figure 4. The predicted probability of travelling in grey seals adults (a) and juveniles (b) with regard to time of year. The solid lines show the median predictions and the dotted lines, the 95% confidence intervals. The rug plots indicate the data coverage used to fit the models.

time spent resting at sea and on land is interchangeable to a degree.

Discussion

There are clear regional differences in harbour seal population trajectories around Britain. Regions in which populations are declining did not show a particularly low proportion of time resting overall or on land. This is unlikely to be because a minimum temporal threshold in time spent resting has been reached because, in comparison to other regions, significantly less time was spent resting in western Scotland, where the population is stable. Other possible indicators of foraging effort such as trip duration and distance (Sharples et al. 2012) also did not correlate with population trajectories. Metrics of foraging effort in top predators (including pinnipeds) have previously been associated with prey availability (Boyd 1997), reduced breeding success and adult survival (Forcada et al. 2005). In fact such research has led to time spent foraging in Antarctic fur seals *Arctocephalus gazelle* being used as an index of krill abundance for manage-

ment purposes (CCAMLR 1995). However, the reliability of foraging effort as a measure of prey availability varies even within a species (Breton et al. 2008); it can be unreliable especially when examining spatial differences between colonies in comparison to temporal trends within colonies. For example, despite evidence that Antarctic fur seals serve as indicators of prey availability, there was no clear indication of relatively high foraging effort associated with a colony showing a constant population trend compared to one showing an increasing trend. In the increasing population, long foraging trips may have been driven by foraging patches of relatively high energy content prey far from the colony (Staniland et al. 2011). Notwithstanding the described limitations, our findings do not provide support for the hypothesis that declining populations of harbour seals are having to work particularly hard to in an attempt to fulfil their energetic requirements due to relatively low prey availability.

In agreement with a study of northwest Atlantic grey seals (Breed et al. 2011), we found distinct sex-specific seasonal trends in the proportion of time foraging and travelling in juveniles and adults. However there was no sex, age or seasonal trends in time spent resting or diving. This

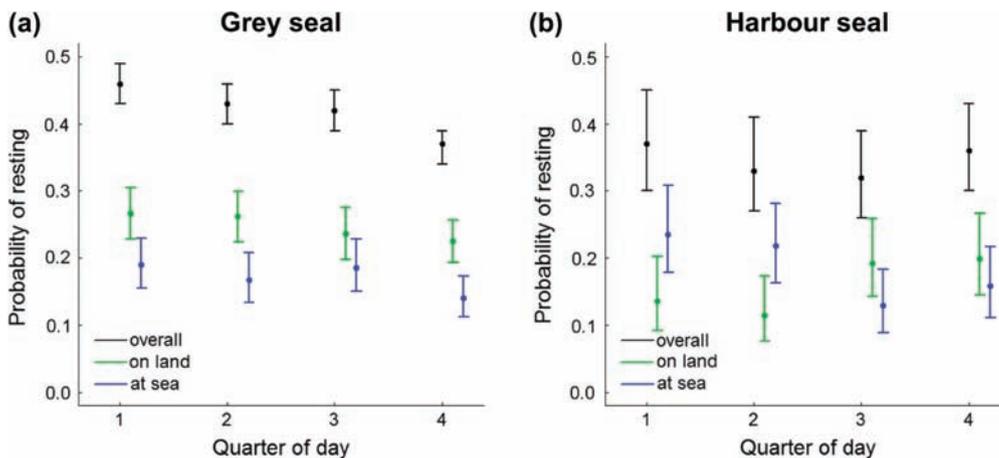


Figure 5. The probability of resting given the time of day for grey (a) and harbour (b) seals. The points show the median estimate and the whiskers the 95% confidence intervals.

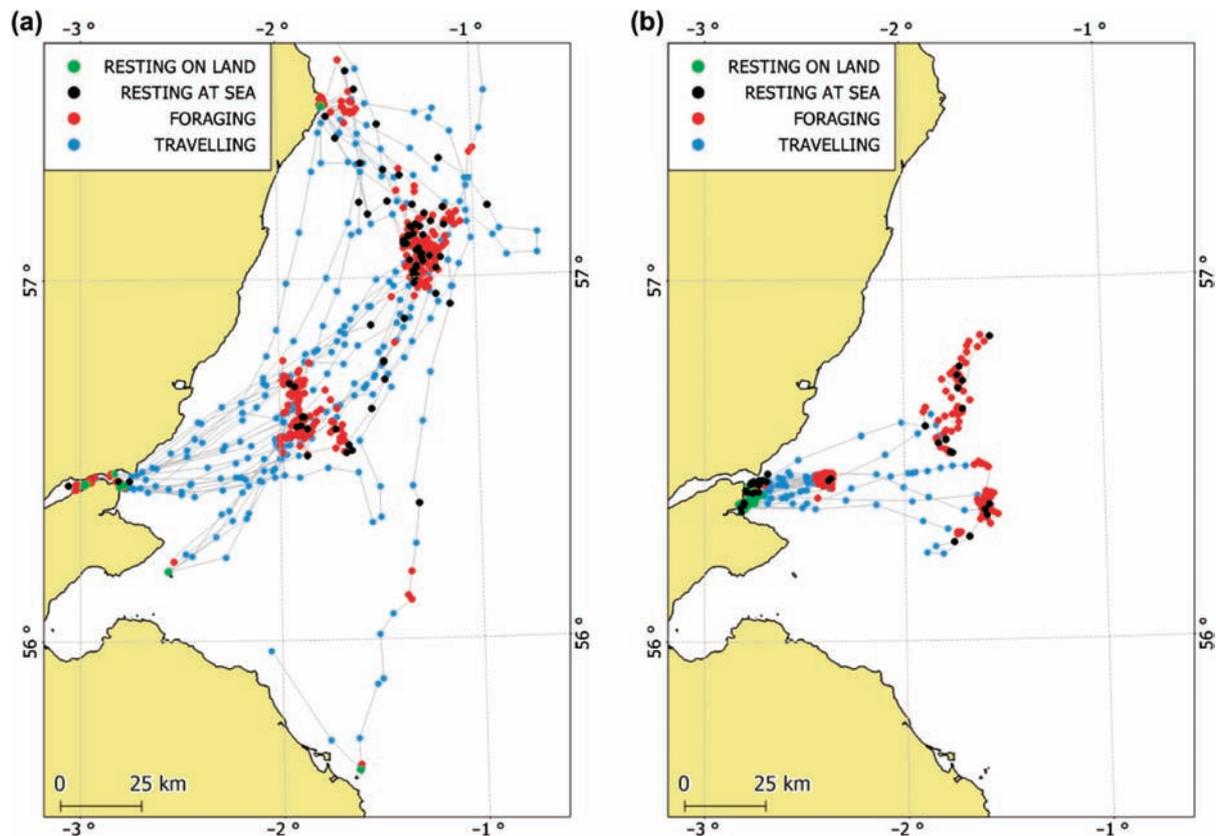


Figure 6. An example of a track characterised into foraging, travelling, resting on land and at sea for a grey (a) and harbour seal (b).

indicates that either grey seals can exhibit little flexibility in the proportion of time spent resting or that they can fulfil their energetic requirements by varying the allocation of resting or diving into their component parts, in response to varying intrinsic and extrinsic drivers. Juveniles, particularly males, increased their time travelling (to the detriment of time foraging), and presumably increased trip distance, in the winter; in winter prey availability is relatively low; for example a main prey species, sandeels, bury themselves in the sediment (Winslade 1974a, b, c) which may make them less available to seals. Juvenile grey seals can become energetically stressed with starvation reported as a main cause of death in juveniles but not in adults (Baker et al. 1998). In addition, Hall et al. (2001) reported lower first year survival in grey seal males than females. Potential reasons for age specific differences in foraging strategies are lower feeding efficiency in juveniles (Weathers and Sullivan 1989, Riotte-Lambert and Weimerskirch 2013) or being out-competed in foraging patches nearer haul out sites by adults (Jones 1987, Breed et al. 2013). These findings about juveniles demonstrate sex-specific behaviour independent of reproductive drivers. Such differences may be driven by differing energy requirements through size dimorphism (Ruckstuhl and Neuhaus 2005), which is evident in juvenile grey seals (SMRU unpubl.). However, differences in foraging strategies have also been found in young of the year (Breed et al. 2011) which are not yet sexually dimorphic (Anderson and Fedak 1987). Furthermore, in juvenile New Zealand sea lions *Phocarctos hookeri*, male trip distance and durations were almost twice as long as females and although present, sexual dimorphism

was an unlikely causal factor (Leung et al. 2012) leading to the suggestion of niche-divergence to reduce intraspecific competition. Alternatively, males of polygynous species may have differing nutritional requirements from females: they need to attain sufficiently large body size at maturity to achieve mating success and thus a more risky foraging strategy, where the balance of energy use tends to the build-up of lean mass rather than blubber, may be favoured (Arnould et al. 1996).

We found no evidence of diurnal segregation which can play a role enabling coexistence of sympatric species (Monterroso et al. 2014). Such temporal segregation may be unnecessary in these seals as although they are both generalist predators, they show some regional dietary differences (Brown et al. 2012) which may reduce direct competition for prey. Furthermore, although grey seals did show some preference for foraging in the last quarter of the day, diurnal segregation may be minimal because trips and thus foraging can encompass multiple days. Despite the coarse temporal resolution that prohibited inclusion of tidal state which is known to affect when individuals haul out (Thompson et al. 1989), we detected a diurnal signal in haul out patterns, most notably in harbour seals. In grey seals, the proportion of time resting on land was lowest in the second half of the day. Although the proportion of time harbour seals rest overall (non diving) varied little with time of day, they showed significant preference to rest on land in the second half of the day. Harbour seals appear to be flexible in when they haul out, linked with availability of tidal haul out sites (Thompson et al. 1989, Hamilton et al. 2014), disturbance (Brasseur et al. 1996), predation pressure (London et al.

2012) and environmental covariates (Watts 1992). In harbour seals, there is evidence of intra-specific density dependent interactions on haul out sites (Neumann 1999) and at mixed haul out sites the smaller harbour seals could be competitively excluded by grey seals leading them to preferentially haul out at a different time of day to grey seals. Further intensive behavioural studies are required to assess whether our findings are a result of temporal segregation of a resource (haul out site) or caused by differing drivers to haul out in these two species. In the former case, we would expect differing diurnal haul out patterns for harbour seal populations hauling out at mixed and single species haul out sites. Such information is required in order to understand the drivers of haul out behaviour in seals and to interpret dual species surveys used to monitor population trends; segregation of species at mixed haul out sites would undermine scalars used to convert counts to population size.

To our knowledge, this study provides the first evidence that in grey seals, resting at sea occurs offshore (mainly between foraging intervals) as well as inshore (associated with tidal haul out site availability). At the temporal resolution of this study (6 h) and levels of location accuracy associated with Argos tags, it was not possible to fully separate resting inshore and offshore, and investigate their allocation with regard to covariates. However, we did find that some individuals of both species spent a substantial percentage of their time (>5%) resting offshore. Our findings are consistent with the presence of extended surface intervals associated with digestion (Sparling et al. 2007). In both species there was substantially more regional variation in the proportion of time spent resting at sea and on land than spent resting overall (Fig. 3). Large variation in time spent hauled out observed here and elsewhere (London et al. 2012) may be feasible due to a degree of interchangeability between resting offshore and on land. Such plasticity in foraging strategies may also explain the large variation in trip distance and duration observed in these species (McConnell et al. 1999, Sharples et al. 2012). We would expect offshore resting may be more favoured in populations that have low marine predation pressure and foraging sites far from land (Thompson et al. 1998). Indeed in regions in which haul out site availability is less tidal (minimising the presence of inshore resting), grey seals, which in Britain generally make longer foraging trips than harbour seals (McConnell et al. 1999, Sharples et al. 2012), showed higher mean proportion of time resting at sea than harbour seals (Fig. 3). However, resting on land must serve a distinct function else there seems little reason to interrupt offshore foraging with lengthy swims ashore. Indeed, Brasseur et al. (1996) showed that if animals are stopped from hauling out, they subsequently increase the time spent hauled out to compensate. Thus in seals that show a central place foraging strategy outwith the breeding season and moult, if they do not need to return to their central place to digest food, the driver for them to return to shore from longer trips is likely to increase with a function of time rather than foraging success. This is likely to have implications for aspects of their foraging strategy. Traditional central place foraging theory predicts that patch time is governed by both prey availability (relative to elsewhere; Charnov 1976) and load capacity (Orians and Pearson 1979). However if digestion can occur at sea the load capacity becomes less limiting. In this case, patch time will

depend on distance to a haul out site, patch quality and time since last haul out.

When interpreting the results of this study, it is important to consider the assumptions made and how they differ from those in other studies, particularly the temporal resolution of the data and the use of both behavioural and movement data to define full activity budgets encompassing four states. In order to include historical Argos data, which comprised the majority of the telemetry data, we investigated activity budgets at a coarse 6 h resolution, similar to the resolution used in previous studies (Breed et al. 2009, 2011). Because we effectively use a majority rule for categorising resting versus diving, and to allocate the components of resting, the effective resolution for attributing an interval to these activities is 3 h. This is unlikely to have led to inaccurate estimates of grey seal activity budgets as they often forage far from their haul out sites. Although this interval is also likely to be appropriate for defining harbour seal haul out events (average duration exceeds 3 h; Cunningham et al. 2009), allocating diving intervals to foraging or travelling at a 6 h resolution was problematic for harbour seals in most regions. This is likely to be because harbour seals stay closer to haul out sites than grey seals and thus, at the temporal resolution considered here, there were very few travelling intervals. Indeed, investigation of harbour seal activity budgets on a finer temporal resolution using data solely from GPS tags allowed diving to be successfully apportioned to foraging and travelling in all individuals (McClintock et al. 2013).

Using both behavioural and movement data, we were able to define activity budgets comprising four states. Behavioural data was used to define resting vs diving and resting on land vs at sea, and then the movement data was used to classify foraging and travelling. Identifying resting at sea allowed us to include all at sea behaviour whereas in previous studies on grey seals (Breed et al. 2009, 2011) using movement data alone, 2–5 km buffers surrounding land or haul out sites had to be used to exclude all inshore behaviour. Furthermore, activities outwith this buffer could only be allocated to foraging or travelling. Such boundaries may result in an underestimate of inshore foraging (Thompson et al. 1991), which is especially important for harbour seals that have a coastal distribution with some individuals staying exclusively within 10 km of the coast (Sharples et al. 2012). Although some of the inshore activity classified as foraging in our study may have represented other activities, such as sleeping under water and socialising, these activities occur in shallow water near haul out sites (Thompson et al. 1991) and thus their influence was minimised by considering parameter estimates based on the deeper depth threshold of 6 m. Resting at sea will, by definition, involve little horizontal movement and so previous studies may have overestimated the proportion of time spent foraging offshore. However, we note that even offshore diving also encompasses other activities with limited horizontal movement that were likely to be classified as foraging in our study, including displaying in male harbour seals (Van Parijs et al. 1997). Recent evidence shows that harbour seals perform resting dives (Ramasco et al. 2014). Although they may be a common occurrence in some individuals, the relatively short duration of bouts (average 2.3 h; 95% CI 2.2–2.4 h) means that, at the resolution of this study, it is unlikely that the presence of these dives would have resulted in overestimation of the proportion of intervals that were assigned to foraging.

In this broad-scale study we defined activity budgets and their intrinsic and extrinsic covariates for two sympatric species allowing us to address multiple questions associated with foraging ecology and the coexistence of sympatric species, and to highlight questions on which future research should be focused. This analysis was only possible by combining data over many years, during which time tag parameters (e.g. depth threshold) have changed. Critically we used the largest temporal resolution, 6 h, to enable comparable data from all tags. Furthermore, we included the key tag parameter, depth threshold at which a dive was recorded, which had a substantial effect on the apparent propensity of some activities. For example, time spent resting at sea increased with increasing depth threshold in harbour seals, demonstrating their substantial use of depths between 1.5 and 6 m (Supplementary material Appendix 3 Fig. A3a). It is worth noting that depth threshold has generally become shallower through time thus its effect is likely to be temporally confounded; this is especially important in grey seals for which the data used extend 20 years. Unlike a previous study of harbour seal activity budgets based on movement and behavioural data (McClinck et al. 2013), we explicitly distinguished resting on land from resting at sea. We found that a substantial proportion of time is spent resting at sea (> 10%) and that, at least in some individuals, some of this time is spent offshore. This resting behaviour within trips highlights the importance of considering activity budgets to understand foraging effort (Boyd et al. 2014). Indeed, regional patterns in traditional indicators of foraging effort such as trip distance and duration did not align with the indicators (time spent diving) used in this study. Finally the substantial proportion of time resting at sea, when underlying habitat may be of little importance or unrelated to foraging, also highlights the potential problem of using all location data to define habitat preference in seals.

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References

- Anderson, S. S. and Fedak, M. A. 1987. Gray seal (*Halichoerus grypus*) energetics – females invest more in male offspring. – *J. Zool.* 211: 667–679.
- Arnould, J. P. Y. et al. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. – *Can. J. Zool.* 74: 254–266.
- Augé, A. et al. 2011. Foraging behaviour indicates marginal marine habitat for New Zealand sea lions: remnant versus recolonising populations. – *Mar. Ecol. Prog. Ser.* 432: 247–256.
- Bailleul, F. et al. 2005. Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. – *Mar. Ecol. Prog. Ser.* 293: 273–282.
- Baker, J. R. et al. 1998. Causes of mortality and non-fatal conditions among grey seals (*Halichoerus grypus*) found dead on the coasts of England, Wales and the Isle of Man. – *Vet. Rec.* 142: 595–601.
- Bonner, W. N. 1972. The grey seal and common seal in European waters. – *Oceanogr. Mar. Biol. Ann. Rev.* 10: 461–507.
- Bowen, D. W. et al. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. – *J. Zool.* 261: 155–163.
- Boyd, I. L. 1997. Foraging and provisioning in Antarctic fur seals: interannual variability in time–energy budgets. – *Behav. Ecol.* 10: 198–208.
- Boyd, C. et al. 2014. Movement models provide insights into variation in the foraging effort of central place foragers. – *Ecol. Modell.* 286: 13–25.
- Brasseur, S. et al. 1996. Deprivation indicates necessity for haul-out in harbor seals. – *Mar. Mammal Sci.* 12: 619–624.
- Breed, G. A. et al. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. – *Ecology* 90: 3209–3221.
- Breed, G. A. et al. 2011. Development of foraging strategies with age in a long-lived marine predator. – *Mar. Ecol. Prog. Ser.* 431: 267–279.
- Breed, G. et al. 2013. Behavioral signature of intraspecific competition and density dependence in colony-breeding marine predators. – *Ecol. Evol.* 3: 3838–3854.
- Breton, A. R. et al. 2008. Multilevel models reveal no cohort-level variation in time spent foraging to account for a collapse in kittiwake (*Rissa tridactyla*) breeding success. – *Ecol. Modell.* 212: 233–243.
- Brown, S. L. et al. 2012. A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. – *J. Mar. Biol. Ass. UK* 92: 1711–1722.
- Burger, A. E. and Piatt, J. F. 1990. Allocation of time and energy flexible time budgets in breeding common buffers against variable prey abundance. – *Stud. Avian Biol.* 14: 71–83.
- Cairns, D. 1988. Seabirds as indicators of marine food supplies. – *Biol. Oceanogr.* 5: 261–271.
- CCAMLR 1995. Convention on the Conservation of Antarctic Marine Living Resources. – CEMP Standard Methods.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – *Theor. Popul. Biol.* 9: 129–136.
- Cunningham, L. et al. 2009. Harbour seal movements and haul-out patterns: implications for monitoring and management. – *Aquat. Conserv. Freshwater Ecosyst.* 19: 398–407.
- Duck, C. D. et al. 2014. The status of UK harbour seal populations in 2013, including summer counts of grey seals. – SCOS BP 14/03.
- Fedak, M. A. and Hiby, A. R. 1985. Population energy requirements of seals. – In: Hammond, P. S. and Harwood, J. (eds), Impact of grey common seals on North Sea Resources, Contract Rep. ENV 665 UK to Comm. Eur. Communities.
- Forcada, J. et al. 2005. The effects of global climate variability in pup production of antarctic fur seals. – *Ecology* 86: 2408–2417.
- Fort, J. et al. 2013. Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. – *J. Avian Biol.* 44: 255–262.
- Furness, R. W. and Tasker, M. 2000. Seabird – fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. – *Mar. Ecol. Prog. Ser.* 202: 253–264.
- Gaspar, P. et al. 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. – *Proc. R. Soc. B* 273: 2697–2702.

- Gentry, R. L. and Kooyman, G. L. 1986. Fur seals: maternal strategies on land and at sea. – Princeton Univ. Press.
- Hall, A. J. et al. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. – *J. Anim. Ecol.* 70: 138–149.
- Hall, A. et al. 2012. Age-length and condition relationships and age distributions among live-captured UK harbour seals, 1999–2012. – SCOS briefing Pap. 12/11
- Hamilton, C. D. et al. 2014. Haul-out behaviour of the World's northernmost population of harbour seals (*Phoca vitulina*) throughout the year. – *PLoS One* 9: e86055.
- Härkönen, T. and Heide-Jørgensen, M. 1990. Comparative life histories of east Atlantic and other harbor seal populations. – *Ophelia* 32: 211–235.
- Härkönen, T. et al. 2008. Seasonal activity budget of adult Baltic ringed seals. – *PLoS One* 3: e2006.
- Harwood, J. and Prime, J. H. 1978. Some factors affecting size of British grey seal populations. – *J. Appl. Ecol.* 15: 401–411.
- Højsgaard, S. et al. 2006. The R package geepack for generalized estimating equations. – *J. Stat. Softw.* 15: 1–11.
- Jones, G. 1987. Competitive interactions among adults and juveniles in a coral reef fish. – *Ecology* 68: 1534–1547.
- Leung, E. S. et al. 2012. Sexual segregation in juvenile New Zealand sea lion foraging ranges: implications for intraspecific competition, population dynamics and conservation. – *PLoS ONE* 7: e45389.
- London, J. M. et al. 2012. Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. – *PLoS ONE* 7: e38180.
- Lonergan, M. E. et al. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. – *J. Zool.* 271: 261–269.
- Lonergan, M. E. et al. 2011. British grey seal (*Halichoerus grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. – *ICES J. Mar. Sci.* 68: 2201–2209.
- Matthiopoulos, J. et al. 2004. Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. – *J. Appl. Ecol.* 41: 476–491.
- McClintock, B. T. et al. 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. – *Ecology* 94: 838–849.
- McConnell, B. J. et al. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. – *Antarct. Sci.* 4: 393–398.
- McConnell, B. J. et al. 1999. Movements and foraging areas of grey seals in the North Sea. – *J. Appl. Ecol.* 36: 573–590.
- McNamara, J. M. and Houston, A. I. 1986. The common currency for behavioral decisions. – *Am. Nat.* 127: 358–378.
- McNamara, J. M. and Houston, A. I. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. – *Phil. Trans. R. Soc. B* 363: 301–319.
- Monterroso, P. et al. 2014. Plasticity in circadian activity patterns of mesocarnivores in southwestern Europe: implications for species coexistence. – *Behav. Ecol. Sociobiol.* 68: 1403–1417.
- Neumann, D. R. 1999. Agonistic behavior in harbor seals (*Phoca vitulina*) in relation to the availability of haul-out space. – *Mar. Mammal Sci.* 15: 507–525.
- Orians, G. and Pearson, N. 1979. On the theory of central place foraging. – In: Horn, D. et al. (eds), *Analysis of ecological systems*. Ohio State Univ. Press, pp. 154–177.
- Pirotta, E. et al. 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. – *Mar. Ecol. Prog. Ser.* 436: 257–272.
- Ramasco, V. et al. 2014. Improving time budget estimates through the behavioural interpretation of dive bouts in harbour seals. – *Anim. Behav.* 94: 117–134.
- Riotte-Lambert, L. and Weimerskirch, H. 2013. Do naive juvenile seabirds forage differently from adults? – *Proc. R. Soc. B* 280: 20131434.
- Royer, F. and Lutcavage, M. 2008. Filtering and interpreting location errors in satellite telemetry of marine animals. – *J. Exp. Mar. Biol. Ecol.* 359: 1–10.
- Ruckstuhl, K. E. and Neuhaus, P. 2005. Sexual segregation in vertebrates: ecology of the two sexes. – Cambridge Univ. Press.
- Russell, D. J. F. et al. 2013. Uncovering the links between foraging and breeding regions in a highly mobile mammal. – *J. Appl. Ecol.* 50: 499–509.
- Russell, D. J. F. et al. 2014. Marine mammals trace anthropogenic structures at sea. – *Curr. Biol.* 24: R638
- Schoener, T. W. 1974. Resource partitioning in ecological communities. – *Science*. 185: 27–39.
- Schwartz, C. C. et al. 2014. Patterns of contrasting activity and allopatric black and sympatric grizzly bears. 74: 1628–1638.
- Sharples, R. J. et al. 2012. Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. – *PLoS ONE* 7: e37216.
- Sparling, C. E. et al. 2007. Eat now, pay later? Evidence of deferred food-processing costs in diving seals. – *Biol. Lett.* 3: 95–99.
- Staniland, I. et al. 2011. Foraging behaviour in two Antarctic fur seal colonies with differing population recoveries. – *Mar. Ecol. Prog. Ser.* 434: 183–196.
- Thompson, P. M. et al. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). – *J. Appl. Ecol.* 26: 521–535.
- Thompson, D. et al. 1991. Movements, diving and foraging behavior of gray seals (*Halichoerus grypus*). – *J. Zool.* 224: 223–232.
- Thompson, P. M. et al. 1998. The influence of body size and sex on the characteristics of harbour seal foraging trips. – *Can. J. Zool.* 76: 1044–1053.
- Thompson, D. et al. 2010. The status of harbour seals (*Phoca vitulina*) in the United Kingdom. – *NAMMCO Sci. Publ.* 8: 117–128.
- Van Parijs, S. M. et al. 1997. Distribution and activity of male harbour seals during the mating season. – *Anim. Behav.* 54: 35–43.
- Vincent, C. et al. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. – *Mar. Mammal Sci.* 18: 156–166.
- Wanless, S. et al. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. – *Mar. Ecol. Prog. Ser.* 294: 1–8.
- Watts, P. 1992. Thermal constraints on hauling out by harbor seals (*Phoca vitulina*). – *Can. J. Zool. Can. Zool.* 70: 553–560.
- Weathers, W. and Sullivan, K. 1989. Juvenile foraging proficiency, parental effort and avian reproductive success. – *Ecol. Monogr.* 59: 223–246.
- Winslade, P. 1974a. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) I. The effect of food availability on activity and the role of olfaction in food detection. – *J. Fish Biol.* 6: 565–576.
- Winslade, P. 1974b. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) II. The effect of light intensity on activity. – *J. Fish Biol.* 6: 577–586.
- Winslade, P. 1974c. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. – *J. Fish Biol.* 6: 587–599.

Supplementary material (available online as Appendix oik.01810 at <www.oikosjournal.org/readers/appendix>). Appendix 1. State assignment. Appendix 2. Details of telemetry deployments: Table A1–A2. Appendix 3. Activity budget covariate figures: Table A3, Fig. A1–A4.