



Coping styles in capital breeders modulate behavioural trade-offs in time allocation: assessing fine-scale activity budgets in lactating grey seals (*Halichoerus grypus*) using accelerometry and heart rate variability

Courtney R. Shuert¹ · Patrick P. Pomeroy² · Sean D. Twiss¹

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Abstract

Balancing time allocation among competing behaviours is an essential part of energy management for all animals. However, trade-offs in time allocation may vary according to the sex of the individual, their age, and even underlying physiology. During reproduction, higher energetic demands and constrained internal resources place greater demand on optimizing these trade-offs insofar that small adjustments in time-activity may lead to substantial effects on an individual's limited energy budget. The most extreme case is found in animals that undergo capital breeding, where individuals fast for the duration of each reproductive episode. We investigated potential underlying drivers of time-activity and describe aspects of trade-offs in time-activity in a wild, capital breeding pinniped, the grey seal *Halichoerus grypus*, during the lactation period. For the first time, we were able to access full 24-h activity budgets across the core duration of lactation as well as characterize how aspects of stress-coping styles influence time allocation through the use of animal-borne accelerometers and heart rate monitors in situ. We found that there was a distinct trade-off in time activity between time spent Resting and Alert (vigilance). This trade-off varied with the pup's development, date, and maternal stress-coping style as indicated by a measure of heart rate variability, rMSSD. In contrast, time spent Presenting/Nursing did not vary across the duration of lactation given the variables tested. We suggest that while mothers balance time spent conserving resources (Resting) against time expending energy (Alert), they are also influenced by the inherent physiological drivers of stress-coping styles.

Significance statement

How animals apportion their time among different behaviours is key to their success. These trade-offs should be finely balanced to avoid unnecessary energy expenditure. Here, we examine how grey seal mothers balance their activity patterns during the short, but energetically demanding, period of pup-rearing. Animal-borne accelerometers provided a uniquely detailed and continuous record of activity during pup-rearing for 38 mothers. We also used heart rate monitors to provide measures of each individual's stress-coping style. We found that mothers balance time Resting against remaining Alert while time Presenting/Nursing was largely independent of all factors measured. Stress-coping styles were found to drive the balancing and variation of all behaviours. This novel indication that differences in personality-like traits may drive whole activity budgets should be

considered when assessing trade-offs in time allocation across a much wider variety of species.

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✉ Courtney R. Shuert
cshuert@gmail.com

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¹ Department of Biosciences, Durham University, Durham DH1 3LE, UK

² Scottish Oceans Institute, University of St. Andrews, St. Andrews KY16 8LB, UK

Introduction

Monitoring changes in fine-scale behaviour is critical to examining trade-offs associated with time allocation. Activity

budgets are a fixed and finite resource where time spent in one behavioural state automatically creates a rebalancing of the remaining time spent in any other behavioural category. Animals must allocate time among a variety of competing interests and demands across their life-history and have been shown to be driven by a range of intrinsic and extrinsic drivers. Sex-specific and age-specific trade-offs in behaviour have been examined extensively in the literature as they are often associated with demographic variables that are important predictors of population trajectories over time (Loison et al. 1999; Wolf et al. 2005; Byrnes et al. 2011; Hastings et al. 2011; Bishop et al. 2017). Conspecific density also plays an important role in driving a wide variety of behavioural trade-offs and can be key in determining reproductive success in a variety of species (Festa-Bianchet et al. 1998; Horning and Mellish 2012; Maniscalco 2014). Environmental factors, such as thermal regimes, are already known drivers of population-level behavioural trade-offs in a variety of taxa, and have been shown to be strong drivers of individuals balancing thermoregulatory needs with that of other behaviours (Liwanag et al. 2009; Turbill et al. 2011; Paterson et al. 2012; Heerah et al. 2013; Udyawer et al. 2017; Pagano et al. 2018). However, life history requirements may dictate that certain elements of time-activity budgets are less plastic than others.

There has also been a growing interest in how individuals differ in stress management (stress-coping styles) that may dictate an individual's response to competing inputs from the environment, be they natural or anthropogenic stressors (von Borell et al. 2007; Koolhaas et al. 1999, 2011; Schmidt et al. 2010; Liu et al. 2014; Briefer et al. 2015; Pohlin et al. 2017). Individuals have been shown to differ in behavioural responses to stress, ranging from more proactive to more reactive coping styles dependent upon the underlying feedback loops associated with the sympathetic and parasympathetic response pathways (Koolhaas et al. 2010). An individual's position on this pro-reactive spectrum can be characterized by a suite of different heart rate characteristics and behavioural traits (Koolhaas et al. 2011). Changes in short-term heart rate variability, such as rMSSD (root mean square of successive differences in interbeat intervals), can be a good indicator of these stress-coping styles and have been measured in a wide variety of species and contexts (Marchant-Forde et al. 2004; Reefmann et al. 2009; Schmidt et al. 2010; Briefer et al. 2015; Grandi and Ishida 2015). To date, few studies have examined the impact of differences in stress-coping style on how individuals balance time-activity budgets in wild animals (e.g. Závorka et al. 2016). However, an individual's stress coping style is likely to influence the trade-offs that are made within activity budgets in response to other intrinsic or extrinsic drivers.

Typically, time allocation studies utilize visual observation methods, often inferring behaviour for an entire population

through intensive scan sampling, but are limited to periods where the individuals of interest are visible (Altmann 1974; Maniscalco et al. 2010; Witter et al. 2012). Recently, accelerometers have allowed collection of remote, fine-scale behaviour free from observer biases (e.g. Naito et al. 2010; Shaffer et al. 2014; Wang et al. 2015), especially relevant for the study of avian and marine mammal behaviour where individuals may remain inaccessible or out of sight much of the time (Goldbogen et al. 2006, 2013; Sakamoto et al. 2009; Stothart et al. 2016). Recording continuously and at high resolution, tri-axial accelerometers can be used to identify changes in body position, dynamic movement patterns, and even changes in affective state (Wilson et al. 2014), even when an animal is outside of its observable period. Collecting behavioural data over a 24-h period for days at a time with the use of accelerometers will overcome the inherent biases associated with traditional observational studies and provide more realistic representations of how individuals balance behavioural trade-offs with respect to intrinsic and extrinsic pressures over time.

Pinnipeds represent an interesting case study for the use of accelerometry to determine fine-scale behavioural trade-offs. Telemetered pinniped research has typically focused on their at-sea behaviour (Biuw et al. 2003; Williams et al. 2004; Skinner et al. 2010; Viviant et al. 2010; Andrews and Enstipp 2016; Jeanniard-du-dot et al. 2017), rather than during the terrestrial phase of pinniped life history including reproduction and nursing. As capital breeding phocids, grey seals (*Halichoerus grypus*), rely on a fixed reserve of energy stores during their lactation period (Fedak and Anderson 1982; Lydersen and Kovacs 1999; Mellish et al. 1999, 2000). Lactating females must balance behaviours that act towards conserving energy (Resting), transferring resources to her pup (Presenting/Nursing), and remaining vigilant (Alert) to protect her pup which together contribute to defining early pup survival (Hall et al. 2001). Over-expenditure during lactation has costs for the mother (e.g. Pomeroy et al. 1999). Balancing these three behavioural states likely represents a trade-off where too much time spent expending energy by remaining Alert may have a detrimental effect on conserving resources (Resting) and effort towards transferring energy to the pup (Presenting/Nursing). Vigilance (Alert) has already been studied extensively in terrestrial mammals in the context of trade-offs in time-activity (Caro 1987; Arenz and Leger 1999; Beauchamp 2007; Pangle and Holekamp 2010).

Pinniped mothers are known to respond to a variety of intrinsic and extrinsic pressures, such as exhibiting differential investment of time and internal energetic resources between pup sexes (Anderson and Fedak 1987), pup developmental stages (Fedak and Anderson 1982; Mellish et al. 2000; McDonald and Crocker 2006), and between years with varying favourability of environmental conditions (McMahon et al. 2016; Desprez et al. 2018) which in turn may lead to

differential survival of offspring (McMahon et al. 2000; Noren 2002; Hastings et al. 2009). Maintaining the high energy throughput associated with capital breeding in grey seal mothers means that optimizing and balancing behaviour and time allocation with the competing demands of intrinsic and extrinsic drivers over time is key for raising a pup without compromising either mother or offspring.

Here, we examine how individual patterns of time allocation, as measured through accelerometry, vary in relation to a range of extrinsic and intrinsic factors, including coping style, with the aim of identifying fundamental trade-offs in time allocation. We focus on three behavioural states (Resting, Alert and Presenting/Nursing) where trade-offs in time-activity likely exist in lactating grey seals as they make up most of a mother's daily activity budget (typically >90% time). Likely extrinsic drivers of behavioural trade-offs include pup sex (Anderson and Fedak 1987), conspecific density (Pomeroy et al. 2000a; Twiss et al. 2003), ambient temperature (Twiss et al. 2002), local topography (access to water; Twiss et al. 2000; Redman et al. 2001; Stewart et al. 2014), and diurnal-nocturnal changes in activity (Culloch et al. 2016; Fraser et al. 2019). Previously, various intrinsic predictors have been found to influence maternal behaviour (maternal mass and length, Pomeroy et al. 1999; phase of lactation and pup developmental stage, Bowen et al. 1992). No study to date has considered intrinsic and extrinsic drivers simultaneously to examine time-allocation trade-offs associated with long-term activity budgets, nor examined the role of individual differences in coping styles in modulating time-allocation patterns in a wild animal. We predict that stress-coping style will be a major determinant of differences in behavioural trade-offs across mothers.

Methods

Data logger deployments

Grey seal activity was determined using head-mounted data-logging tri-axial accelerometers (AXY-Depth, Technosmart Europe, Italy) as described in Shuert et al. (2018). Over two consecutive breeding seasons, 38 adult female grey seals were equipped with accelerometers for the core duration of lactation while on land. Adult female grey seals were captured on the Isle of May in Scotland (56.1° N, 2.55° W) between the months of October and December in 2015 and 2016. Accelerometers were applied during an initial handling event around day 5 of lactation and removed around day 15, prior to the cessation of lactation. At each handling event, mothers were chemically immobilized via a mass-specific dose of tiletamine-zolazepam ('Zoletil', Virbac, U.K.; see Pomeroy et al. 2000b). Upon sedation, each mother and pup were weighed to the nearest 0.2 kg using a portable digital scale

and tripod as part of a research program on grey seal demography (Pomeroy et al. 1999; Bennett et al. 2007). Accelerometers were housed in custom-designed ballistic nylon pouches attached onto dry pelage using a thin layer of superglue (Loctite, formula 422; Fig. 1) and were configured to sample at 50 Hz for the 2015 breeding season ($n_{ind} = 18$) and 25 Hz (due to an error in the firmware) during 2016 ($n_{ind} = 20$). Seven mothers were sampled in both 2015 and 2016.

As an indicator of stress-coping style we measured resting heart rate variability (HRV; Koolhaas et al. 1999, 2010; von Borell et al. 2007; Coppens et al. 2010; Liu et al. 2014; Briefer et al. 2015) for individual seals. Over the course of accelerometer deployments, study females were also equipped with modified heart rate monitoring activity belts (FirstBeat Technologies Ltd. TM). Each heart rate monitor was placed on the back with the central transmitter housing on the midline with leads extending down both flanks to silver chloride electrodes located immediately posterior to the fore flippers (Fig. 1). A small section of pelage was clipped to match the size of the electrode, held in place by a small plastic donut packed with medical-grade electrogel, and secured with a small cover plate on each donut. The heart rate monitors sample (1000 Hz) and transmit inter-beat interval data (IBIs, milliseconds) to a portable base station located up to 200 m from instrumented seals, rather than logging data. While this means that the heart rate data were not sampled continuously over lactation, data were collected over multiple 5-min periods where the animal was at rest for at least 95% of the 5 min and not engaged in high-levels of activity during the 5 min. Recordings were made for each individual seal morning and afternoon (daylight hours only) and across the duration of lactation.

Raw IBI values were checked for artefacts using the default options in the FirstbeatTM Sports software (v. 4.5.0.2) installed on the receiver station, which automatically corrected potentially missing beats (extreme long IBIs) by interpolation, and deleted spurious extra beats (extreme short IBIs; Sami et al.



Fig. 1 Example showing placement of head-mounted accelerometers and heart rate monitor on a study female with her pup in view

2004). Corrected IBI data were also compared to 1 min duration ECG data for 12 individuals and was found to be highly accurate (mean difference between Firstbeat™ IBI data and ECG measurements was 0.87 ± 0.16 ms; SDT, unpublished data). In addition, we filtered IBI data further by identifying invariable sequences of IBIs (two or more consecutive identical inter-beat intervals; flats) or monotonically changing IBIs (two or more identical non-zero changes in IBIs; stairs) using custom R scripts. Only those 5-min traces with less than 50% of these flats and stairs were included in subsequent analyses (2015: mean traces per seal (\pm standard error, SE) = 24 ± 6 ; 2016: mean traces per seal = 37 ± 7). We computed the root mean square of successive differences in inter-beat-intervals (rMSSD; ms) for each of these 5 min traces using the R package ‘RHRV’ (Rodriguez-Linares et al. 2017). We used the median rMSSD for each individual across the entire season as our measure of resting HRV to assess whether stress-coping styles would have any influence over time-activity budgets.

Accelerometer-derived activity budgets

Accelerometer data were transformed and summarized by 33 feature variables that characterize various elements of static and dynamic acceleration, corresponding to body position and movement, respectively, as well as elements of power spectrum density and frequency within the signal (Shuert et al. 2018). These variables were used to classify the entirety of the accelerometry data for the duration of the deployed time for each individual into 6 behavioural states at the resolution of 1-s. The behavioural states included were Resting, Alert, Flipping pup, Locomotion, Presenting/Nursing, and Comfort Movements. Video footage was used to label accelerometry data to train a random forest model that was then used to classify each female’s activity budget as detailed in Shuert et al. (2018). It was not possible to record data blind because our study involved focal animals in the field. For the purposes of this study, we focus on three of these behaviours that make up the greater part (> 90%) of a female’s activity budget during lactation and are therefore more likely to exhibit trade-offs in time-activity allocation; Resting, Alert, and Presenting/Nursing (Table 1). It should be noted that these

are behavioural categories determined exclusively from accelerometry data and do not provide information on the location of a female’s pup nor any other contextual information that might be typically found in an ethological study. Therefore, the behaviour Presenting/Nursing represents a specific body position which we associate with nursing effort on the part of the grey seal mother (see Table 1), rather than a discrete measure of milk transfer or interaction with a pup. Activity budgets were summarized by consecutive day and night period, split by the timing of civil twilight in order to match previous efforts to study activity (e.g. Murie and Lavigne 1991; Harris et al. 2001; Culloch et al. 2016); day light hours included civil twilight at both ends of what constituted a day.

Factors influencing behaviour and model parameterization

Predictors of time spent in each of the three key behavioural states (Resting, Alert, and Presenting/Nursing) were modelled separately using binomial GLMMs with a logit link function. Predictors were included as fixed-effects and were classified as either intrinsic to each female-pup pair or extrinsic variables acting upon each female-pup pair. As target mother arrival on the colony was closely monitored, the parturition date for our study females in each breeding season was estimated to within a day and therefore allowed for an estimate of maternal post-partum mass. Intrinsic fixed effects included initial mother post-partum mass as an indicator of size and condition, the stage of the pup on a given day (classed as stage I to IV according to Kovacs and Lavigne 1986; Woldstad and Jenssen 1999), pup sex, and the phase of lactation (Lphase: 11+ days post-partum). Each mother’s resting heart rate variability (rMSSD) was also included as an intrinsic variable to evaluate the influence of stress-coping style on whole activity budgets (Coppens et al. 2010; Monestier et al. 2015). Weather variables were collected continuously across each breeding season from a weather station located in the centre of the island (Supplemental Fig. 1). For the purposes of this analysis, extrinsic fixed effects included daily maximum temperature

Table 1 Description of behaviour states for assessing time trade-offs in lactating female grey seals, a summary of static heave acceleration (stZ; median with 1st and 3rd quartile in brackets) found to be the most important variable for classifying behaviour in head-mounted

Behaviour	Description	Accel. (stZ)	Prop.
Resting	Seal is motionless, head on ground	0.720 (0.044, 0.836)	0.607 \pm 0.11
Alert	Seal is stationary, head is up and moving, may look at pup	0.817 (0.722, 0.878)	0.303 \pm 0.11
Presenting/Nursing	Seal is rolled laterally so that nipples are presented to pup	0.173 (−0.228, 0.711)	0.051 \pm 0.05

accelerometers, as well as the mean proportion (\pm SD) of time spent in each behavioural state across deployments as classified through accelerometry (behaviour definitions and acceleration summary adapted from Shuert et al. 2018)

(DMT), daily mean wind speed (Mwind), and total daily precipitation (Precip). We included date, modelled as a polynomial of days since October 1st, to represent seasonal changes in colony density which roughly follows a negative second order polynomial pattern, with the highest density mid-way through the season. Grey seal mothers remain with their pup throughout lactation and occupy a relatively small area (typically ranging no more than c. 20 m from their birth site; Pomeroy et al. 2000b). Therefore, we recorded each mother's locations within the colony, based on 7 geographic regions on the island that seals use (see definitions in Supplemental Fig. 1) to represent gross differences in colony topography and access to water.

A preliminary analysis found that the behavioural data were overdispersed. Mother identity was included as a random effect in all models to not only account for overdispersion, but also to account for individual variability in behaviour (Bolker et al. 2009). Behavioural data were modelled as the proportion of time spent in the behaviour of interest, weighted appropriately for the total number of seconds in each day and night period from the accelerometer data, as each day of the study lost about 5 min of daylight. As this was the first opportunity to access the full suite of night behaviour, the proportion of time spent in each behaviour was parameterized for each consecutive day and night (dn) for the length of each deployment with dn included as a factor in all models. Intrinsic and extrinsic models were designed a priori and are listed in Table 2 (a and b). Pup sex was included in all models as it has already been shown to influence how a grey seal mother partitions her time (Anderson and Fedak 1987; Kovacs 1987). As a result, our null models presented here include pup sex and dn to capture what is already known to influence activity budgets in grey seal mothers.

Candidate models were ranked based on Akaike information criterion, corrected for small sample size (AICc; Anderson et al. 1998) and model deviance. Models were initially designed in two different groups including intrinsic factors and extrinsic factors separately. This was done in order to tease apart the potential trade-offs associated with separate influences of potential intrinsic or extrinsic drivers of behaviour, without masking any important factors that may be lost within model selection methods. Top models were selected using AICc model selection methods (Burnham and Anderson 2002). Those factors included within 2 delta AICc were considered to have extensive support in modelling, while those with ≤ 5 delta AICc were considered to have minor support. Models with more than 7 delta AICc were not considered further (Burnham and Anderson 2002; Burnham et al. 2011). Model covariates with extensive or minor support from each of the two model groups (intrinsic, extrinsic) were combined into a reduced model list with the heart rate

Table 2 Initial predictors for generalized linear mixed effects models (GLMM) including (a) intrinsic variables and (b) extrinsic variables used to assess time spent Resting, Alert, and Presenting/Nursing with female ID included as a random factor. Intrinsic predictors include the phase of lactation (Lphase), date (modelled as a second-order polynomial), and pup stage. Maternal size was characterized by estimated maternal postpartum mass (MPPM). Extrinsic predictors include daily maximum temperature (DMT), mean wind speed (Mwind), total daily precipitation (Precip), date, and colony location. All models included pup sex and day/night (dn), including the null. Following initial reduction, rMSSD was added to models with extensive and minor support

	No.	Binomial GLMM predictors
(a) Intrinsic models	1	Lphase + Date* + PupStage + PupSex + MPPM + dn
	2	Date* + PupStage + PupSex + MPPM + dn
	3	Lphase + PupStage + PupSex + MPPM + dn
	4	Date* + PupSex + MPPM + dn
	5	Lphase + PupSex + MPPM + dn
	6	PupStage + PupSex + MPPM + dn
	7	PupStage + PupSex + dn
	8	PupSex + dn (null)
(b) Extrinsic models	1	DMT + Mwind + Precip + Date* + ColLoc + PupSex + dn
	2	DMT + Precip + Date* + ColLoc + PupSex + dn
	3	DMT + Mwind + Date* + ColLoc + PupSex + dn
	4	DMT + ColLoc + PupSex + dn
	5	Precip + ColLoc + PupSex + dn
	6	Mwind + ColLoc + PupSex + dn
	7	ColLoc + PupSex + dn
	8	DMT + PupSex + dn
	9	Mwind + PupSex + dn
	10	Precip + PupSex + dn
	11	PupSex + dn (null)

All continuous variables were scaled and centred to meet model assumptions

* Date modelled as a second-order polynomial

variability metric, rMSSD, and competed against the null for each of the three behavioural states to identify potential trade-offs in time allocation and the respective drivers of those trade-offs (Burnham et al. 2011). Selected models were described by their deviance and Akaike weight and relative evidence ratios, calculated as the ratio of model weight between two models of interest (Burnham and Anderson 2002; Burnham et al. 2011). All models were built using the 'glmmTMB' package, ranked using the 'bbmle' package, and covariates model averaged with the 'MuMIn' package in R (version 3.5.0; Bolker and Team 2017; Magnusson et al. 2017; Barton 2018).

Results

Resting

A post hoc analysis of intrinsic and extrinsic models found that grey seal mother size and all weather variables were likely ‘pretending variables’, as they failed to reduce model deviance compared to those models that did not include each of these factors (Anderson 2008; Burnham et al. 2011). As a result, models including these factors were removed from model competition for time spent Resting (see Supplementary Table 1). Model weights were recomputed after the removal of pretending and unsupported variables. Minor support (≤ 5 delta AICc) was found for the inclusion of pup stage as a predictor of time spent Resting in addition to the inclusion of pup sex and the effects of day and night (dn; Table 3(A)). Compared to the average across all pup stages, mothers with stage II pups rested significantly longer (Wilcoxon rank sum; $W = 15,146$, $p < 0.001$), while mothers with pups at stage IV rested significantly less ($W = 35,062$, $p = 0.006$; Fig. 2). Mothers also spent significantly less time resting with female

pups ($W = 57,330$, $p = 0.006$) and rested significantly more at night ($W = 28,550$, $p < 0.001$; Table 4). Little to no support was found for more complicated models including colony location or other intrinsic variables, with the exception of date. Time spent Resting was highest at the start and end of the season, as indicated by positive relationship for the parabolic effect of our date variable (Table 4).

Extensive support was found for the effect of resting HRV (rMSSD; ≤ 2 delta AICc, Table 3(A), Supplementary Table 1) compared to models without this variable, yielding a combined evidence ratio of 5.6 above the models that omitted rMSSD, and holding 69% of the model weight (Table 3(A)). Grey seal mothers with higher rMSSD tended to rest for longer than those with lower HRV, with an apparent inflexion point in the sigmoid-like relationship at around 55 ms (Fig. 3a, Table 4). The combined evidence ratio for the inclusion of rMSSD along with pup stage and date was 11.7 above the null model (pup sex and dn only; Table 3A). Final models, rankings, and recomputed Akaike weights are included in Table 3A. Variable estimates were model-averaged across these final top models (Table 4).

Table 3 Final models for predicting time spent (A) Resting, (B) Alert, and (C) Presenting/Nursing in lactating female grey seals with extensive and minor support, following the removal of several pretending variables as determined by a post hoc analysis. Models were ranked based on Akaike information criterion, corrected for small sample size (AICc).

Time spent Resting and Alert were best described by pup stage, date (* modeled as a second order polynomial), and the heart rate variability metric rMSSD. Time spent Presenting/Nursing was best described by location on the colony and rMSSD. Pup sex and differences in day and night activity (dn) were included in every model

Model formula	<i>k</i>	Delta AICc	Weight	Deviance
(A) Resting				
Date* + PupStage + rMSSD + PupSex + dn	8	0.0	0.410	1367.099
PupStage + rMSSD + PupSex + dn	6	2.0	0.149	1373.224
rMSSD + PupSex + dn	5	2.3	0.131	1375.521
Date* + PupStage + PupSex + dn	7	2.4	0.123	1371.555
Date* + PupSex + dn	6	2.6	0.111	1373.815
PupStage + PupSex + dn	5	4.6	0.042	1377.810
PupSex + dn (null)	4	4.9	0.035	1380.179
(B) Alert				
Date* + rMSSD + PupSex + dn	7	0.0	0.401	1304.548
Date* + PupStage + rMSSD + PupSex + dn	8	0.3	0.344	1302.803
rMSSD + PupSex + dn	5	3.3	0.079	1311.888
Date* + PupSex + dn	6	3.5	0.069	1310.115
PupStage + rMSSD + PupSex + dn	6	4.3	0.046	1310.908
Date* + PupStage + PupSex + dn	7	4.5	0.043	1309.020
PupSex + dn (null)	4	7.1	0.012	1317.758
PupStage + PupSex + dn	5	8.1	0.007	1316.715
(C) Presenting/Nursing				
PupSex + dn (null)	4	0.0	0.440	587.326
ColLoc + rMSSD + PupSex + dn	11	1.4	0.220	574.359
rMSSD + PupSex + dn	5	1.6	0.190	586.933
MPPM + ColLoc + rMSSD + PupSex + dn	12	7.1	0.150	573.090

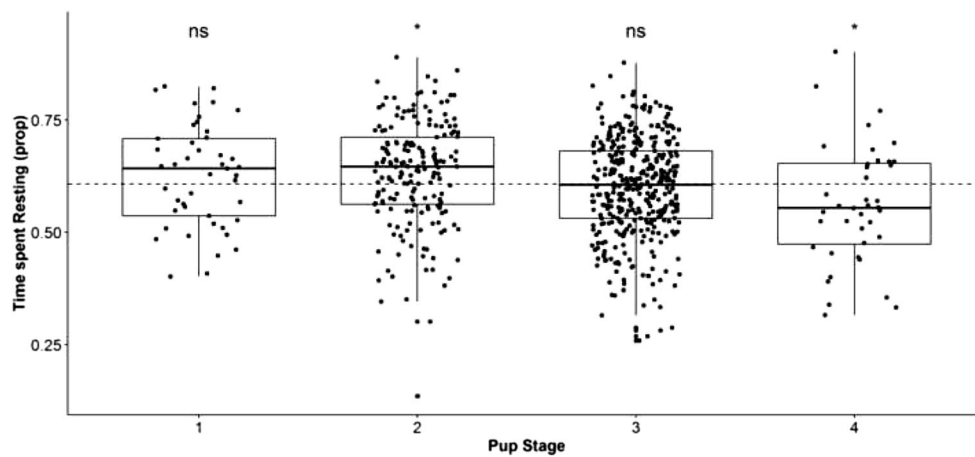


Fig. 2 Boxplot of time spent resting as a function of pup stage in grey seals. The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and individual data points. Grey seal mothers spent significantly longer Resting when pups were

stage II than average (dashed line), and significantly less in stage IV, as indicated by the (*) above each boxplot. Stage I and III were not significantly different than average (ns). Significance was determined using Wilcoxon rank sum tests

Alert

As with models predicting time spent Resting, time spent Alert was best explained by a model including date, pup stage, and rMSSD following the elimination of variables in the post hoc reduction from the larger pool of models (Supplementary Table 2), carrying 34.4% of the total model weight. Minor support (≤ 5 delta AICc) was identified for less complicated models including these variables, but the full model still had an evidence ratio of 4.354 above the next best model and 28.667 above the null (Table 3(B)).

Grey seal mothers with a lower resting HRV (lower rMSSD) spent a greater portion of their time Alert than those with a more variable heart rate (Fig. 3b), with an apparent inflection point of the sigmoid-like relationship again at around 55 ms. Mothers spent significantly more time alert with female pups than male pups (Wilcoxon rank sum; $W = 43,820$, $p = 0.002$; Table 5). Grey seal mothers also spent significantly less time Alert at night ($W = 74,664$, $p < 0.001$; Table 5). Mothers spent significantly less time Alert during stage II of pup development than the overall mean ($W = 49,104$, $p = 0.001$) and a significantly longer time alert in stage IV ($W = 8946.5$, $p = 0.006$; Fig. 4). As with Resting, time spent Alert was found to be influenced by the effect of date, where Alert was found to be highest at the mid-point of the season as indicated by the negative beta parameter for both terms of the polynomial relationship (Table 5). Beta estimates for top models predicting time spent Alert were model averaged across all top models and can be found in Table 5.

Presenting/Nursing

Extensive support was found for the inclusion of colony location and rMSSD, in addition to the mandatory inclusion of

pup sex and dn, in our models of time spent Presenting/Nursing (Supplementary Table 3). However, these models were equivalent in predictive power to that of the null model (Table 3(C)), and therefore must be regarded with caution. No support was found for any other intrinsic or extrinsic model variables, with the exception of maternal post-partum mass (MPPM), in predicting time spent Presenting/Nursing, though MPPM did not have any support in the final model table (> 7 delta AICc; Table 3(C)). All models equivalent to those listed in Table 3(C) but without rMSSD were found to have no support in final models and were ultimately removed ($>> 7$ delta AICc).

There was no significant difference between time spent Presenting/Nursing male and female pups (Wilcoxon rank

Table 4 Model-averaged variable estimates of top binomial GLMMs describing time spent Resting in lactating grey seals. Top model predictors included date (modelled as a second-order polynomial), pup stage (against stage II), and rMSSD with pup sex (positive condition is female) and day vs. night (dn; positive condition is night) included in all models. In order to meet model assumptions, rMSSD was scaled and centred

Variable	Estimate	Std. error	95% confidence	
			Upper	Lower
(Intercept)	0.513	0.196	0.897	0.128
Date—poly 1	0.045	0.049	0.141	−0.051
Date—poly 2	0.046	0.049	0.142	−0.050
PupStage	−0.070	0.067	0.061	−0.201
rMSSD*	0.059	0.051	0.158	−0.040
PupSex (F)	−0.138	0.084	0.026	−0.302
dn (night)	0.371	0.078	0.523	0.218

*Scaled and centred

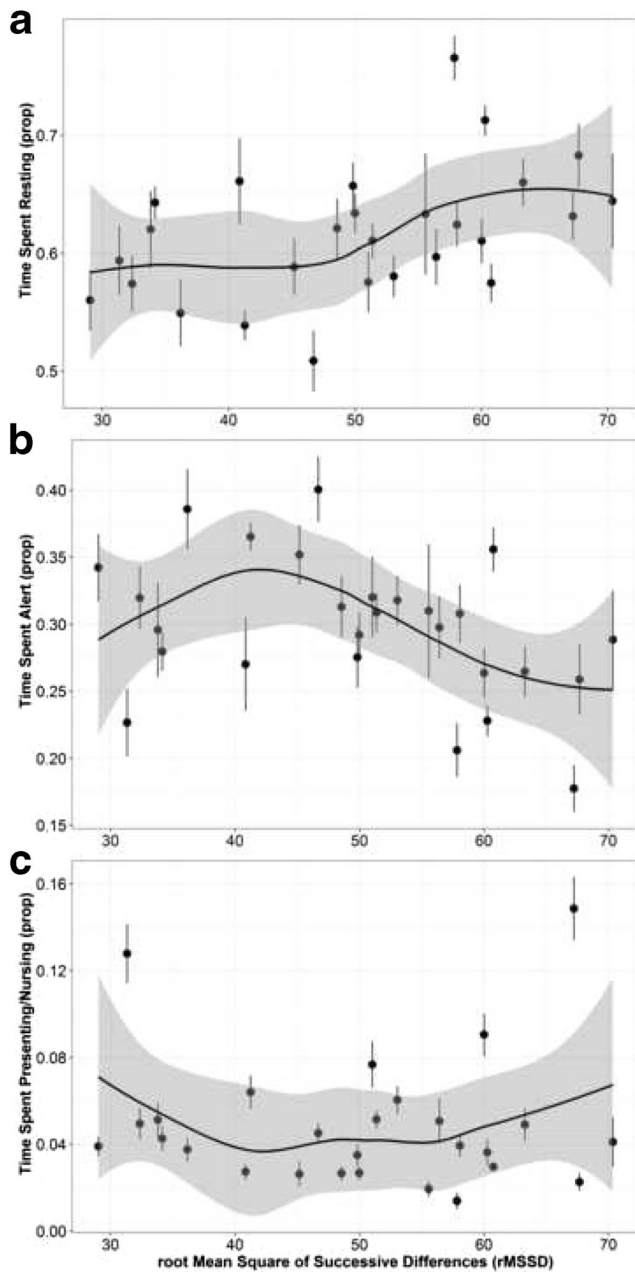


Fig. 3 Scatter plot of time spent (a) Resting, (b) Alert, and (c) Presenting/Nursing as a function of the root mean square of successive differences (rMSSD; ms) describing resting heart rate variability in grey seal mothers. Point values represent the mean time spent in each behaviour by each female, with standard error represented by the black bars around each point. The solid line represents a loess-smoothed trend line with 95% confidence intervals around the line in grey

sum; $W = 53,655$, $p = 0.252$), but mothers tended to spend significantly more time Presenting/Nursing at night ($W = 46,121$, $p = 0.019$; Table 6). While there was variability in the response of time spent Presenting/Nursing in relation to rMSSD, the relationship appears mostly flat (Fig. 3c). Presenting/Nursing time varied significantly across the seven colony locations (Kruskal-Wallis rank sum = 92.634,

$p < 0.001$; Fig. 5). Grey seal mothers in Karen’s Gully (KG) and the Loan Road (LR), areas with access to freshwater pools, had the highest average time Presenting/Nursing, while those in Cross Park (XP), an area with no freshwater access, had the lowest average time Presenting/Nursing (Fig. 5). Beta parameter estimates were model averaged for top model variables of time spent Presenting/Nursing and can be found in Table 6.

Discussion

Grey seal maternal behaviour over a continuous multi-day period during lactation was analysed using accelerometry data, focusing on three core behaviours that constitute over 90% of a typical activity budget. Overall, it was found that time spent both Resting and Alert by grey seal mothers were best explained by complimentary models including the effect of a pup’s developmental stage, the influence of time as expressed through the polynomial variable of date, and the mother’s resting HRV (rMSSD). Significant differences were also found between pup sexes as well as difference between day and night periods with respect to these two behaviours. Time spent Presenting/Nursing, on the other hand, was found to be relatively constant across coping styles over lactation, though all final models were equal in predictive power to that of the null model. Mothers of male or female pups did not differ in time spent Presenting/Nursing, though they did allocate more time to this activity overnight. Colony location also influenced time spent Presenting/Nursing, indicating that topographical features, such as access to freshwater pools, may drive behaviour.

Table 5 Model averaged variable estimates of top binomial GLMMs describing time spent Alert in lactating grey seals. Top model predictors included date (modelled as a second-order polynomial), pup stage (against stage II), and rMSSD with pup sex (positive condition is female) and day vs. night (dn; positive condition is night) included in all models. In order to meet model assumptions, rMSSD was scaled and centered

Variable	Estimate	Std. error	95% confidence	
			Upper	Lower
(Intercept)	-0.816	0.175	-0.473	-1.159
Date—poly 1	-2.060	1.439	0.760	-4.880
Date—poly 2	-1.932	1.390	0.792	-4.656
PupStage	0.035	0.058	0.148	-0.078
rMSSD*	-0.090	0.052	0.011	-0.191
PupSex (F)	0.190	0.089	0.365	0.015
dn (night)	-0.427	0.083	-0.264	-0.589

*Scaled and centred

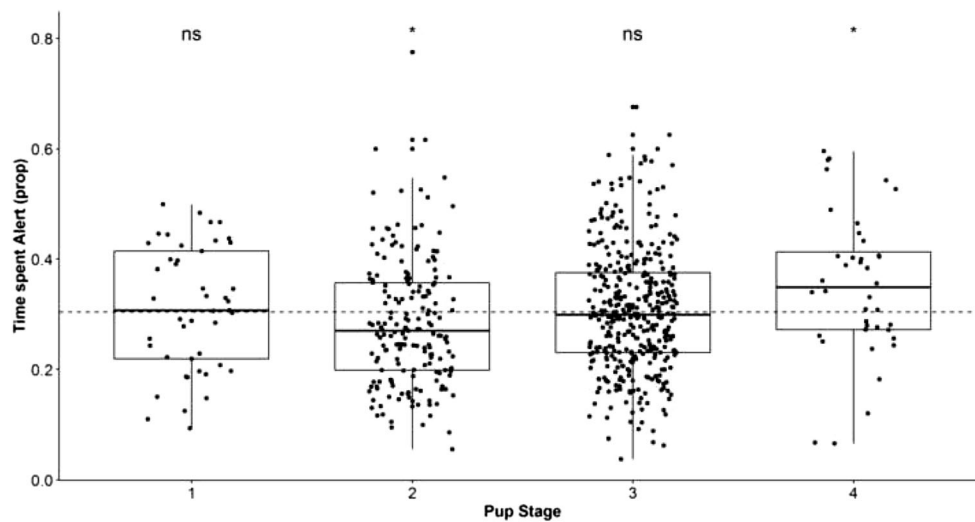


Fig. 4 Boxplot of time spent Alert as a function of pup developmental stage. The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and individual data points. The dashed horizontal line represents the grand mean of time spent Alert. Grey seal mothers spent significantly less than average time Alert

when pups were in stage II, while spending more time Alert late in lactation when pups were at stage IV, as indicated by the (*) above each boxplot. Stages I and III were not significantly different than average (ns). Significance was determined using Wilcoxon rank sum tests

Trade-offs between conserving energy and vigilance

While time allocation does not represent an exact measure of energy expenditure, it does provide a useful proxy for how individuals balance conserving energy through inactive behaviours against those active behaviours that may lead on from remaining vigilant, such as aggression or fleeing. Time spent Resting and Alert appear to represent a key trade-off in grey seal mothers; both behaviours were best predicted by identical model variables with opposing effects. The resulting relationships indicate that these two behaviours are complimentary with regard to the sex of a pup, its developmental stage, time, and the mother's resting HRV. Given the evidence presented here, we argue that a trade-off in the conservation of internal resources through Resting and appropriately expending energy while Alert represents a key trade-off in time allocation over the course of lactation for grey seals.

Interestingly, these two behaviours appeared to be subject to the changing density across the colony, as indicated by the opposing relationships between date for Resting and Alert. The Isle of May birth curve, and therefore number of seals ashore, like many other breeding rookeries follows a normal distribution with a peak in density towards the middle of the season around mid-November (Pomeroy et al. 2000a, b; Hall et al. 2001). While we do not have daily estimates of colony density across the study period, the results with respect to trading off time spent Resting and Alert respond as one might expect. Grey seal mothers spent more time Alert and less time Resting mid-season when colony density is highest. Grey seals mothers, at higher densities, must remain vigilant to keep track of and protect their pups from conspecifics and other

threats (Pomeroy et al. 2000a; Twiss et al. 2003). Mothers were found to spend significantly more time Resting and less time Alert with pups in developmental stage II, while the opposite was found for pups in developmental stage IV as they approached weaning. During the early stages of development, pups are generally fairly immobile and do not tend to stray far from their mothers (Kovacs 1987). Milk fat content peaks

Table 6 Model-averaged variable estimates of top binomial GLMMs describing time spent Presenting/Nursing in lactating grey seals. Top models included the effect of colony location (ColLoc against KG, sublocation codes can be found in Fig. 5 and Supplemental Fig. 1) and rMSSD as well as pup sex (positive condition is female) and day vs. night (dn, positive condition is night) included in all models. In order to meet model assumptions, rMSSD was scaled and centred

Variable	Estimate	Std. error	95% confidence	
			Upper	Lower
(Intercept)	-2.832	0.416	-2.016	-3.647
ColLoc: LR	0.155	0.392	0.923	-0.613
ColLoc: RT	-0.261	0.460	0.640	-1.162
ColLoc: TC	-0.299	0.524	0.728	-1.326
ColLoc: TH	-0.104	0.298	0.480	-0.688
ColLoc: XP	-0.346	0.530	0.692	-1.384
ColLoc: CH	-0.371	0.646	0.895	-1.637
rMSSD*	0.079	0.113	0.300	-0.181
PupSex (F)	-0.030	0.212	0.385	-0.445
dn (night)	0.099	0.173	0.438	-0.240

*Scaled and centred

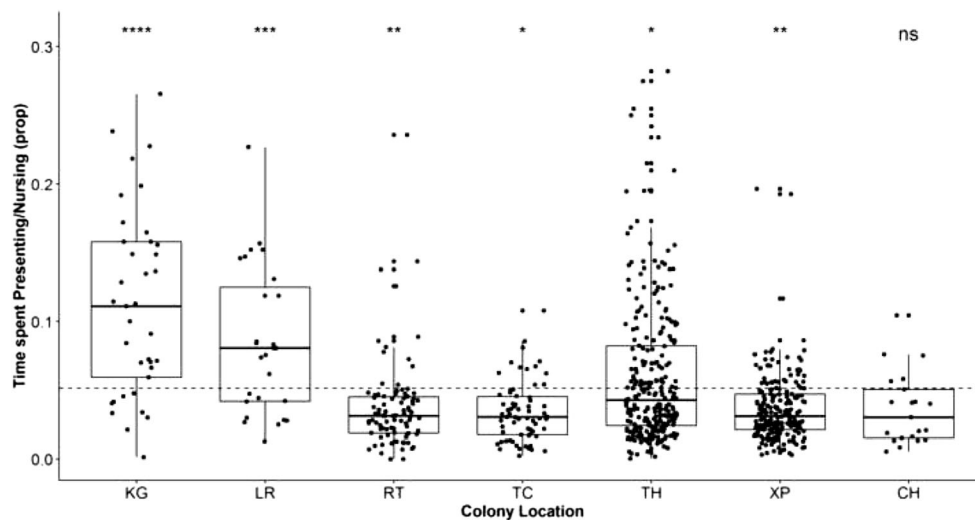


Fig. 5 Boxplot of time spent Presenting/Nursing within each colony location (see Supplemental Fig. 1 for location boundaries and water source locations). The boxes show the median, interquartile range, whiskers (indicating the 90th and 10th percentiles), and individual data points. The dashed horizontal line represents the overall mean time spent Presenting/Nursing. Locations with access to several freshwater sources include Karren's Gully (KG), Loan Road (LR), and Tabet Hole (TH),

while the remaining sites had no or extremely limited access to freshwater pools (Rona Top (RT); Tennis Court (TC); Cross Park (XP); Chapel (CH)). Grey seal mothers at KG and LR spent the longest average time Presenting/Nursing, while those in XP and TC had the least. Significance of deviation from the mean (as determined from a Wilcoxon rank sum) indicated by '****' ($p < 0.0001$), '***' ($p < 0.001$), '**' ($p < 0.01$), '*' ($p = 0.05$) or 'ns' across the top

during early development (Mellish et al. 1999) and pups have the highest ratio of milk intake to mass gained during the early days of lactation (Iverson et al. 1993). Stage II of pup development (median days 5–9 of lactation; Woldstad and Jenssen 1999) may therefore be an important developmental milestone whereby pups must lay down their initial fat stores while both mothers and pups remain relatively inactive, maximizing mass-transfer. As pups approach stage IV near the end of lactation, mothers are approaching estrus and likely remain more vigilant due to more frequent interactions with males (Anderson and Fedak 1985; Tinker et al. 1995; Lidgard et al. 2001; Bean et al. 2004; Twiss et al. 2006; Bishop et al. 2017).

Previous work on grey seals in the UK indicate that mothers expend up to 10% more energy over gestation and lactation for male pups than female pups and spend significantly more time defending and nursing male pups than female pups (Anderson and Fedak 1987; Kovacs 1987). While it was found that grey seal mothers spent significantly more time Alert and significantly less time Resting with female pups than with male pups, it is unclear how much regional differences influence patterns of maternal investment, but the results presented here indicate that populations may experience different pressures on time allocation with regard to pup sex.

Trade-offs between the acquisition of resources and vigilance behaviours have been examined in a variety of predator and prey contexts in terrestrial mammals, with varying degrees of density-dependence identified (Caro 1987; Burger and Gochfeld 1994; Hunter and Skinner 1998; Pangle and

Holekamp 2010). In herding prey species, higher conspecific density can mean that certain individuals are able to spend less time Alert for predators, devoting a greater proportion of their time activity towards foraging or maternal care (Burger and Gochfeld 1994; Hunter and Skinner 1998). These trade-offs are also applicable where individuals must strike a balance between the energetic cost of foraging as a function of distance and search time and the acquisition of energy upon locating sufficient resources in the environment (Hill et al. 2003; Lagarde et al. 2008; Therrien et al. 2008; Watanabe et al. 2012; Patrick et al. 2014; Battaile et al. 2015; Flack et al. 2016; Costelloe and Rubenstein 2018). These examples principally illustrate the relationships between conserving or acquiring energy and expending energy to ensure survival.

Grey seal mothers have been shown to have poor pupping success following a year with exceptional resource output into a larger pup (Pomeroy et al. 1999). Preliminary analyses indicate that Resting and Alert have very different energetic costs across individuals, as indicated by significantly different mean heart rate (HR) associated with these behaviours. For the same seals studied in this paper, mean HR (\pm SE) across $n = 6,099$ 100-beat traces where the seal was Resting for $> 50\%$ of those beats was 84.4 ± 0.18 bpm. By contrast, mean HR across $n = 2,504$ 100-beat traces where the seal was Alert for $> 50\%$ Alert 92.6 ± 0.28 bpm (SDT, unpublished data). Mean heart rate has been shown to be a reliable proxy of total energy expenditure across a wide range of taxa and behaviours, where higher mean heart rate indicates more energy spent on an activity (Signer et al. 2011; Turbill et al. 2011; Hawkes et al. 2014; Portugal et al. 2016, 2018). Balancing time spent

Resting and Alert may be key to lactating grey seals as they attempt to optimize resource availability for their current offspring while minimizing the impact of the associated longer-term costs on the next breeding cycle, though the actual energetic costs of engaging in these two behaviours is currently unknown. These differences in energy costs for Resting and Alert behaviours certainly indicate that there may be tangible energetic consequences that may result from individual differences in time-activity trade-offs, but these costs need to be investigated further. Tracking these behaviours across years may reveal consistent mothering strategies that may relate to different ways of managing these trade-offs with respect to ultimate fitness outcomes.

Measures of heart rate variability, such as rMSSD, have been linked to a continuum of stress-coping styles in laboratory experiments, also known as the pro-reactive spectrum (Koolhaas et al. 1999). Individuals that display low HRV tend to be those classed as proactive and exhibit stereotypical, routine action patterns in a variety of contexts (Coppens et al. 2010). Those individuals that tend towards higher HRV show a more reactive coping style, where the inputs of the surrounding environment tend to elicit responses and dictate the degree of responsiveness to a greater extent than internally regulated control (Coppens et al. 2010). Our study shows that differences in stress-coping styles appear to be important in determining the balance point of trade-offs in whole activity budgets. Grey seal mothers at the proactive end of the spectrum (lower values of rMSSD) spent generally more time Alert and less time Resting than those with a more reactive stress-coping style (Fig. 3a, b). While we did not investigate the frequency of these behaviours in time, proactive individuals may be regularly engaging in Alert vigilance behaviour interspersed with Resting and other behaviours to maintain constant and consistent vigilance effort over time as a mechanism for mitigating overall stress responses, rather than reacting to stressors as they occur (Twiss et al. 2012). These results here may explain in part the observed differences in fitness outcomes for the same population of grey seals (Twiss et al. 2012), but needs to be investigated further.

Few efforts to date have focused on differences between day and night behaviour in grey seals. An early study by Anderson (1978) concluded that behaviour did not differ between day and night other than a higher frequency of 'looks' during day and twilight hours (Anderson 1978). More recently, two studies have found that grey seal mothers Rested significantly more and were Alert significantly less during nighttime hours, though these studies did not monitor behaviour throughout the entire night (Culloch et al. 2016; Fraser et al. 2019). The current study used accelerometers to measure behaviour through the day and night hours, and has confirmed unequivocally that Resting occurs at night along with a marked reduction in vigilance. Alert and other vigilance-

type behaviours likely decrease at night due to a decrease in visual acuity, relying more on other sensory inputs to maintain contact with their pup and to intercept incoming threats (Schusterman and Balliet 1971; Schusterman 1974; Culloch et al. 2016). Given the evidence for significant differences between night and day for all behavioural categories examined here, previous studies that (explicitly or implicitly) used time-activity data gathered only during daylight hours as a proxy for behavioural energy usage or behavioural maternal investment (e.g. Kovacs and Lavigne 1986; Twiss et al. 2000) may be misleading. Artificial light pollution has already been shown to significantly alter behaviour for many coastal species and is identified as an ever increasing problem (Davies et al. 2013, 2014; Kamrowski et al. 2013; Yorzinski et al. 2015). If seals are exploiting night as a means of energy conservation and rebalancing time-activity trade-offs because of decreased visual acuity among conspecifics, artificial light pollution may impact this. While the Isle of May is largely undisturbed by human impact, encroaching human settlements towards mainland breeding sites may alter the nighttime activity in grey seals and other land-breeding phocid species, especially for areas of newly formed breeding colonies and more ephemerally populated haul-out sites along the coasts of the UK.

Patterns in Presenting/Nursing

The results presented here show that Presenting/Nursing behaviour remains constant across lactation, but differs across some colony locations, between day and night, and with respect to rMSSD. These modelled effects, however, were equal in predictive power to our null model and therefore must be regarded as tentative patterns. Intuitively, consistency in Presenting/Nursing effort across lactation should be highly selected for in order to maximize the likelihood that energy can be transferred to the pup. While the number of nursing attempts, or time spent Presenting/Nursing here, is not an accurate measure for amount of energy transferred (Cameron 1998), a theoretical minimum in Presenting/Nursing effort must exist and is likely strongly selected for in these seals. Given that we are also unable to follow the behaviour of the pup through accelerometry, Presenting/Nursing effort remains a loose approximation of maternal investment and can also be heavily influenced by proximity to the pup, the pup's effort to nurse, milk production capacity, and hormone levels (Robinson et al. 2015, 2016). Likewise, seals should not overexert their energy output during lactation, or they risk jeopardizing subsequent breeding attempts (Pomeroy et al. 1999; McMahan et al. 2016; Bubac et al. 2018). Pup survival is highly dependent on the mass at which it is weaned (Hall et al. 2001), a

common feature across a wide range of taxa (Pilastro et al. 1994; Festa-Bianchet et al. 2000; Hall et al. 2001; Harding et al. 2005; Ozgul et al. 2010; Bowen et al. 2015; Weitzman et al. 2017). As a result, mothers are likely less able to be flexible in trading-off time spent Presenting/Nursing with other behaviours over lactation in order to maximize energy transfer to her pup.

Bowen et al. (1992) found no pup sex dependent differences in grey seal mother energy expenditures on Sable Island (Canada), while studies in the UK indicated differences in investment between pup sexes (Anderson and Fedak 1987). Here, we found no detectable difference in time spent Presenting/Nursing across pup sexes. These conflicting results may indicate that some regional or colony-specific differences may be at play. Resting HRV had some support in models of time spent Presenting/Nursing, but did not show any clear patterns (Fig. 3c). This lack of distinct pattern further supports our conclusion that consistency in Presenting/Nursing effort is highly selected for, irrespective of individual coping style. By using accelerometers, we also found that grey seal mothers are often engaging in Presenting/Nursing effort significantly more overnight. Presenting/Nursing more overnight likely help to stabilize maternal effort over time, especially when social and aggressive interactions may limit the amount of time during the day that mothers can nurse.

The greatest source of apparent variability in time spent Presenting/Nursing was found in the different sub-regions of the island. The study colony (Isle of May) is topographically heterogeneous (see Supplemental Fig. 1; Twiss et al. 2000). In particular, access to water varies considerably, and previous work has demonstrated that lactating females prefer access to fresh water (Twiss et al. 2000, 2002; Redman et al. 2001; Stewart et al. 2014). The thick blubber layer of all phocids provides insulation and grey seals will often use freshwater pools to achieve the benefits of evaporative cooling (Rommel et al. 1995; Boily and Lavigne 1996; Twiss et al. 2002; Khamas et al. 2012; Paterson et al. 2012). With the increased metabolic demands of lactating while fasting, grey seal mothers may also prefer access to freshwater as a means to drink to meet water demands (Stewart et al. 2014). Areas with the poorest access to temporary freshwater pools (Cross Park – XP, Tennis Court – TC, and Rona Top – RT; Fig. 5) tended to have mothers that spent significantly less time Presenting/Nursing on average than those containing permanent and stable freshwater sources. Therefore, time spent travelling to and from pools to drink or cool off may potentially impact time spent Presenting/Nursing day to day. Alternatively, some grey seal mothers may simply go without drinking, minimizing geographic movement and energy used for

activity as a means of compensating for increased expense of burning more internal resources to free up body water (Reilly and Fedak 1990). It remains to be seen whether either strategy may impact energy leftover for lactation and how this may affect pup development. Locomotory behaviours were poorly identified in the current study design (see Shuert et al. 2018) which prevents an accurate assessment of movement across the colony to and from freshwater sources, without the aid of additional sensors like GPS or magnetometers for dead-reckoning.

No support was identified for extrinsic environmental variables influencing behaviour in the current investigation. Weather variables were measured as summaries over an hour at a single location on the island, therefore it is likely that the spatial and temporal resolution of the environmental data was too coarse to link to individual behavioural decisions with respect to thermoregulatory or water balance needs. Spatial differences in local weather variables across the island may have also contributed to differences in Presenting/Nursing behaviour, but it was not possible to assess environmental variables at such a fine spatial resolution in the current study. A fine-scale analysis of environmental conditions associated with time and energy management in grey seals may reveal more about behavioural responses to extrinsic drivers, especially given the projected changes in climate variability for the autumnal breeding season in the UK (Jenkins et al. 2008).

Conclusions

Using the high-resolution data from accelerometers, we were able to identify behavioural trade-offs between rest (Resting) and vigilance (Alert) in a capital breeding pinniped. Stress-coping styles, measured through the metric rMSSD, have an important influence on how individuals resolve this trade-off throughout the duration of lactation. Time devoted to Presenting/Nursing as a behavioural state is more fixed within an individual, but potentially varies across individuals depending upon local topography. Therefore, only certain aspects of time-activity budgets are labile and available for modification of allocated time as individuals attempt to balance current breeding activity while maintaining enough resources to successfully complete lactation the next season. Incorporating the dynamics of these trade-offs on whole activity budgets as well as the modulating effect of stress-coping styles on behaviour will enhance our understanding of how individuals optimize energy usage trajectories over time.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were adhered to in this study. All animal procedures were performed under UK Home Office project licence #60/4009 and conformed to the UK Animals (Scientific Procedures) Act, 1986. All research was approved ethically by the Durham University Animal Welfare Ethical Review Board as well as by the University of St. Andrews Animal Welfare and Ethics Committee.

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