Title: "Stress-coping styles are associated with energy budgets and variability in energy management strategies in a capital breeder."

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Authors: Courtney R. Shuert[1,*], Patrick P. Pomeroy[2], Sean D. Twiss[3]

[1] Conservation and Research, Assiniboine Park Conservancy, Winnipeg, Canada

[2] Scottish Oceans Institute, University of St. Andrews, St. Andrews, UK

[3] Department of Biosciences, Durham University, Durham, UK

[*]corresponding author: Courtney Shuert, cshuert@gmail.com

Abstract

Individuals vary in their stress-coping styles, characterized by specific behavioural and physiological traits that influence their response to stressors. Theory suggests that these traits are linked to underlying metabolic mechanisms that affect energy management strategies. Despite the potential of this powerful comparative approach, few studies have explored how stress-coping styles relate to energy management strategies. Using heart rate telemetry data from a large, capital-breeding pinniped, the grey seal (*Halichoerus grypus*), we sought to investigate the relationship that stress-coping styles (via individual resting heart rate variability, rHRV) may have on energy management strategies. Background energy expenditures, a proxy for metabolic rate and other background processes, and daily energy expenditures were found to be individually repeatable in grey seal mothers across successive breeding seasons. Proactive individuals (low rHRV) exhibited consistently higher background and daily energy expenditures than reactive females (high rHRV). However, reactive phenotypes were more variable overall in energy management strategy, highlighting greater flexibility in their energy management strategy. Our results highlight key energetic trade-offs associated with stress-coping styles in grey seal mothers during this short but critical life-history stage; proactive individuals tended to exhibit a single pattern of energy management, expending greater energy while incurring greater risk of over-spending, than those with a more reactive phenotype.

Introduction

Personality differences are the product of co-evolved behavioural and physiological traits that are consistent and repeatable within individuals across time. These inter-individual differences have broad ranging impacts on individual fitness and population ecology, such as predation risk of bold exploratory behaviour, population effects of high dispersal of individuals, or in explaining genetic differences in animal size and behaviour (Bijleveld et al., 2014; Careau and Garland Jr., 2012; Zablocki-Thomas et al., 2019). Underlying these impacts is the way that individuals of differing personalities respond behaviourally and physiologically to changes in their environment (stressors). These individualistic responses to short-term stressors have been evaluated in a number of ways, including controlled behavioural experiments and *in situ* observations both in laboratory and wild contexts (Blas et al., 2007; Cockrem, 2022; Liu et al., 2014; Sih et al., 2015; Wilson et al., 2019). As personality reflects inter-individual differences in behaviours such as activity level, different personality types are also likely to expend energy at different rates, resulting in long-term inter-individual differences in metabolic rate and energy expenditure (Biro and Stamps, 2010; Careau et al., 2008).

One aspect of personality, stress-coping styles, is defined as a set of behavioural and physiological stress responses which fall on a continuum ranging from more proactive to more reactive coping styles. Individuals tending towards a proactive coping style often exhibit greater boldness, aggression, and are generally more fixed in their action patterns than those tending toward a more reactive phenotype (Koolhaas et al., 1999). Proactive individuals have a higher sympathetic reactivity and lower hypothalamus-pituitary-adrenal (HPA) axis responsiveness than more reactive phenotypes (Koolhaas et al., 1999). Evolutionarily, these stress-coping styles are thought to be maintained within a population as a result of contrasting trade-offs in behaviour and physiology in relation to the prevailing biophysical and/or social environments (Coppens et al., 2010). Proactive individuals are thought to perform best in stable-state conditions, exhibiting a consistent level of investment or energy expenditure over time, while reactive individuals tend to be more variable overall in energy expenditure and may be more adaptable in unstable conditions (Monestier et al., 2015).

In accordance with the concept of the co-evolution of personality and underlying metabolism, proactive individuals are thought to require larger energy reserves or more efficient physiological pathways to afford the high energy life-style (Careau et al., 2010), or trade-off with other aspects of life-history strategies such as early reproduction against shorter lifespan (pace-of-life syndromes; e.g. (Montiglio et al., 2018). While contrasting theories exist as to whether physiological phenotypes predict differences in behaviour (Careau and Garland Jr., 2012) or whether correlated selection of behavioural traits instead drives physiological adjustments (Bijleveld et al., 2014), only a few studies have directly investigated these two contrasting theories in practice. Previous work linking metabolism and personality differences has so far been limited to controlled studies in laboratories (Careau et al., 2008) or where controlled tests of behaviour can be applied (Careau et al., 2019). One approach to understanding how individuals balance energetic demands is through the lens of energy management strategies, which can reveal across-individual differences in relative energy partitioning over time (Halsey et al., 2019; Portugal et al., 2016) or within-individual consistencies in management strategy (Shuert et al., 2020b). Metrics derived from heart rate data have been shown to provide robust proxies of individual energy management strategies (Halsey et al., 2019; Portugal et al., 2016). In addition, measures of resting heart rate variability (rHRV) can provide an indicator of individual differences in stress-coping styles (Carravieri et al., 2016; de Jong et al., 2000; Marchant-Forde et al., 2004; Rodriguez-Linares et al., 2017; Twiss et al., 2020; Twiss et al., 2021; von Borell et al., 2007). Measures of rHRV represent the variability in inter-beat intervals of an individual while at rest. This variability is driven by the interacting influences of sympathetic (response to stress) and parasympathetic/vagal (self-maintenance, allostasis) inputs from the autonomic nervous system (Kitajima et al., 2021; von Borell et al., 2007) Relatively low rHRV is indicative of a more proactive individual, while high rHRV indicates a more reactive individual. However, no empirical evidence has been provided for the effects that stress-coping styles may have on energy management strategies.

Here, we examine individual energy management strategies in relation to stress-coping style using heart rate telemetry in lactating grey seals (*Halichoerus grypus*) as a model system. Grey seals, like many phocids, exhibit an energy-intensive, contracted lactation period while fasting on land, known as capital breeding (e.g. Pomeroy et al., 1999). Over the past decade, studies in grey seals have revealed consistent individual differences in stress-coping styles determined from behavioural patterns (plasticity in vigilance (Twiss et al., 2012a) and underlying physiological indicators (rHRV; (Twiss et al., 2021). Furthermore, these studies indicated that individuals with more reactive stress-coping styles (determined either behaviourally or physiologically) show more variable reproductive expenditure (measured as daily maternal mass loss rate) and short-term fitness outcomes (measured as the resulting pup daily growth rate) compared to more proactive mothers (Twiss et al., 2012b; Twiss et al., 2020). Shuert et al. (2020a) also demonstrated differences in activity budgets (measured from accelerometry-derived behaviour) in relation to individual stress-coping style (via rHRV). Further, multi-season data also revealed within- and across-individual differences in energy management, highlighting that deviations in energy management strategy resulted in suboptimal outcomes for pups, where individual mothers were seen to abandon lactation much earlier than expected within the population (Shuert et al., 2020b). As lactation in seals is so contracted, ending lactation early means less energy transferred to the pup which can result in low survival probability in those offspring because mass at weaning is a key predictor of survival (Hall et al., 2001). Correctly balancing energy management is therefore key to ensuring that energy transfer is maximized to offspring, while maintaining adequate internal resources for self-maintenance (Pomeroy et al., 1999). Here, we aimed to evaluate the relationships between stress-coping styles and aspects of energy usage and management. To do this, we first evaluated the repeatability of energy usage in grey seal mothers over multiple consecutive breeding seasons. We then investigated the associations that stress-coping styles may have with energy use and management strategies among grey seals.

Methods

Over three successive autumnal breeding seasons, forty-six grey seal mothers were captured early in lactation and equipped with heart rate monitors (FirstBeat Technologies, Ltd.) on the Isle of May, Scotland. Details on the capture, handling, and deployment of heart rate monitors have been published elsewhere (Shuert et al., 2018; Twiss et al., 2020; Twiss et al., 2021). In brief, each female was captured at approximately day 5 of lactation and sampled for various health metrics. During this time, each individual was equipped with a heart rate monitor as well as an accelerometer (Shuert et al., 2018). All biologgers were removed on approximately day 15 of an average 18-day lactation period for this species (Pomeroy et al., 1999). Each heart rate monitor provided millisecond precision measurements of inter-beat-intervals through the detection of RR peaks. These data were transmitted in real-time to a portable receiving station located at a distance of 50-200 m from focal seals during subsequent observation periods without disturbing normal seal behaviour (Twiss et al., 2021). Inter-beat interval data were collected on subsets of focal individuals for 1-6 hr each day during their lactation periods, collected over an average of 10 days per individual in each season, providing daily samples for most individuals. These data provided an indicator of stress-coping style and daily heart rate metrics. It should be noted that not all individuals instrumented within a single breeding season are present at the same time; individuals remain ashore for 18-21 days, but the entire breeding season spans 8 weeks. There is a constant influx of arrivals that provide for new deployments, just as previously instrumented seals are ready to depart the island. Thus, the number of focal seals to observe and record heart rate data on each day is relatively small.

Stress-coping styles were determined from measures of resting heart rate variability (rHRV) for each individual (Pohlin et al., 2017; Rodriguez-Linares et al., 2017; von Borell et al., 2007). As detailed in Twiss et al. (2020), 5-minute traces of inter-beat interval data from individual seals while at rest were used to extract resting heart rate variability (von Borell et al., 2007), measured as the root mean square of successive differences (rMSSD) between inter-beat-intervals using the ‘RHRV’ package (Rodriguez-Linares et al., 2017). Resting periods were identified through time-matched accelerometry data that demonstrated the individual was unmoving during the 5-minute period (Shuert et al., 2018; Twiss et al., 2020). Individual rHRV was represented by their median rMSSD across each year they were present on the colony and equipped with heart rate monitors (Twiss et al., 2020). rMSSD provides an easily interpretable indication of sympathovagal balance within individuals, and has been found to be less affected by respiratory cycles (Pohlin et al., 2017; von Borell et al., 2007). rMSSD specifically has been shown to be a robust indicator of consistent and highly repeatable individual differences in stress-coping styles in seals across multiple breeding seasons (Twiss et al., 2020) and for other species (de Jong et al., 2000; Marchant-Forde et al., 2004). At rest, individuals with more proactive stress-coping styles exhibit lower resting heart rate variability (represented by a lower rMSSD), while more reactive individuals tend to have higher resting heart rate variability (von Borell et al., 2007, Pohlin et al., 2017, Twiss et al. 2020).

To determine energy management strategies for each female, daily heart rate (f_H, beats min^{-1}) statistics were extracted as described in (Shuert et al., 2020b) as robust proxies for energy management patterns. In brief, the inter-beat interval data for each individual was divided into successive non-overlapping 15-min segments, spanning all observation periods for each individual, and all behaviours that individuals engaged in, not just resting periods. The mean heart rate was computed for each segment. 15-min segments were chosen to minimize the potential bias associated with brief bradycardia periods when an animal was at rest (Castellini, 1996; Halsey et al., 2019). Minimum daily mean heart rate (min-f_H) was then computed as the lowest daily value of mean heart rate. This provided a proxy for metabolism and other metabolic processes (‘background energy expenditure’; Portugal et al., 2016). Mean daily heart rate (mean-f_H) was computed as the daily average of all 15-min segment mean values for an individual within a given day. This provides a proxy of ‘daily energy expenditure’ (Portugal et al., 2016). The difference between these two measures (min-f_H subtracted from mean-f_H) was then attributed to all other auxiliary energetic processes and activity (aux-f_H, ‘auxiliary energy expenditure’; (Portugal et al., 2016). Shuert et al. (2020b) used these proxies to model the energy management strategy across individuals (i.e. population level) and within each individual as the slope of the relationship between mean-f_H and min-f_H using a mixed-effects modelling framework. The resulting slope of the line served as an indicator of energy management strategy adopted by individuals within each breeding season, where a slope of less than 1 indicated a compensation energy management strategy, highlighting that an individual compensated for higher daily energy expenditures by lowering background energy expenditures, and vice versa. Slopes of 1 or higher indicated either an independent or performance energy management strategy, respectively (Careau and Garland Jr., 2012; Halsey et al., 2019). Grey seals fast during the brief, but intense lactation which spans about 18 days for this population. Mothers consequently have extreme physiological demands within a relatively discrete and defined energy budget, and over-expenditure may lead to a mother curtailing lactation prematurely in order to conserve her longer-term reproductive capacity (Pomeroy et al., 1999; Shuert et al., 2020b). A compensation energy management strategy was found across individuals (population level), but some variability of within-individual energy management slopes between years was noted (Shuert et al., 2020b). Following Shuert et al. (2020b), we defined a typical (compensation) energy management strategy as a slope of <1 and an alternative strategy as a slope of >1. Grey seal mothers are under extreme energetic constraints and those that maintain a compensation energy management strategy were more likely to complete the full duration of lactation, likely resulting in higher offspring survival (Hall et al., 2001; Shuert et al., 2020b).

While previous work has demonstrated that the stress-coping styles of individual grey seal mothers measured during the breeding season are highly repeatable across years (for at least 5 years (Twiss et al., 2020), it is unclear whether individuals' patterns of energy usage and energy management strategies may be repeatable across years. For all individuals, the repeatability of both daily background energy expenditure (min-f_H) and daily mean energy expenditure (mean-f_H) was assessed. Repeatability for each energy expenditure proxy was evaluated over 1000 bootstrapped iterations, resampled from the energy expenditure data, within the rptR package in R (Stoffel et al., 2017). We included each breeding season (year) as well as maternal daily mass-loss rate as covariates in the repeatability models to control for gross-interannual differences in environmental conditions which may have impacted seal body condition and/or behaviour, and to control for morphometric differences, respectively, as they have been shown to be important factors for predicting energy usage over a breeding season (Pomeroy et al., 1999; Shuert et al., 2020b; Twiss et al., 2021). Maternal daily mass-loss rate (expressed as kg day^{-1}) was calculated as a linear slope between initial mass recorded early on in lactation and the final mass recorded near the end of lactation when the heart rate monitors were removed. The significance of repeatabilities were assessed through a likelihood ratio test where the results of the repeatability model were tested against a model without the effect of individual. Individual repeatability estimates (R_i) were extracted from the variance component of the model following (DeRango et al., 2019). Based on literature about the pro-reactive spectrum of coping styles, where reactive individuals express greater flexibility in both behavioural and physiological traits, we expected reactive individuals to exhibit lower repeatability in both measures of energy management (min-f_H and mean-f_H) relative to more proactive individuals.

To understand the potential relationships between stress-coping styles and energy usage and management, we evaluated several relationships using a linear mixed effects modelling framework. All variables were standardized to be centred around zero. First, we modeled the effect of rHRV (our indicator of an individual's stress-coping style) on seasonal mean of background energy expenditure (min-f_H) and seasonal mean daily energy expenditure (mean-f_H), with each individual included as a random effect to account for repeated measures. We also investigated the potential constraints that stress-coping styles may have on females exhibiting typical patterns of energy management by exploring how stress-coping styles influence deviance in energy management slopes within a similar mixed-effects modelling framework. Deviance was calculated as absolute difference from the population mean for the energy management slope described above. A greater deviance indicates greater difference from the population mean. As field-based measures of rHRV and energy management likely contain small measurement errors (Shuert et al., 2020b), each regression was also evaluated for regression dilution as per Halsey and Perna (2019). The amount of regression dilution, if present, was evaluated comparing ordinary least-squares (OLS), semi-major axis (SMA), and ranged major axis (RMA) methods using the 'lmodel2' package in R (Legendre, 2018). The results of the regression dilution analyses are reported in the Supplementary Materials.

Energy management envelopes provide a representation of population-level patterns of energy management by evaluating the distribution of data between daily values of min-f_H and mean-f_H (Shuert et al., 2020b). This approach sets graphical boundaries around the range of combinations of min-f_H (x-axis) and mean-f_H (y-axis) expressed within the population across all three breeding seasons (Shuert et al., 2020b). The lower boundary is defined by a 1:1 line, where background energy expenditure (min-f_H) equals daily energy expenditure (mean-f_H), meaning that background energy expenditure is the sole contributor to daily energy expenditure. The upper boundary is defined by a 95th quantile regression of mean-f_H against min-f_H. These boundaries define the envelope which captures the range of 95% of possible daily energy expenditures ('scope of energy management'; more information provided in the Supplementary Materials). We then evaluated the relative distribution and positioning of individual seals within this envelope with respect to their stress-coping style as indicated by their rHRV value.

All animal procedures were performed under UK Home Office project license #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.

Results

Controlling for annual differences and maternal daily mass-loss rates, daily background energy expenditure (min-f_H) was repeatable within individuals (*adj*-R = 0.308, bootstrapped confidence interval (CI) = 0.14 – 0.454; Likelihood ratio test $p < 0.001$). Daily energy expenditure (mean-f_H) was also repeatable between years (*adj*-R = 0.326, CI = 0.154 – 0.474, Likelihood ratio test $p < 0.001$). Individual repeatabilities (R_i) were variable, with some seals exhibiting higher individual repeatability than others (min-f_H R_i median = 0.301, range = 0.077 – 0.800; mean-f_H R_i median = 0.326, range = 0.096 – 0.743). Individuals that exhibited higher repeatability for min-f_H also showed higher repeatability for mean-f_H (Figure 1). Individuals exhibiting higher repeatability of both min-f_H and mean-f_H tended to be those with lower rHRV (indicative of more proactive individuals; Figure 1).

Resting HRV (rHRV) was a significant predictor of seasonal mean background (min-f_H) and mean daily energy expenditure (mean-f_H). Individuals with a lower rHRV, reflecting a more proactive stress-coping style, tended to have significantly higher background energy expenditures than those with a higher rHRV (mixed effects model slope rHRV: -0.71 ± 0.081; Figure 2A). Likewise, lower rHRV individuals also tended to exhibit higher daily energy expenditures than individuals with a higher rHRV (rHRV: -0.74 ± 0.077; Figure 2B). There was little influence of regression dilution within these relationships given that similar slopes were observed across estimation methods (Supplementary Materials). Full model results can also be found in the Supplementary Materials.

Individuals with lower rHRV (‘proactive’) were found to exhibit less deviance from the population mean (values closer to 0) in annual energy management slopes, while individuals with a higher rHRV (‘reactive’) tended to exhibit greater deviance in energy management slope (rHRV: 0.02 ± 0.007; Figure 3). Regression dilution highlighted possible alternative relationships in the data with a higher slope value, but all regression approaches represented positive associations between rHRV and energy management slope deviance (Supplementary Materials). Full model results are reported in the Supplementary Materials.

Across all individuals and years, the energy management envelope formed a wedge shape (Figure 4) with a wider range of, but lower values of, daily energy expenditure at lower values of background energy expenditures. At higher background energy expenditure values, higher daily energy expenditure was observed, but the range of daily energy expenditure values becomes increasingly narrow. Within this overall energy management envelope, low rHRV individuals (indicating more proactive stress-coping styles) tended to cluster towards the narrowest section of the relationship, where background energy expenditure and daily energy expenditure were greater, but the range of daily energy expenditure values was most restricted. Conversely, higher rHRV (reactive) were widely distributed throughout the energy management envelope (Figure 4; Supplementary Materials).

Discussion

Here we provide evidence that energy management strategies vary with stress coping styles in a capital breeding pinniped. Capital breeding pinnipeds do not feed during lactation and exhibit some of the highest sustained metabolic rates in mammals (Mellish et al., 2000), which places tremendous constraints on energy management during this critical life-history stage (Shuert et al., 2020b). As might be expected across capital breeding pinnipeds, grey seals tend to exhibit energy management strategies falling under a compensation model during lactation, meaning that periods of higher daily energy expenditure are compensated for by lowering background energy costs, and vice versa (Shuert et al., 2020b). However, we demonstrate here that not only are individuals relatively consistent across years in their specific pattern of expressing and balancing background and daily expenditures, but that more reactive (high rHRV) individuals tend to express a wider deviance of energy management patterns than more proactive (low rHRV) individuals.

Well established behavioural hallmarks of reactive stress-coping styles include shyness, high levels of HPA reactivity to threats, as well as slower and more thorough exploratory behaviour (Carere et al., 2010; Collins et al., 2020; Coppens et al., 2010; Ferlazzo et al., 2020; Koolhaas et al., 1999). Conversely, proactive individuals tend to exhibit greater boldness, more rapid but superficial exploratory behaviour, and higher levels of aggression (Coppens et al., 2010). Previous work on lactating grey seals has demonstrated that more proactive mothers tend to express more consistent patterns of maternal attentiveness across situations (Twiss et al., 2012b) and higher levels of non-resting behaviours, such as vigilance, relative to more reactive mothers (Shuert et al., 2020a). Our proxy of daily energy expenditure here incorporates both the presumed metabolic contributions to maintenance energy expenditure (background energy expenditures) along with those from other auxiliary processes, such as activity (Portugal et al., 2016). Our results concur with theoretical frameworks contending that proactive individuals likely have higher metabolic rates to facilitate their high energy lifestyle, whereas reactive individuals are likely to have a greater degree of flexibility in energetic phenotype in order to facilitate increased reactivity (Bijleveld et al., 2014; Carere et al., 2010; Twiss et al., 2020).

Our results imply that there are key differences in metabolic flexibility between pro- and reactive individuals. Variation across the more reactive mothers was greater than the variation among more proactive mothers. This was evidenced by the range of within individual repeatabilities for background and daily energy expenditures mapping onto rHRV (Figure 1). While there has been some debate about the value of individual repeatabilities in spatial behaviours, such as space-use patterns (Dingemanse et al., 2022; Stuber et al., 2022; Vander Wal et al., 2022), here we argue that the range of repeatabilities may present a better way to capture the personality-specific gradient of flexibility in metabolism. This aligns with the theory that proactive phenotypes tend to exhibit more consistent behaviour and expenditures as a result of being less reactive to environmental fluctuations and are generally less flexible in behaviour and energetic investment (Bijleveld et al., 2014; Koolhaas et al., 1999; Koolhaas et al., 2010). Proactive mothers tended to have a highly repeatable, less flexible background energy expenditure (min-f_H), our approximation of metabolic and other background processes, and daily energy expenditure (mean-f_H) than females with a more reactive phenotype. Experimental manipulations of great tit (*Parus major*) clutch sizes found that proactive females tended to invest more consistent energy into a breeding cycle based on a long-term perception of environmental conditions, while reactive females tended to be more variable in investment to match the current environmental conditions (Nicolaus et al., 2015). Similar results were found in our grey seal mothers, where reactive females tended to be more variable in both behavioural measures of maternal attentiveness (Twiss et al 2012) and reproductive expenditure across years than their proactive counterparts (Twiss et al., 2020).

Mathot et al. (2019) conducted a meta-analysis of maintenance energy expenditure (*sensu* metabolic rates) and behaviour. They found that specific behaviours, directly associated with energy gain or expenditure (such as foraging, boldness, or maximum swim speed) were correlated in a positive manner with metabolic rates across taxa, with those behaviours associated with extreme stress responses (e.g. escape behaviours) exhibiting the strongest correlation (Mathot et al., 2019). However, this same meta-analysis highlighted that single behaviours commonly used as measure of personality (e.g. exploration tendencies) do not scale well with metabolic rate (Mathot et al., 2019). These results have been corroborated with studies of other species in the wild where personality traits determined exclusively by single behavioural attributes did not always scale well with metabolism across contexts (Careau et al., 2019). Similarly some that assess coping style exclusively from behavioural measures suggest no relation to glucocorticoid metabolites implying that behavioural coping styles do not match physiological differences (Santicchia et al., 2020; Santicchia et al., 2022). However, we argue along with others that stress-coping style (i.e. pro-reactivity) and stress-reactivity are two independent dimensions of the HPA-axis (Zhang et al., 2020). Stress-coping styles determined using rHRV likely provides a more robust indicator of an individual's position on the pro-reactive spectrum. This is because such measures are based on the underlying physiological drivers of behaviour (Carravieri et al., 2016; Killen et al., 2014; Koolhaas et al., 2010; Twiss et al., 2020; von Borell et al., 2007), rather than comparing one, or a few, behavioural traits whose expression is likely impacted by multiple internal and external drivers at any one point in time.

The majority of grey seals included in our study tended to energy management strategies falling under a compensation model during this stage of life history as reported in previous work (Shuert et al., 2020b). Our results indicate that proactive grey seal females tended to a single pattern of energy management during lactation, investing in a larger energy budget overall at the cost of having less flexibility in their potential range of energy management. As such, proactive individuals were more constrained in energy management and may therefore be at a greater risk of 'overspending' above the limits of the energy management envelope. Reactive females on the other hand tended to be more variable overall in their energy management strategy, investing less energy on average, but retaining a greater range of energy adjustment potential. Individuals with reactive phenotypes, as a result, tended to have higher variability in slopes for energy management within a compensation energy management strategy, while possibly incurring less risk of over expending energy. While previous work on grey seals found some evidence for stress-coping styles driving differences in the variability of maternal expenditure (Twiss et al., 2020), other mechanisms may also drive this variability in energy trade-offs along a pro-reactive continuum. Breeding grey seals on sites like the Isle of May need periodic access to water sources during lactation, both for thermoregulatory needs (Redman et al., 2001) and likely for consuming fresh water while fasting (Stewart et al., 2014). In warm dry years, previous work has noted there is a behavioural or energetic impact in needing to access these pools, such as travel to and from freshwater sources (Redman et al., 2001; Stewart et al., 2014; Twiss et al., 2007). Shuert et al., (2020b) found that the portion of the energy management envelope occupied largely by reactive females saw the greatest change in the upper limits of energy expenditure envelope during years of sub-optimal weather patterns during the breeding season. Reactive stress-coping styles highlighted here appear to occupy the widest space within an energy management envelope and thus may be more capable of adjusting energy investment and expenditure as a result of increased scope.

We postulate that the width of the energy management envelope represents metabolic scope, the difference between minimum and maximum rates of metabolism (Pörtner and Farrell, 2008), and that individuals with a more reactive stress-coping style exhibit the greatest width and flexibility therein. Differing personality types or stress-coping styles exhibit differences in metabolic scope as indicated by our results, which may lend evidence towards differences in pace-of-life (Réale et al., 2010). However, evidence to support a relationship between metabolic scope and pace-of-life thus far appears to be mixed in other research efforts. Leaders of schooling fish were found to have lower aerobic scope and a lower maximal metabolic rate than their follower counterparts, suggesting a trade-off between high-performance individuals and swimming capabilities (Ward et al., 2018). Conversely, a study on round goby (*Neogobius melanostomus*) indicated that bolder individuals tended to have higher sustained metabolic rates, but found no difference in aerobic scope or maximum metabolic rates between personality types (Behrens et al., 2020). As argued above, using simple behavioural categorisations, however, may not adequately capture the covariance of personality-based measures with aerobic scope (Mathot and Frankenhuis, 2018). In theory a greater metabolic scope should support greater plasticity of behaviour, equating to a greater range of residual variation in the expression of behaviour across a population (Biro et al., 2018). Greater plasticity in metabolic scope can also support more flexibility in energy allocation, such as toward growth across variable resource conditions (Nilsson-Örtman and Brönmark, 2022), and trade-offs in behavioural prioritization relative to reproductive costs (Keicher et al., 2024). Given our results here, we argue that the upper limit of the relationships between background and daily energy expenditures presents a viable field-based measure of metabolic scope for grey seals, and potentially other, species. Our results indicate that, due to greater behavioural flexibility and reactivity, reactive females may benefit from a lower daily and background energy expenditure with a greater metabolic scope within individuals. Conversely, proactive individuals tend to invest more consistent energy into breeding at the cost of a lower flexibility in metabolic scope.

Evidence suggests that reactive stress-coping styles may have less sensitivity to oxidative stress and greater immune responses, potentially contributing to a longer observed lifespan than their proactive counterparts (Costantini et al., 2008; Costantini et al., 2012). While pace-of-life theory has often been applied to understanding differences in correlated traits between closely related species or populations, it is also applicable to our understanding of inter-individual differences in stress-coping styles and personality (Réale et al., 2010). Pace-of-life theory focuses on differences between fast and slow life-histories. For iteroparous animals, these correlated traits typically associated with either a fast or slow life-history likely provide no direct fitness benefit for lifetime reproductive output as reproductive episodes occur multiple times over an individuals' lifetime. Instead, others have argued that correlated pace-of-life syndromes provide a range of plasticity for the relationships between behaviour and physiology (Montiglio et al., 2018) to create a trade-off between current and future reproduction. As such, it is argued that the trade-offs for pace-of-life, and likely 'payoff structures' (as discussed in Mathot and Frankenhuis, 2018), are instead expressed as a balance of consistency against flexibility of energy investment across years. In the current study, we are only evaluating these trade-offs within a specific context, the value of which has been argued elsewhere (Biro, 2024). Using the approach presented here, integrated with measures of reproductive output and survival, may contribute to our understanding differences in pace-of-life in further study.

We have identified some limitations in our study that warrant future investigation. Grey seals tend to be site-faithful, often returning to the same breeding colony and often to within the same few metres of previous pupping sites (Pomeroy et al., 1994; Pomeroy et al., 2000). Site fidelity means that, across years, an individual may experience similar microhabitats (Stewart et al., 2014; Twiss et al., 2000), local conspecific densities, and neighbour identities (Pomeroy et al., 2000), potentially influencing social interactions (Pomeroy et al., 2000) and local thermoregulatory differences (Stewart et al., 2014, 20; Twiss et al., 2007). These environmental influences may impact the time spent at rest and the quality of that rest (Mortlock et al., 2024a; Mortlock et al., 2024b; Mortlock et al., 2025). In this study we were not able to directly tease apart the relationship between individual identity (and therefore coping style) and site-choice (i.e. phenotype-environment matching; Holtmann et al., 2017; Wolf and Weissing, 2010), though some investigations in this colony suggest there is no preference among different stress-coping styles (*unpublished data*). At the Isle of May, most pregnant females select similar types of habitats in which to give birth: Relatively flat while subject to inundation by the tide, but with access to pools of freshwater (Redman et al., 2001). Microhabitat does vary at very fine (metre by metre) spatial resolution (Twiss et al., 2000), but despite being ‘site-faithful’ most seals select pupping sites that differ by tens of metres (median inter-annual site fidelity = c. 50m) across years. Therefore, individual mothers will experience different microhabitats in successive years, and our study considers individuals measured over multiple years. While our rHRV metric is derived from data gathered while all individuals are in the same resting behavioural state, microhabitat differences (such as thermal environment), can impact sleep quantity and quality (e.g. wild boar, *Sus scrofa*; Mortlock et al., 2024a). We defined resting as periods where the individual was unmoving based on accelerometry (Shuert et al., 2018; Twiss et al., 2020), which could include both true sleep and wakeful rest. It is likely that individual differences in the amount and fragmentation of sleep (and wakeful rest) exist among lactating grey seals, as found in other wild mammals (neonate fallow deer, *Dama dama*; Mortlock et al. 2024a, 2025, and adult wild boar, *Sus scrofa*; Mortlock et al. 2024b). Identifying sleep in free-ranging mammals is challenging, though recent research has developed surface-mounted devices capable of electrophysiological recordings of sleep in wild marine mammals (Kendall-Bar et al., 2022; Kendall-Bar et al., 2023). Future work may consider finding new ways to quantify these fine-scale differences across the breeding colony, such as through temperature loggers (e.g. using iButton Miniature Data Loggers; https://i-button.co.uk/) or fine-scale movement analyses. New developments in biologging technology, such as the inclusion of EEG devices, long-term recording capabilities, and beyond will help to further enrich this picture of the impact that other variables may have on variation in background and daily energy expenditures.

Grey seals are a long-lived pinniped, and it was beyond the scope of this study to evaluate lifetime reproductive output. Despite this challenge, our work provides a tool for assessing if pace-of-life syndromes exist in grey seal mothers. Specifically, we have presented evidence of some of the linkages between stress-coping styles and energy management to support an extended definition of pace-of-life theory across multiple years in a fully wild population (Dammhahn et al., 2018). Combining our evidence here across multiple studies (Shuert et al., 2020a; Shuert et al., 2020b; Twiss et al., 2012b; Twiss et al., 2012a; Twiss et al., 2020), we see that a continuum of pace-of-life syndromes could be exhibited during this reproductive period for grey seals along covarying behavioural (pup-checking rates, activity budgets) and physiological (energy expenditure, energy management, energetic scope) traits within a stress-coping style framework. While this terrestrial phase of grey seal life-history has been well documented for the trade-offs associated with stress-coping styles, further work is needed to investigate if, and how, stress-coping styles impact the remainder of the yearly cycle for grey seals and over a lifetime of an individual. Outside of the brief, but intense lactation period, grey seals are largely found out at sea foraging (Breed et al., 2009). Flexibility, or lack thereof, in energetic investments due to differences in stress-coping style may drive consistent individual differences in spatial foraging patterns (Patrick et al., 2014), diving behaviour (Hamilton et al., 2018), migratory patterns (Shuert et al., 2023), and diet specialization and diving abilities (McHuron et al., 2018) as a result of inherent differences in physiological capacity or metabolic scope. For grey seals and other species, evaluating the impact of stress-coping styles in other contexts may contribute to a greater understanding of the mechanisms underpinning consistent individual differences in behaviour. Developments in telemetry approaches that permit recordings of heart rate, rHRV, and movement will yield data where similar analyses to ours could be conducted even when individuals are not directly observable presenting an exciting opportunity for future study.

Data Accessibility Statement

The data and code for this manuscript can be found in the following Dryad repository (https://doi.org/10.5061/dryad.stqjq2cbm).

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Author Contributions

C.R.S., S.D.T. and P.P.P. conceived of the study, participated in the field work and collected data; C.R.S. performed data analyses with support from P.P.P. and S.D.T.; C.R.S. wrote the paper with input from all authors. All authors have read and approved of the final manuscript.

Conflict of Interest

The authors declare no conflict of interests.

Ethics Statement

All animal procedures were performed under UK Home Office project license #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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Figures

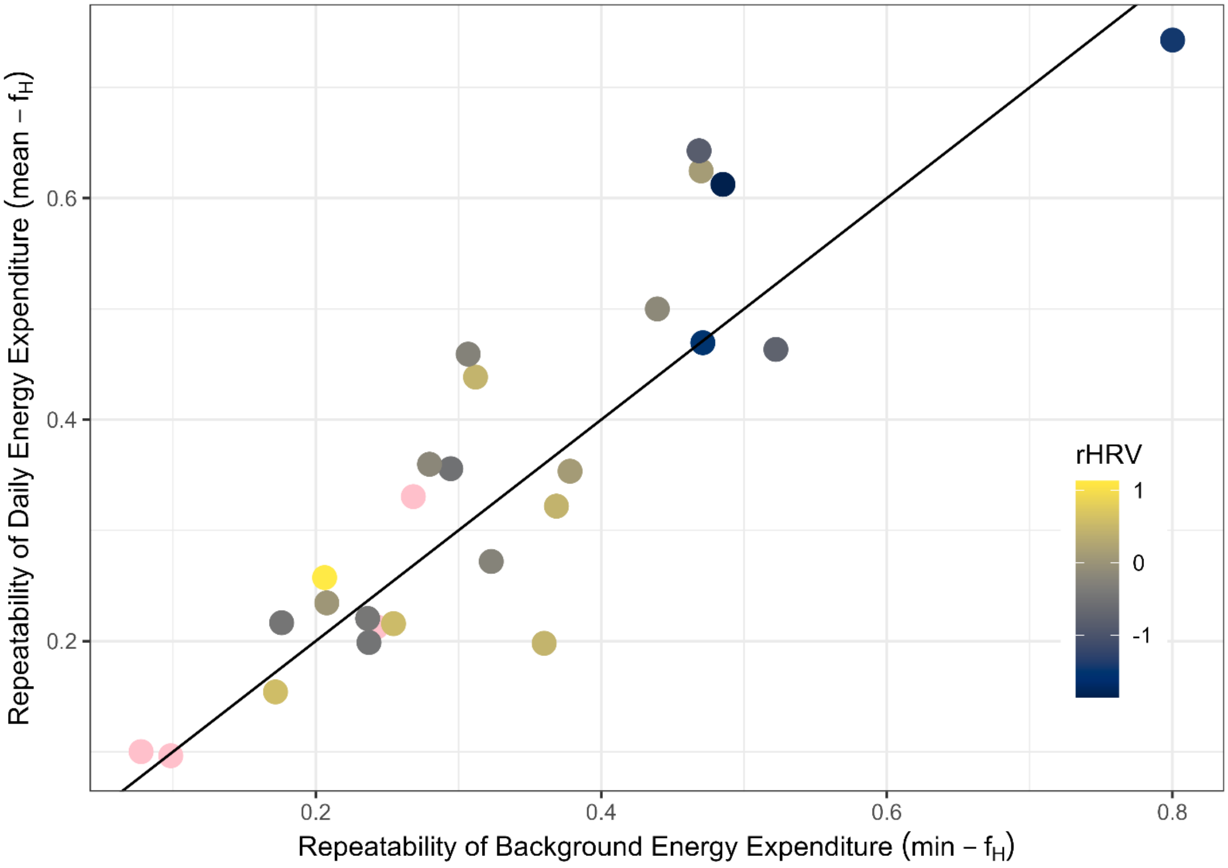


Figure 1: Individual repeatability values (R_i) for background and daily energy expenditures. Individual repeatabilities (R_i) were extracted for each seal by computing the variance component for each individual from the group variance of the random effects within a linear model. Individual seals displayed remarkable consistency in repeatability for background and daily energy expenditures, as evidenced by the close relationship to a 1:1 line (solid black line). Each individual (point) is also coloured by their rHRV, highlighting that individuals with more proactive stress-coping style (lower rHRV) tended to have the highest repeatabilities for both background and daily energy expenditures. Those individuals in pink did not have enough data over a season to compute a reliable rHRV estimate.

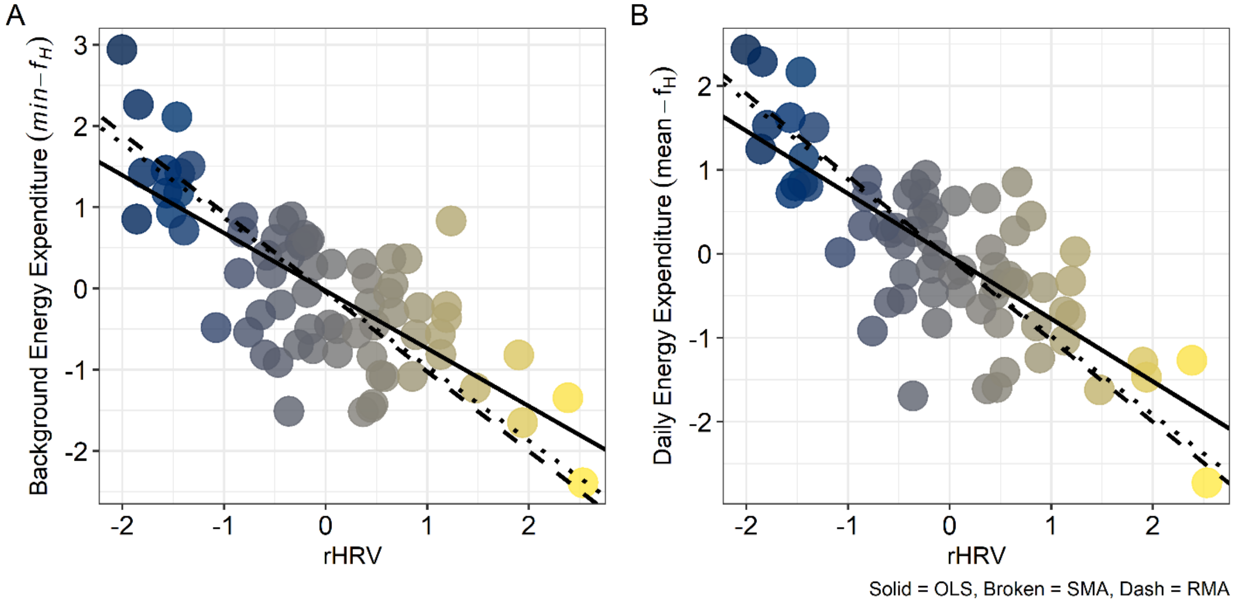
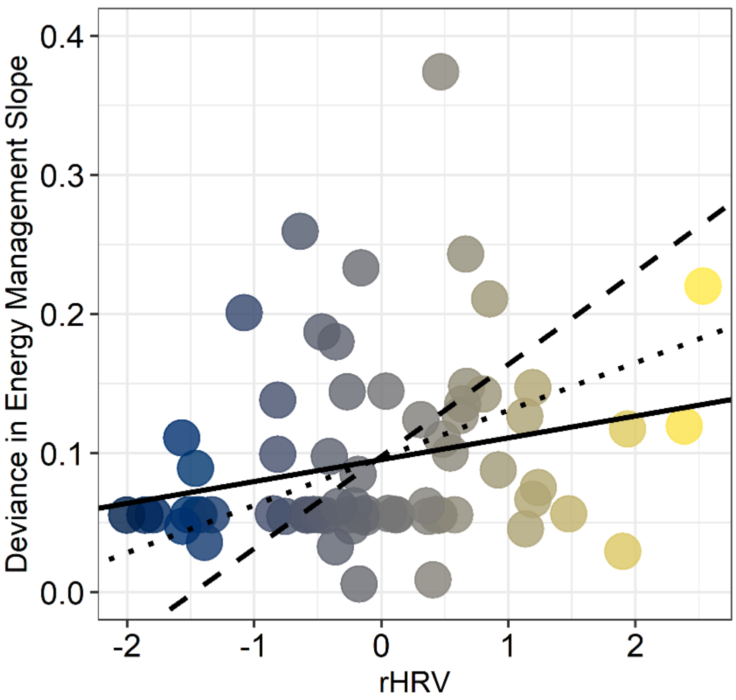


Figure 2: Background and daily energy expenditure are related to resting HRV. Standardized rHRV predicted background energy expenditure (standardized min-f_H) and daily energy expenditures (standardized mean-f_H) in grey seal mothers. Individuals with higher values for rHRV (indicative of reactive phenotypes, lighter yellow points) had lower background energy expenditures and daily energy expenditures than females tending towards lower values for rHRV (proactive phenotype, darker blue points). Regression dilution highlighted from best fits resulting from ordinary least squares (OLS; solid line), semi-major axis (SMA; broken line), and ranged major axis (RMA; dashed line) regression approaches.



Solid = OLS, Broken = SMA, Dash = RMA

Figure 3: Energy management slope variability in relation to resting HRV (stress-coping style). Individuals with positive standardized rHRV (more reactive phenotypes) show greater deviance in energy management slope relative to the population mean (a value of zero), indicating greater variability across years. Regression dilution highlighted by best fits resulting from ordinary least squares (OLS; solid line), semi-major axis (SMA; broken line), and ranged major axis (RMA; dashed line) regression approaches.

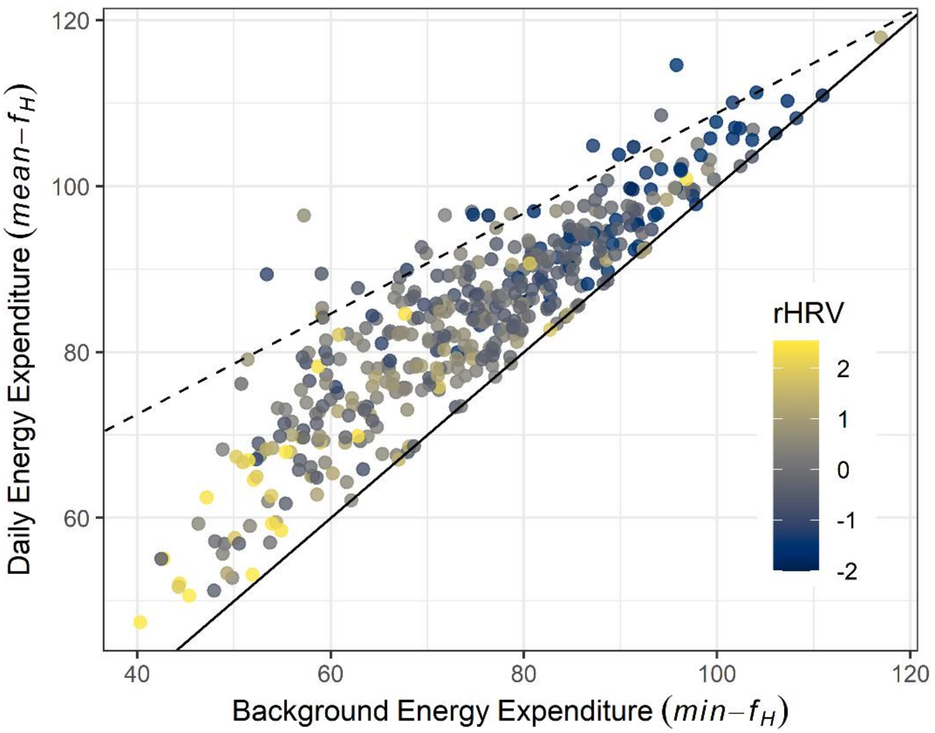


Figure 4: Pro- and reactive individuals differ in their positions within the energy management envelope. Daily measures of background (min-f_H) and daily energy expenditure (mean-f_H) pooled across three breeding seasons, bounded by a 1:1 line (solid), indicating when minimum energy expenditures match daily energy expenditure estimates, and the upper 95th quantile regression (Shuert et al., 2020b). Lower rHRV (proactive) individuals tended to occupy the narrowest section of the performance envelope as a result of higher background and daily energy expenditures, while higher rHRV (reactive) individuals tended to exhibit more flexibility in values throughout the performance envelope.

Title: "Stress-coping styles are associated with energy budgets and variability in energy management strategies in a capital breeder."

Journal: Proceedings of the Royal Society B

Authors: Courtney R. Shuert[1,*], Patrick P. Pomeroy[2], Sean D. Twiss[3]

[1] Conservation and Research, Assiniboine Park Conservancy, Winnipeg, Canada

[2] Scottish Oceans Institute, University of St. Andrews, St. Andrews, UK

[3] Department of Biosciences, Durham University, Durham, UK

[*]corresponding author: Courtney Shuert, cshuert@gmail.com

Supplementary Materials

Quantile regression was fitted across all daily values of background energy (min-f_H) against daily energy expenditures (mean-f_H) to highlight the upper limits of energy management across all individuals, following (Shuert et al., 2020). The regression fit was assessed at the 95th quantile ($\tau = 0.95$) for all available years using the 'quantreg' package in R (Koenker, 2018) and resulted in a slope of 0.604 (Confidence interval: 0.567 – 0.705) as fit. The resulting relationship was compared against a 1:1 line and included in the main text as Figure 3. While the main modelling effort leveraged mixed-effects models, regression dilution was also assessed for each relationship. Following (Halsey and Perna, 2019), regression dilution was assessed between stress-coping styles (as determined from resting heart rate variability (rHRV); (Twiss et al., 2020) and seasonal energy management parameters using three regression methods. Regression methods included ordinary least squares (OLS), semi-major axis (SMA), and ranged major axis (RMA) fits (Legendre and Legendre, 1998) of rHRV predicting min-f_H and mean-f_H as well as the deviance (absolute difference from across-individual mean) in seasonal energy management slope. Regression dilution methods were fit using ‘lmodel2’ package in R (Legendre, 2018). Full model fits of the resulting slopes are included in both Figures 1 and 2 and are also presented in Table S1. Full model output for mixed-effects models relating stress-coping styles to energy management parameters are included below in Table S2.

Table S1: Regression dilution of stress-coping styles modulating energy management. Regression dilution was assessed using three methods (ordinary least squares, OLS; semi-major axis, SMA; ranged major access, RMA) for relationships across individuals for the impact that stress-coping styles (represented by rHRV) had with seasonal energy management parameters, including background energy (min-f_H), daily energy expenditure (mean-f_H) and deviance in energy management slope (dev. EM Slope). Slopes are presented for each case with the resulting 95% confidence interval below in brackets.

	min-f_H	mean-f_H	dev. EM Slope
OLS	-0.712	-0.749	0.014
	(-0.872, -0.552)	(-0.899, -0.599)	(-0.001, 0.030)
SMA	-0.976	-0.976	0.066
	(-1.150, -0.829)	(-1.138, -0.837)	(0.052, 0.083)
RMA	-0.913	-0.933	0.034
	(-1.139, -0.722)	(-1.137, -0.759)	(0.0004, 0.081)

Table S2: Fixed effects of model regressions. Full model output for each regression of stress-coping style (rHRV) and maternal daily mass-loss rate (MDML) as predictors of energy management strategy parameters, including background energy (min-f_H), daily energy expenditure (mean-f_H) and deviance in energy management slope (dev. EM Slope). Parameter estimate included with 95% confidence interval included below.

	min-f_H	mean-f_H	dev. EM Slope
Intercept	-0.035	-0.038	0.096
	(-0.206, 0.134)	(-0.204, 0.126)	(0.081, 0.112)
rHRV	-0.691	-0.710	0.011
	(-0.865, -0.517)	(-0.875, -0.546)	(-0.005, 0.027)
MDML	0.062	0.105	-0.016
	(-0.109, 0.233)	(-0.051, 0.261)	(-0.033, -0.001)

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