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Biologging reveals individual variation in behavioural predictability in the wild

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Abstract

1. Recent research highlights the ecological importance of individual variation in behavioural predictability. Individuals may not only differ in their average expression of a behavioural trait (their behavioural type) and in their ability to adjust behaviour to changing environmental conditions (individual plasticity), but also in their variability around their average behaviour (predictability). However, quantifying behavioural predictability in the wild has been challenging due to limitations of acquiring sufficient repeated behavioural measures.
2. We here demonstrate how common biologging data can be used to detect individual variation in behavioural predictability in the wild and reveal the coexistence of highly predictable individuals along with unpredictable individuals within the same population.
3. We repeatedly quantified two behaviours—daily movement distance and diurnal activity—in 62 female brown bears *Ursus arctos* tracked across 187 monitoring years. We calculated behavioural predictability over the short term (50 consecutive monitoring days within 1 year) and long term (across monitoring years) as the residual intra-individual variability (rIIV) of behaviour around the behavioural reaction norm. We tested whether predictability varies systematically across average behavioural types and whether it is correlated across functionally distinct behaviours, that is, daily movement distance and amount of diurnal activity.
4. Brown bears showed individual variation in behavioural predictability from predictable to unpredictable individuals. For example, the standard deviation around the average daily movement distance within one monitoring year varied up to fivefold from 1.1 to 5.5 km across individuals. Individual predictability for both daily movement distance and diurnality was conserved across monitoring years. Individual predictability was correlated with behavioural type where individuals which were on average more diurnal and mobile were also more unpredictable in their behaviour. In contrast, more nocturnal individuals moved less and were more predictable in their behaviour. Finally, individual predictability in daily movement distance and diurnality was positively correlated, suggesting that individual predictability may be a quantitative trait in its own regard that could evolve and is underpinned by genetic variation.
5. Unpredictable individuals may cope better with stochastic events and unpredictability may hence be an adaptive behavioural response to increased predation risk.

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Coexistence of predictable and unpredictable individuals may therefore ensure adaptable and resilient populations.

KEYWORDS

animal personality, behavioural syndrome, double hierarchical model, movement, residual intra-individual variability, *Ursus arctos*

1 | INTRODUCTION

Similar to the study of classical ecological niches, where populations may be composed of individual specialists with distinct niches (Araújo et al., 2011), the field of animal personality studies behavioural niche specialisation where over repeated measures individuals may have a lower or higher average expression of a given behaviour (i.e. behavioural type) than the population average (Figure 1a). The coexistence of different behavioural types in the wild has been demonstrated for a range of behaviours, such as food resource selection (Courbin et al., 2018),

movement (Abrahms et al., 2018; Spiegel et al., 2017), activity (Hertel, Leclerc, et al., 2019; Nakayama et al., 2016), habitat selection (Leclerc et al., 2016), mating strategy (van Oers et al., 2008) and aggressiveness towards conspecifics (Araya-Ajoy & Dingemanse, 2017). A facet of behaviour that only recently gained attention in the study of animal personality is the variability of behaviour around the behavioural type (Figure 1b) after also accounting for variation in plastic responses to changing environmental conditions (i.e. behavioural reaction norm: Dingemanse et al., 2010). Individuals may not only vary in their average behaviour but also in their residual intra-individual variability

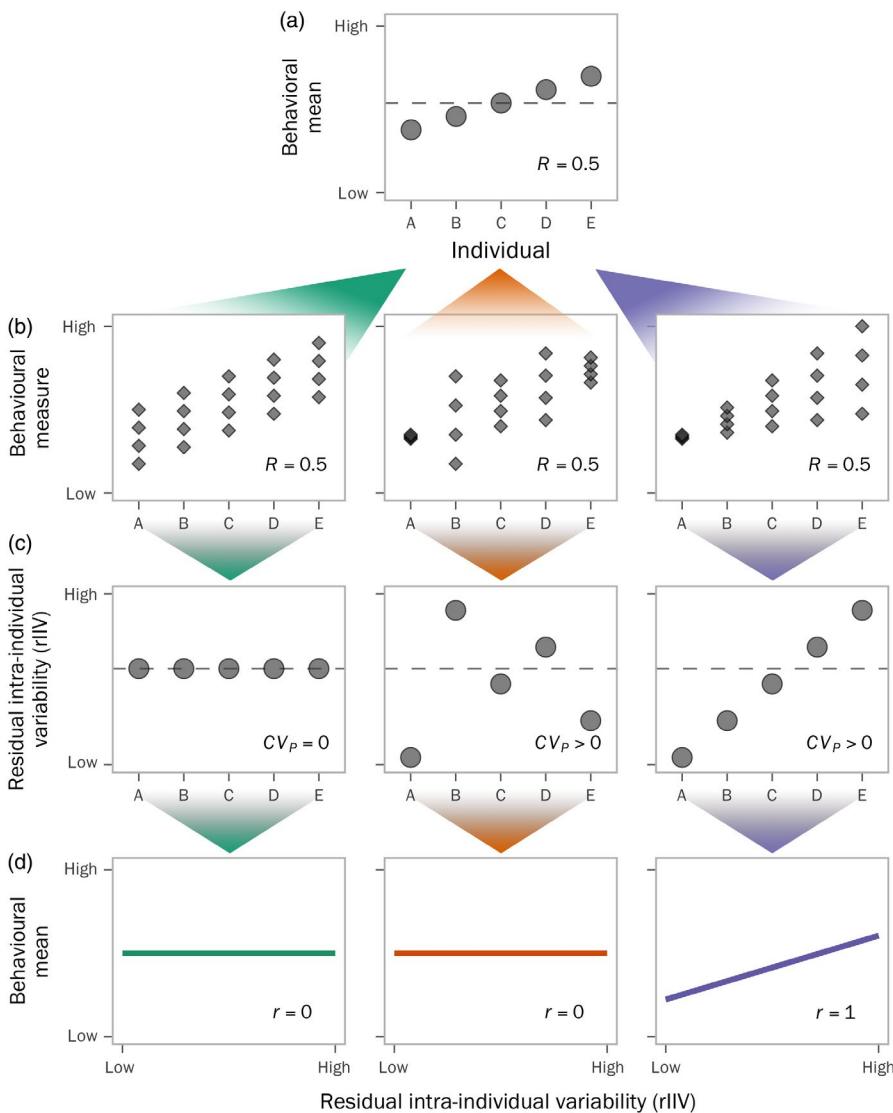


FIGURE 1 Conceptual depiction of possible relationships between an individual's mean behaviour (behavioural type) and its variability of behaviour around the behavioural type (behavioural predictability). (a) Behavioural type of five individuals relative to the population average behaviour (dashed line). Among-individual repeatability (R) characterises how much of the population wide behavioural variation is explained by among-individual differences. (b) Behavioural type and R can assume the same values under different structures of within individual behavioural variability. Within individual variability may be equal (green), or vary among individuals (orange and purple). (c) Accordingly, behavioural predictability measured as residual intra-individual variability (rIIV), that is, after controlling for environmental effects, may be equal (green) among individuals, in which case rIIV does not differ from the population mean residual (dashed line) and the coefficient of variation in predictability (CV_p) approaches 0. Alternatively, rIIV can vary among individuals (orange, purple), implicating a gradient from behaviourally predictable to behaviourally unpredictable individuals. Low rIIV indicates higher behavioural predictability relative to individuals with high rIIV indicating low predictability. (d) Finally, variation in behavioural predictability can be correlated with behavioural types (purple) or uncorrelated (orange)

of behaviour around that mean (Westneat et al., 2015), a phenomenon commonly termed behavioural predictability (Figure 1c; Biro & Adriaenssens, 2013; Cleasby et al., 2015; Stamps et al., 2012). Under individual variation in behavioural predictability, some individuals are unpredictable and are producing a broad range of behavioural values, whereas more predictable individuals express behaviours that are narrowly centred around their own average. Individual variation in predictability may arise statistically due to an incomplete model in which covariates which animals plastically adapt their behaviour to are not sufficiently controlled for (Westneat et al., 2015). As such, variation in predictability may account for important hidden biological processes. Variation in predictability may, however, also be adaptive, for example in predator–prey relations (Briffa, 2013), for conspecific social niche partitioning (Bergmüller & Taborsky, 2010), or predictability may increase with experience over age (Fischer et al., 2014). The analogue of behavioural predictability in a foraging context would be intraspecific dietary niche variation (Araújo et al., 2011) with a spectrum from dietary specialists occupying a narrow dietary niche co-occurring with dietary generalists occupying a wide dietary niche within populations of the same species (Estes et al., 2003; Wilson & Yoshimura, 1994). Dietary specialised individuals may be at an advantage under stable environmental conditions (Kassen, 2002; Vander Zanden et al., 2010) whereas generalists fare better under environmental stochasticity or anomalies (Abrahms et al., 2018). Individual variation in behavioural predictability could have similar important implications for individual performance relative to environmental dynamics.

The existence of variation in behavioural predictability is data demanding and difficult to quantify and, as a result, has rarely been investigated in experimental studies (Jolles et al., 2019; Mitchell et al., 2016). So far only one study has studied variation in predictability under realistic field conditions (Westneat et al., 2012) where the presence of predators and conspecifics is expected to have strong and long-lasting effects on individual behaviour. We here aim to close this gap by using biologging data to elucidate the extent of individual variation in behavioural predictability in routine movement and activity behaviours of animals in the wild. A major challenge in estimating variation in predictability is that it requires large samples of repeated measures per individual and balanced sample sizes across individuals (Cleasby et al., 2015). Biologging data such as GPS location or accelerometer data from animal tracking devices provide a means of obtaining such high and relatively equal sampling intensities of behaviour over all instrumented individuals in a population.

1.1 | Biological relationships of mean and variance

Only a few studies have tested whether behavioural predictability is systematically correlated with behavioural types (Figure 1d; Jolles et al., 2019; Matich et al., 2011; Stamps et al., 2012). Potier et al. (2015) showed that foraging great cormorants *Phalacrocorax carbo* consistently differed in dive durations. Individuals which dove for shorter periods applied this foraging tactic more consistently, whereas individuals with longer dive times were more flexible in

their diving behaviour. Conversely, Mitchell et al. (2016) found that in the closed environment of an experimental tank, more active guppies *Poecilia reticulata* showed lower intra-individual variability in activity and were hence more predictable in their behaviour than their more sedentary conspecifics. Elsewhere, no relationship could be found between an individual's behavioural type and its predictability (Stamps et al., 2012). From a neuroendocrinological perspective, bolder and more proactive individuals seem to have less inhibitory control and are hence more predictable in their behavioural responses, whereas shy, reactive individuals are more flexible to adjust their behaviour to the environment (Coppens et al., 2010). This is in line with findings from black-legged kittiwakes where bolder birds displayed more repeatable foraging behaviour than shy birds (Harris et al., 2020). Furthermore, behavioural types of functionally distinct behaviours can be correlated among individuals into behavioural syndromes (Dingemanse et al., 2012; Réale et al., 2007; Sih et al., 2004). If behavioural predictability is a repeatable trait in itself (Biro & Adriaenssens, 2013), we might expect that the expression of this trait, quantified from functionally distinct behaviours, could also be correlated among individuals into *predictability syndromes*. Based on this assumption, individuals with high predictability in one behaviour could also express high predictability in other behaviours, which in turn would strongly support the idea of coexisting unpredictable and predictable individuals in the same population. Alternatively, trade-offs between many behaviours may lead to a mix of positive, negative and neutral among-individual correlations in predictability estimates across behaviours, simply because low levels of predictability in one suite of behaviour may be compensated for in functionally distinct other suites of behaviours (Forsman, 2015).

1.2 | Statistical relationships of mean and variance

Behavioural predictability can be quantified statistically by partitioning the phenotypic variance into its among-individual and residual components. Typically, behavioural ecologists quantify how much behavioural variance in a population can be attributed to among-individual differences in average behaviour, that is, behavioural types (Figure 1a). Univariate and multivariate mixed modelling techniques are effective tools to partition these variances (Dingemanse & Dochtermann, 2013). Mixed models assume homogeneity of variance across individuals (the levels of a random intercept), however, this assumption is rarely verified and often violated (Schielzeth et al., 2020). The average behavioural types of individuals, as well as the population level 'among individual repeatability' (R) can assume the same values under different scenarios of residual intra-individual variability around the mean, that is, homogenous (Figure 1b green) or heterogeneous (Figure 1b orange). The extension of a mixed model into a double-hierarchical generalized linear model (DHGLM) allows to relax the assumption of equal residual variance for all individuals by explicitly modelling the residual variance. DHGLMs allow to simultaneously model differences in the average and in the residual variance in a 'mean' and 'dispersion' model. The

'mean' model includes fixed and random effects just as typical linear mixed effects models do. The dispersion part of the model uses the residual variance, that is, the unexplained variance from the mean model, as its response variable. As in the 'mean' model, the dispersion model includes an intercept, which correspond to the average residual standard deviation in the population. Fixed effect coefficients indicate whether a given factor or gradient increases or decreases the variance relative to the intercept. By including individual identity as a random effect, one can estimate how much individuals depart from the population residual variance (residual intra-individual variation: rIIV, Figure 1c, Cleasby et al., 2015). When individuals are equally variable, rIIV equals the population intercept (Figure 1c green). Alternatively, higher values of rIIV indicate that an individual produces a wider range of phenotypes compared to the average behavioural variance in the population, it hence behaves more unpredictably. In contrast, individuals with low rIIV only express a narrow range of behavioural values and behave more predictably (Figure 1c orange). Similar to the population's repeatability (R), variation in rIIV can be quantified as the coefficient of variation in predictability (CV_p). Higher CV_p values indicate a population composed of a mixture of predictable and unpredictable individuals (Figure 1c orange and purple) while low values indicate individuals are homogenous in their expression of behavioural variation (Figure 1c green). When individuals at one of the extremes of a behavioural type gradient (i.e. higher or lower average behaviour) display higher behavioural predictability (and vice versa) this results in a functional correlation of behavioural type and behavioural predictability (Figure 1d purple).

Note that such mean–variance between correlations can arise mathematically, for example for data measured on a ratio scale (i.e. data that have a lower bound at 0) or for specific distributions where the mean is equal to its variance or standard deviations (e.g. Poisson and exponential distributions respectively). In such cases, individuals with mean values close to 0 will inevitably have small variances. Any change in mean must therefore be accompanied by an equal change in variance. Mean–variance relationship can also occur when data distributions deviate from normality.

1.3 | Study system

We here use the brown bear *Ursus arctos* a highly adaptable ecological generalist, as model species to test theoretical predictions about individual variation in predictability and its relation to an individual's behavioural type, in the wild. Our study population in south-central Sweden has previously been demonstrated to show considerable among-individual variation for routine behaviours such as daily movement distance, diurnal activity and habitat selection for roads, bogs and clearcuts (Hertel, Leclerc, et al., 2019; Leclerc et al., 2016). Moreover, female bears exhibit behavioural syndromes and vary along a gradient from nocturnal/less mobile to diurnal/more mobile individuals (Hertel, Leclerc, et al., 2019). Female brown bears maintain non-territorial, stable multiannual home ranges which overlap considerably among females (Frank et al., 2018). Pronounced long-lasting individual

differences in behaviour have been suggested to facilitate home range overlap through intraspecific temporal (Hertel et al., 2017) and spatial (Leclerc et al., 2016) niche partitioning. Brown bears inhabiting less anthropogenically altered landscapes and with no hunting are preferably day active but increase nocturnality in reaction to increased human presence (McLellan & McLellan, 2015; Ordiz et al., 2014). When approached experimentally by humans on foot, humans rarely notice the presence of a bear, while bears, after their initial flight response, change their activity pattern to become more nocturnal for up to 3 days after the encounter (Ordiz et al., 2013). These studies demonstrate individual variation in mean bear behaviour but they also suggest that bears may differ in their behavioural variability around their mean if certain behavioural types are more likely to be disturbed by humans. A functional among-individual correlation between diurnality and daily movement distance has been demonstrated (Hertel, Leclerc, et al., 2019), with more diurnal individuals also moving farther and we suggest that those diurnal, far moving bears are more likely to encounter humans or traffic than their more elusive behavioural counterparts. Furthermore, adult female brown bears in our population produce a litter every 2–3 years (i.e. females keep their cubs for 1 or 2 years after birth, Van de Walle et al., 2018). Females with cubs have been shown to move over shorter distances than solitary females, probably because cubs constrain the movement capacity of their mother (Hertel, Zedrosser, et al., 2019) and at the same time family groups are more diurnal than solitary bears, most likely to protect cubs from encounters with potentially infanticidal adult males (Steyaert et al., 2013).

1.4 | Objectives

We used movement and accelerometer data of 62 female brown bears to study behavioural predictability in diurnal activity and movement behaviour the wild. We expected that cubs of the year constrain females to behave more predictably. We further expected among-individual variation in behavioural predictability. Specifically, we hypothesised that behavioural types are correlated with behavioural predictability and predict that more diurnal and farther moving behavioural types will be less predictable in their behaviour as they are more exposed to human disturbances (traffic, recreationists or berry pickers) when active during the day and will alter their behaviour after an encounter as has been shown previously (Ordiz et al., 2013). Alternatively, movement activity has been shown to be negatively correlated with predictability in experimental environments (Mitchell et al., 2016) and bolder individuals seem generally more predictable (Harris et al., 2020; Jolles et al., 2019). In our case, this means that more diurnal and active bears should accept encounters with humans more readily and be more predictable as a result. Last, we predicted that individuals with a more predictable diel activity pattern are also more predictable in their daily movement distances as the means of these two functionally distinct behaviours are correlated (Hertel, Leclerc, et al., 2019). We decomposed behavioural variance into its short-term (i.e. within a given bear monitoring year) and long-term effects (i.e. across all years an individual was

monitored) which allowed us to test whether behavioural predictability is stable or varies within individuals, for example, across changing reproductive status or with age (Westneat et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

We used movement and activity data collected in south central Sweden (~N61°, E15°) as part of a long-term, individual-based monitoring project (Scandinavian Brown Bear Research Project; www.bearproject.info). Bears were immobilised from a helicopter (Arnemo & Fahlman, 2011) and fitted with GPS–GSM neck collars with dual-axis motion sensors (Vectronics Aerospace GmbH). A vestigial premolar tooth was collected from all bears not captured as a yearling to estimate age based on the cementum annuli in the root (Matson et al., 1993). We used data of female bears after separation from their mother (>2 years) and of all reproductive stages (solitary, with cubs of the year, with 1-year-old offspring). We used GPS relocation data collected at 1 hr intervals and acceleration data from dual-axis motion sensors averaged at 5 min intervals to estimate diurnality and movement distance for 50 consecutive days from 1 July to 20 August in 2007–2017 (i.e. a monitoring year is defined as a bear monitored from 1 July to 20 August in a given calendar year). We estimated diurnality from acceleration data as relative activity during daylight hours corrected for changes in daylight length (Hoogenboom et al., 1984):

$$\text{diurnality index} = \frac{\frac{AD}{DD} - \frac{AN}{DN}}{\frac{AD}{DD} + \frac{AN}{DN}}, \quad (1)$$

where AD and AN are the sum of the acceleration values during the day and night, respectively, and DD and DN are the duration of the day and night respectively. Diurnality ranges from –1 (strictly nocturnal) to 1 (strictly diurnal). We calculated daily movement distance as the sum of Euclidian distances between consecutive hourly GPS positions within a day. Because missing GPS positions lead to missing distance calculations which may lead to an under-estimation of the daily movement distance, we only included days with at least 18 of 24 possible relocations. Movement distance was independent from the number of relocations because missing fixes usually occur under closed canopy cover, habitat that bears select for resting. We included bears for which both diurnality and movement distance was recorded and included all monitoring days on which either one of the behaviours was recorded.

2.2 | Model fitting

We fitted a bivariate double-hierarchical generalized linear models (DHGLMs) with diurnality and daily movement distance as response variables using the R package *BRMS* (Bürkner, 2017) based on the Bayesian software Stan (Carpenter et al., 2017; Stan Development Team, 2018). DHGLMs allow for the simultaneous estimation of a

‘mean model’ and a ‘dispersion model’. Fixed and random effects can be fitted to both parts of the model. The model can therefore not only estimate whether individuals differ in their mean expression of a behaviour (i.e. behavioural type, ‘mean model’) but also whether they differ in their residual standard deviation (rIV) around this behavioural mean (i.e. behavioural predictability, ‘dispersion’ model). Importantly, population mean residual standard deviation (the intercept of the dispersion model) and individual specific residual standard deviation (rIV) are estimated on the log scale to ensure that standard deviations are always positive (see Cleasby et al., 2015 for details). We additionally estimated the correlation between the random intercepts in the mean model and residual model (i.e. the correlation between behavioural mean and rIV) for both diurnality and movement distance, the among-individual correlation of behavioural means (i.e. behavioural syndrome), and the among-individual correlation of rIVs. The response variables movement distance and diurnality were analysed using a Gaussian distribution after being standardised (mean = 0, SD = 1) to facilitate model fitting. Because some days were missing behavioural measures for either diurnality or movement distance, we fitted each model to the subset maximising the number of days with behavioural measures (diurnality $n = 7,532$, movement distance $n = 7,485$). Among individual differences and regression coefficients for fixed effects were estimated on the subset of days for which data of the given behaviour were available while among individual correlations of means and rIV were based on days with behavioural measures for both diurnality and movement ($n = 6,835$).

2.2.1 | Mean model

We included diurnality and daily movement distance as response variables with similar fixed and random effects model structures into a multivariate mixed model to model differences in average behaviour. For both, diurnality and daily movement, we added a population intercept (β_0) and controlled for the effects of the shortening daylength gradient (as a linear effect over ordinal day of year, Z-transformed to mean = 0 and SD = 1), reproductive status (solitary, with cubs, or with 1-year-old offspring) and their interactions by fitting these terms as fixed effects. In addition, we controlled for a linear effect of age on daily movement distance. For diurnality, data exploration suggested a decrease in diurnal activity for younger bears and we therefore allowed the effect of age (Z-transformed to mean = 0 and SD = 1) to vary within age categories of younger bears (3–4 years old) and adult bears (>4 years old).

To decompose behavioural variance which cannot be explained by the models’ fixed effects into short-term (annual scale) and long-term (multiannual scale) effects, we fitted random intercepts for each year a bear was monitored (BearYear, observation year nested in individual) and for each individual (BearID). We accounted for individual level variation in seasonal shifts in behaviour with random slopes (slope.day) over ordinal day of year for BearYear and BearID respectively (Figure S2). There are no systematic effects of study

year on diurnality or movement behaviour (Hertel, Leclerc, et al., 2019), and we therefore did not include a year effect in the model. Please refer to the Supporting Information, Equations S1–S3 for a mathematical notation of the mean model and covariance. Note that the mean part of a DHGLM does not contain a term for the residual variance, since this term is modelled separately in the ‘dispersion’ part of the model.

2.2.2 | Dispersion model

We modelled the residual standard deviation of each diurnality and movement distance measure (on the log scale). We added a population intercept (γ_0) and included age (scaled) and reproductive status as fixed effects in the dispersion part of the model. We fitted random intercepts for BearYear and BearID. The dispersion model hyperparameter ω^2 reflects, on the log scale, how strongly individuals (ω^2_{BearID}) or monitoring years ($\omega^2_{\text{BearYear}}$) differ in their residual standard deviation, measured on the log scale (fig. 3 in Cleasby et al., 2015). It allows to assess the consistency of individual differences in predictability through time (Mitchell et al., 2016).

We estimated the full correlation matrix among all random effects, that is, the random intercepts and random slopes of the bivariate mean model and the random intercepts of the bivariate dispersion model, on both the observation year (BearYear) and individual (BearID) level. Please refer to the Supporting Information S5, Equations S1–S6 for a mathematical notation of the mean model, dispersion model and their covariance. Due to the aim of this paper we concentrate on correlations between behavioural type and predictability and on cross-trait among-individual correlation of behavioural means (i.e. behavioural syndrome) and rIIV (i.e. predictability syndrome) in the main test. We report the full correlation matrix of the fitted model in the Supporting Information S6.

Environmental covariates like home range habitat composition, or road density had no effect on mean or rIIV of movement or diurnality behaviour and were therefore not included in the model presented in the main part of the manuscript (Figure S4).

2.2.3 | Priors and model validation

Given that response variables were Z-transformed (mean = 0, SD = 1) we used weakly informative normal priors ($N(0, 1)$) for fixed effects, half-normal priors ($N(0, 1)$) for random effects, and an LKJ(2)–correlation prior for the correlation of random effects (McElreath, 2020). We ran four chains to evaluate convergence which were run for 10,000 iterations, with a warmup of 6,000 iterations and a thinning interval of 4. All estimated model coefficients and credible intervals were therefore based on 4,000 posterior samples and had satisfactory convergence diagnostics with $\hat{R} < 1.01$, and effective sample sizes >400 (Vehtari et al., 2020).

Posterior predictive checks recreated the underlying Gaussian distribution of distance moved well but did not perfectly capture the data distribution of daily diurnality. As mentioned in the introduction, non-normality of data can affect mean–variance relationships. We therefore refitted the model with a log-transformed response variable (not shown) which confirmed that our model conclusions using a Gaussian distribution were robust. Importantly, this last step confirmed that any correlation between behavioural type and predictability is unlikely to be a mathematical artefact generated by data distributions deviating from normality. Specifically, movement data (which are strictly positive and bound by 0) were normally distributed and average values were far from the lower bound of 0. We report the mean and 95% credible intervals, calculated as the highest posterior density intervals, for all parameters in our statistical models to assess whether parameters were statistically different from 0. All statistical analyses were performed in R 4.0.0 (R Core Team, 2020). Primary data and code to reproduce all analyses are provided under (Hertel & Royauté, 2020).

2.3 | Short-term and long-term behavioural repeatability and behavioural types

Each bear had year specific intercepts for each year it was monitored (BearYears) and one individual specific intercept (BearID). We calculated intercept repeatability (R_{int} , Equation 2), a standardised index representing the proportion of variance (V) across all BearYears that is explained by long-term consistency of individuals (Araya-Ajoy et al., 2015).

$$R_{\text{int}} = V_{\text{BearID}} / (V_{\text{BearYear}} + V_{\text{BearID}}). \quad (2)$$

Behavioural measures taken closely in time (i.e. within a BearYear) are often more similar (Bell et al., 2009) because prevailing environmental conditions are temporally autocorrelated. Our hierarchical approach allowed us to partition repeatability into its short-term within-year (BearYear) and long-term across-year (BearID) components. We calculated the unconditional long-term repeatability (Equation 3) and the conditional short-term repeatability (Equation 4), that is, conditional on time-related change over monitoring years, for movement and diurnality (Araya-Ajoy et al., 2015).

$$R_{\text{long-term}} = V_{\text{BearID}} / (V_{\text{BearYear}} + V_{\text{BearID}} + V_{\text{residual}}). \quad (3)$$

$$R_{\text{short-term}} = (V_{\text{BearYear}} + V_{\text{BearID}}) / (V_{\text{BearYear}} + V_{\text{BearID}} + V_{\text{residual}}). \quad (4)$$

Mind that conversely to classic mixed effects model, the residual variance (V_{residual}) here refers to the population intercept of the residual model (γ_0). We converted this intercept into a variance by taking its exponent and squaring the resulting value since the dispersion model uses a log scale to estimate residual standard deviations.

We also calculated repeatability of individual random slopes (slope. day) to assess whether individuals showed long-term consistency in

their temporal adjustment of behaviour over the 50-day study period (Equation 5).

$$R_{\text{slope}} = V_{\text{BearID.slope-day}} / (V_{\text{BearYear.slope-day}} + V_{\text{BearID.slope-day}}). \quad (5)$$

We extracted long-term individual behavioural types for diurnality and movement as the mean and credible interval of the posterior distribution of the random intercept for each individual. Short-term behavioural types were calculated by summing the predicted value of the random intercept BearYear to the predicted value of the random intercept BearID of the given individual and we extracted the mean and credible interval of this posterior distribution. The model was fitted on Z-transformed response variables. To facilitate ecological interpretation we added the population level intercept and coefficients of important covariates (i.e. reproductive status) to the random intercept and back transformed the resulting 'realised' behavioural type onto the original scale (i.e. km and diurnality index units).

2.4 | Short-term and long-term individual predictability

We estimated individual variation in predictability over short time-scales (i.e. within one BearYear) and over long time-scales (i.e. BearID) as the coefficient of predictability (CV_p , Equation 6). CV_p is a standardised metric quantifying among BearID and among BearYear variation in the predicted standard deviation from the mean residual standard deviation (rIIV).

$$CV_p = \sqrt{(\exp(\omega^2) - 1)}. \quad (6)$$

We extracted the posterior distribution of the rIIV for each level of the random intercept of BearID as an indicator for long-term behavioural predictability. Similar to the behavioural type, short-term behavioural predictability was calculated by summing the rIIV for a given BearYear and the respective random intercepts for the corresponding individual (BearID). When rIIV is high, the residual standard deviation around the behavioural mean is high indicating higher behavioural variability. rIIV is estimated on the log scale, for biological interpretation we added the population level mean standard deviation (intercept) and coefficients of reproductive status to rIIV, and exponentiated and back transformed the resulting 'realised' rIIV to facilitate biological interpretation of individual variation in residual standard deviation of behaviour.

2.5 | Correlation of behavioural type and behavioural predictability

We extracted the mean and 95% credible interval for the among-individual correlation of behavioural means and predicted standard deviation of residual variance (rIIV) on the short-term scale (BearYear), and on the long-term scale (BearID).

2.6 | Behavioural syndrome, predictability syndrome

We extracted the mean and 95% credible interval for the among-individual correlation of behavioural means on the short-term scale (BearYear), and on the long-term scale (BearID). We extracted the mean and 95% credible interval for the among-individual correlation of rIIVs of diurnality and movement on the short-term scale (BearYear), and on the long-term scale (BearID).

Since reproductive status (three-level factor) was an important covariate in the model, with solitary bears as reference level in the intercept, repeatability, CV_p estimates and correlations among variance components are reflective of solitary bears. We refitted the model with a dummy-centred covariate for reproductive status, producing estimates for an average bear (irrespective of reproductive status). All estimates were almost identical for solitary bears and an average bear (Supporting Information S7, Table S2).

3 | RESULTS

We analysed data of 62 female brown bears (BearID) monitored over 187 monitoring years (BearYears) with 1–12 monitoring years per individual (Figure S1). Within a given bear monitoring year, we recorded daily movement distance on 7–50 days (median 41 days) and diurnality on 13–50 days (median = 42 days). Bears ranged in age between 3 and 25 years in a given monitoring year (Figure S1). The average daily movement distance for solitary females was 8.5 km (back-transformed intercept for movement β_0 in Table 1 and centred at the 25th of July). Females moved over shorter distances when accompanied by cubs of the year (back-transformed $\beta_0 + \beta_{\text{StatusCub}} = 6.3$ km) or yearling offspring (back-transformed $\beta_0 + \beta_{\text{StatusOffspring}} = 7.7$ km, Figure S6). Solitary females moved over shorter distances later in the season, while females with 1-year-old offspring and females with cubs of the year increased daily movement distances over the autumn ($\beta_{\text{Ordinal day} \times \text{Status}}$, Table 1). Daily movement distances decreased slightly with age (β_{Age} , Table 1).

On the population level, solitary females distributed activity equally into the dark and light hours of the day (back transformed intercept for diurnality $\beta_0 = -0.04$, Table 1), whereas females accompanied by offspring (back-transformed $\beta_0 + \beta_{\text{Offspring}} = 0.22$) and in particular females accompanied by cubs of the year (back-transformed $\beta_0 + \beta_{\text{StatusCub}} = 0.28$) were considerably more diurnal (Figure S6). All females increased diurnality with shortening day length over the season ($\beta_{\text{Ordinal day}}$, Table 1). Diurnality initially decreased for 3–4-year-old bears but was unaffected by age in adult bears ($\beta_{\text{Age:ageclass}}$, Table 1).

3.1 | Short-term and long-term behavioural repeatability and behavioural types

Bears were highly consistent in their diurnality behaviour over time ($R_{\text{int.diurnality}}$ mean [95% credible interval] = 0.72 [0.6, 0.83]) but less consistent in their daily movement distance ($R_{\text{int.movement}} = 0.34$

	Movement distance	Diurnality
Mean model		
<i>Fixed effects</i>		
Intercept	0.21 [-0.12, 0.30]	-0.18 [-0.35, -0.02]
Ordinal day	-0.1 [-0.14, -0.06]	0.26 [0.21, 0.32]
Status		
Cubs	-0.73 [-0.88, -0.58]	0.92 [0.76, 1.08]
Offspring	-0.27 [-0.52, -0.04]	0.76 [0.5, 1.02]
Ordinal day × status		
Ordinal day × cubs	0.34 [0.26, 0.41]	-0.08 [-0.19, 0.02]
Ordinal day × offspring	0.17 [0.06, 0.29]	0.1 [-0.06, 0.26]
(movement) age	-0.13 [-0.2, -0.04]	
(diurnality) age:ageclass		
Age:subadult		-0.25 [-0.43, -0.07]
Age:adult		0 [-0.12, 0.13]
<i>Random effects</i>		
Among BearID		
$sd_{intercept.BearID}$	0.24 [0.15, 0.34]	0.56 [0.44, 0.69]
$sd_{slope.day}$	0.07 [0.01, 0.12]	0.11 [0.01, 0.19]
$r_{intercept-slope}$	-0.08 [-0.62, 0.56]	0.01 [-0.49, 0.49]
Among BearYear		
$sd_{intercept.BearYear}$	0.34 [0.29, 0.4]	0.34 [0.3, 0.4]
$sd_{slope.day}$	0.15 [0.12, 0.18]	0.23 [0.19, 0.27]
$r_{intercept-slope}$	-0.32 [-0.54, 0.08]	0 [-0.23, 0.22]
Dispersion model		
<i>Fixed effects</i>		
Intercept	-0.21 [-0.26, -0.15]	-0.56 [-0.62, -0.5]
Status		
Cubs	-0.4 [-0.51, -0.29]	0.24 [0.14, 0.34]
Offspring	-0.3 [-0.46, -0.13]	0.18 [0.02, 0.34]
Age	-0.01 [-0.06, 0.05]	-0.02 [-0.07, 0.04]
<i>Random effects</i>		
Among BearID		
ω^2_{BearID}	0.12 [0.05, 0.19]	0.16 [0.11, 0.21]
$r_{intercept.BearID-\omega_{BearID}}$	0.44 [-0.06, 0.8]	0.7 [0.39, 0.9]
Among BearYear		
$\omega^2_{BearYear}$	0.23 [0.2, 0.27]	0.22 [0.19, 0.26]
$r_{intercept.BearYear-\omega_{BearYear}}$	0.68 [0.54, 0.8]	0.27 [0.07, 0.46]

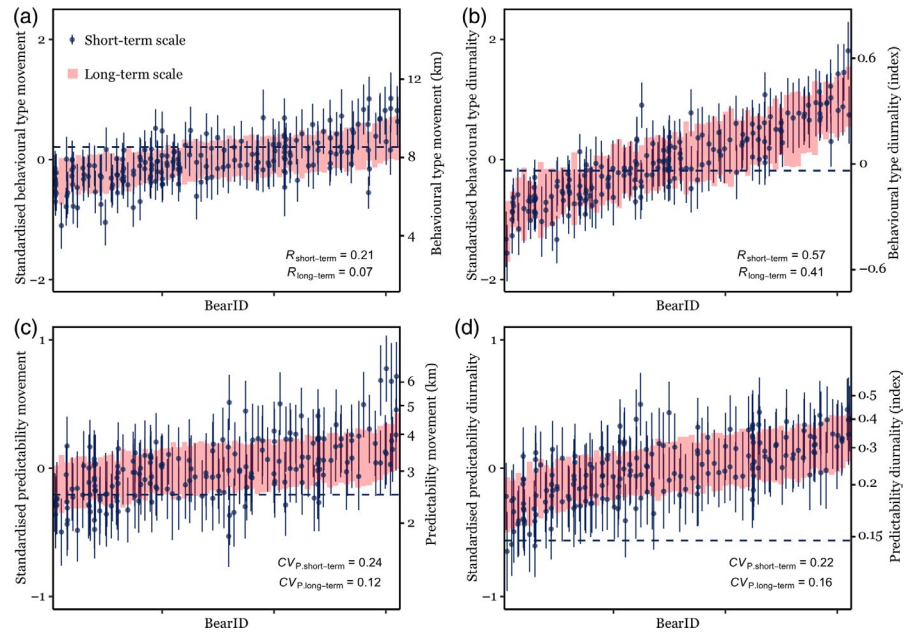
TABLE 1 Estimates and 95% credible intervals (in parentheses) of fixed and random effects on daily movement distance and diurnality (mean model) and residual standard deviation of daily movement distance and diurnality (dispersion model) in brown bears. Variation in mean behaviour and residual standard deviation of behaviour (rIIV) was estimated among bear monitoring years (BearYear) and among individuals (BearID). The correlation between mean behaviour and rIIV was calculated on both the BearYear and BearID level. Estimates are based on double hierarchical mixed models. Italics indicate estimates which were not different from 0 based on their 95% credible intervals

[0.15, 0.55]). This means that individual differences in diurnality were maintained across study years ($R_{BearID.diurnality} = 0.41$ [0.31, 0.53]). In contrast, individual differences in daily movement distance were only repeatable over a yearly period but did not carry over long, multi-year periods ($R_{BearID.movement} = 0.07$ [0.02, 0.12]). When controlling for time-related change in behaviour across monitoring years, short-term repeatability for both diurnality and movement increased markedly ($R_{BearYear.diurnality} = 0.57$ [0.49, 0.65], $R_{BearYear.movement} = 0.21$ [0.16, 0.26]). This confirms that behavioural observations within a year were more similar than observations across years and corroborates the

need to account for a temporal hierarchical structure in the model. Variance partitioning therefore suggested that diurnality was conserved over long time-scales within an individual, whereas movement was only repeatable on an annual time-scale.

Individuals in a given year differed in the rate at which they adjusted movement and diurnal activity over the 50-day study period (Among BearYear: $sd_{slope.day}$ in Table 1; Figure S3) but temporal adjustments were only weakly repeatable over multiple years ($R_{slope.movement} = 0.2$ [0, 0.41], $R_{slope.diurnality} = 0.19$ [0, 0.41]). There was no relationship between the average behaviour of a bear in

FIGURE 2 Behavioural type (a–b) and behavioural predictability (c–d) for daily movement distance (a, c) and diurnality (b, d) in 49 female brown bears followed over 174 monitoring years. Red shaded boxes indicate the 95% credible interval for long term, that is, multiannual behavioural types (measured as behavioural means, a–b) and behavioural predictability (measured as residual intra-individual variability, rIIV, c–d). Circles and error bars indicate the mean and 95% credible interval for short term, that is, annual estimates. Estimates are grouped by individual and sorted by multiannual estimates. Behaviours were Z-transformed for model fitting and rIIVs are estimated on the log scale, the second y-axis shows estimates in original units (i.e. km and diurnality index units)



a given year and its rate of change in behaviour over the 50-day study period (Among BearYear: $r_{\text{intercept-slope}}$, Table 1).

Behavioural types therefore varied from individuals which moved less on average than the population average to ones that moved more on average, but individuals were also capable of adjusting their movement patterns across multiple years (Figure 2a). To illustrate the magnitude of this variability: the individual that moved most on average in any given monitoring year moved three times longer daily distances (11.7 km, a solitary female) than the individual that moved least (3.9 km, a female with cubs of the year, Figure S6). However, when averaging these patterns over multiple years of tracking, this discrepancy decreased to a 1.3-fold difference (behavioural type gradient from an average of 7.4 km to an average of 9.6 km for the least and most moving individual, respectively, Figure S6). Patterns of individual variation were much more conserved for diurnality where individual behavioural types ranging from more nocturnal to more diurnal individuals showed little among year variability (Figure 2b).

3.2 | Short-term and long-term individual predictability

The population level mean residual standard deviation was estimated to be 2.5 km for movement (back-transformed intercept of the dispersion model $\exp(y_0) = 0.21$) and 0.19 for diurnality (back-transformed intercept of the dispersion model $\exp(y_0) = -0.56$, Table 1). Females with cubs of the year and females accompanied by 1-year-old offspring were more predictable in their movement distance than solitary females (y_{Status} , Table 1; Figure S6). Contrarily, females with cubs of the year were less predictable in their diurnality behaviour than solitary females or females with 1-year-old offspring (y_{Status} , Table 1; Figure S6). Bear age did not affect predictability (y_{Age} , Table 1). The predicted standard deviation

from the mean residual standard deviation (rIIV) for movement varied across individuals (ω^2_{BearID} , Table 1, $CV_{P\text{BearID.movement}} = 0.12$ [0.06, 0.19]) and across bear monitoring years ($\omega^2_{\text{BearYear}}$, Table 1, $CV_{P\text{BearYear.movement}} = 0.24$ [0.2, 0.28]), demonstrating differences in the behavioural predictability of movement across individuals and monitoring years (Figure 2c). The most predictable individual in a given monitoring year had a standard deviation of 1km around its behavioural mean for daily movement distance (a female with cubs of the year). On the other extreme, the least predictable individual in a given year had a standard deviation of 5.4 km (a solitary female, Figure S6). Individual differences in predictability were less pronounced on the long-term multi-annual scale and ranged from a standard deviation of 2.2 km to 3km around an individual's average behavioural type (Figure S6). Similarly, we found evidence for differences in predictability among individuals ($CV_{P\text{BearID.diurnality}} = 0.16$ [0.1, 0.21]) and among monitoring years ($CV_{P\text{BearYear.diurnality}} = 0.22$ [0.19, 0.26], Figure 2d) for diurnality. The standard deviation from the average behavioural type ranged from 0.11 for the most predictable individual in a given year to 0.39 for the least predictable individual in a given year (a female with cubs, Figure S6). Individual predictability for diurnality was similar over multiple monitoring years and ranged from 0.15 to 0.25. Long-term among-individual differences in behavioural predictability were therefore stronger for diurnality than for movement.

3.3 | Behavioural predictability correlates with behavioural type

Movement behavioural type was correlated with movement predictability at both temporal scales (long-term scale: $r_{\text{intBearID}-\omega\text{BearID.movement}} = 0.45$ [0.01, 0.84], Table 1; Figure 3a, annual scale: $r_{\text{intBearYear}-\omega\text{BearYear.movement}} = 0.68$ [0.55, 0.81], Table 1; Figure 3b). Individuals which moved over

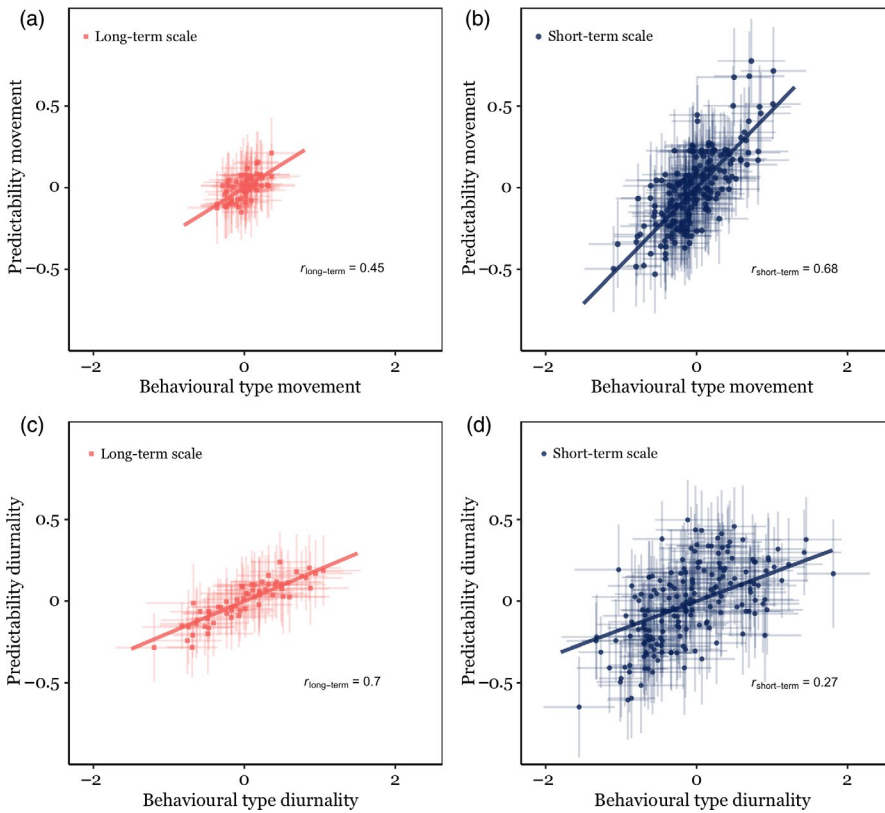


FIGURE 3 Among individual correlation (r) between behavioural type and behavioural predictability in movement (a and b) and diurnality (c and d). Long-term posterior means and 95% credible intervals are shown in red (a, c) and short-term posterior means and 95% credible intervals are shown in blue (b, d)

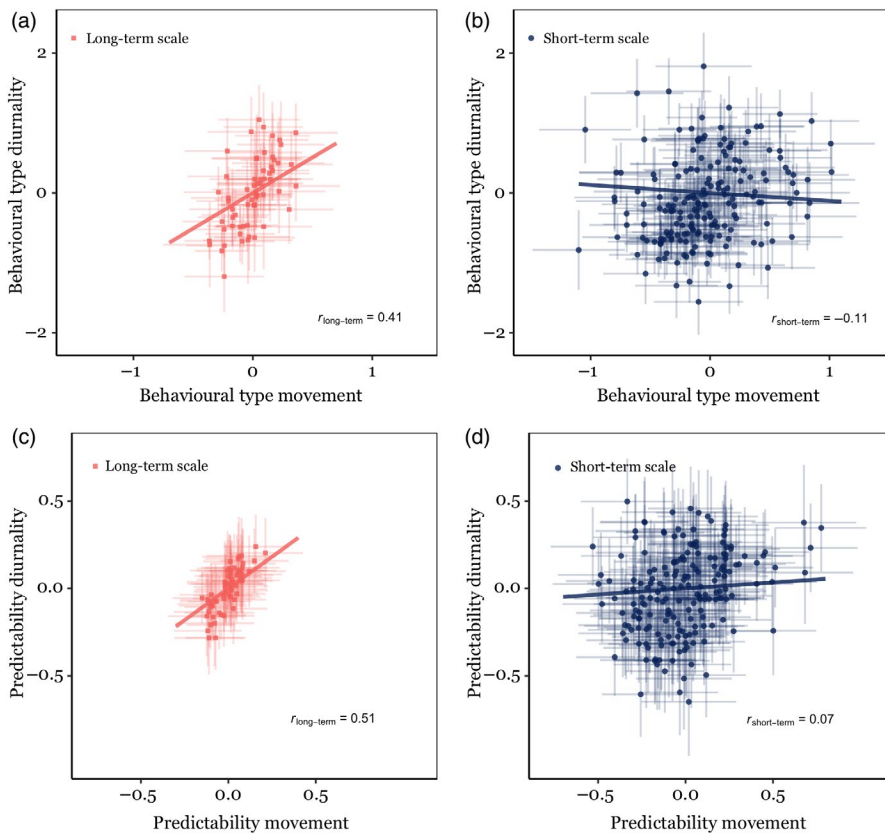


FIGURE 4 Among-individual correlation (r) of movement and diurnality behaviour types (i.e. behavioural syndrome, a and b) and among individual correlation (r) of behavioural predictability in movement and diurnality (c and d). Red squares represent multiannual posterior means and 95% credible intervals of behavioural types (a) and behavioural predictability (c) in movement and diurnality. Red lines show the multiannual correlation. Blue circles represent annual posterior means and 95% credible intervals respectively (b, d)

longer daily distances on average were therefore less predictable in their behaviour as indicated by a higher rIIV value. In contrast, sedentary individuals which moved over shorter daily distances on average

also had also more predictable daily movement distances. Similarly, nocturnal individuals were more predictable, whereas diurnal individuals were more unpredictable. This trend was mostly expressed

over the long-term scale ($r_{\text{intBearID} \sim \omega \text{BearID} \cdot \text{diurnality}} = 0.7$ [0.44, 0.93], Table 1; Figure 3c) but decreased substantially on an annual basis ($r_{\text{intBearYear} \sim \omega \text{BearYear} \cdot \text{diurnality}} = 0.27$ [0.08, 0.47], Table 1; Figure 3d) suggesting that bears adjust their diurnal activity to yearly conditions.

3.4 | Behavioural syndrome and predictability syndrome

We found a positive among-individual correlation between average daily movement distance and average diurnality ($r_{\text{intBearID} \cdot \text{movement} \sim \text{intBearID} \cdot \text{diurnality}} = 0.41$ [0.08, 0.76]). Individuals that moved over short daily distances were more nocturnal while individuals that moved over longer daily distances were more day active (Figure 4a). The correlation was entirely based on long-term individual effects and a short-term within-year correlation was not supported ($r_{\text{intBearYear} \cdot \text{movement} \sim \text{intBearYear} \cdot \text{diurnality}} = -0.11$ [-0.31, 0.09], Figure 4b). Likewise, we found a behavioural predictability syndrome. Movement–unpredictable individuals (i.e. high rIIV) were also more unpredictable in their diurnality behaviour compared to individuals with predictable daily movement distances and diurnality ($r_{\omega \text{BearID} \cdot \text{movement} \sim \omega \text{BearID} \cdot \text{diurnality}} = 0.51$ [0.09, 0.87], Figure 4c). Similar to the behavioural syndrome described above, this predictability syndrome was solely generated by long-term individual differences (short-term correlation: $r_{\omega \text{BearYear} \cdot \text{movement} \sim \omega \text{BearYear} \cdot \text{diurnality}} = 0.07$ [-0.13, 0.28], Figure 4d).

4 | DISCUSSION

We here demonstrate that individuals may not only vary in their average behavioural type but also in their behavioural predictability around that behavioural type. Using accelerometer and movement data of brown bears we reveal a continuum from predictable to unpredictable individuals for daily movement distance and diurnal activity. For example, the standard deviation around an individual's average daily movement distance varied up to fivefold from 1.1 to 5.5 km across individuals. Importantly, behavioural predictability was correlated with the average behavioural type. Furthermore, behavioural types and behavioural predictability were positively correlated for both traits. For example, a more predictable individual had an average daily movement distance of 7.4 km with a predicted standard deviation of 2.3 km and was on average more nocturnal (-0.27) with little variation (0.16). A less predictable individual on the other hand moved 9.6 ± 3 km and was on average more diurnal (0.26) but also less predictable in when during the day it was active (0.24). Our findings show evidence for a to-date little studied aspect of individual differences, that is, among individual differences in behavioural predictability.

We here show that movement data can reveal significant individual variation in behavioural predictability as they record behaviour of many members of a population over long monitoring durations (Hertel et al., 2020) offering the opportunity to receive numerous repeated measures, a prerequisite when studying

predictability (Cleasby et al., 2015). This finding is important given that a key assumption of mixed models, the common analytical approach in animal personality studies, is that individuals are homogenous in variance around their individual means (Cleasby et al., 2015; Schielzeth et al., 2020). Our results highlight that this assumption is not met under realistic field conditions. Whether and how such variation in predictability is linked to mean behavioural types is still poorly understood. As predicted based on the ecology of our species, behavioural predictability was not randomly distributed among the expression of behavioural types, but variability around the behavioural type systematically increased towards more diurnal and mobile behavioural types. Our findings contradict previous results obtained in the laboratory where more active individuals tend to be predictable and less active individuals unpredictable (Mitchell et al., 2016). More diurnal and mobile bears are more likely to encounter humans and could hence be considered as more risk-taking compared to nocturnal and less mobile bears. Indeed, our observed pattern of systematic variation in predictability across a behavioural type gradient which enhances disturbance risk could have two alternative explanations. Either, diurnal bears simply encounter more disturbances (Ordiz et al., 2013), which were not statistically accounted for in the model and the observed pattern of higher variance around the diurnal behavioural mean could be entirely explained by behavioural plasticity (Westneat et al., 2015). In this case, a complete model accounting for these unknown human encounters would explain the observed pattern and no among-individual variation in predictability should remain. Alternatively, the increased behavioural variability of diurnal individuals could be an anticipatory predator, that is, human, avoidance strategy. Unpredictable behaviour is a mechanism to reduce predation risk (Briffa, 2013; Humphries & Driver, 1970) and for diurnal individuals which face a higher risk of encounters, displaying unpredictable movement and temporal behaviour could be an adaptive strategy to prevent a predator from anticipating its future behaviour (Richardson et al., 2018). Although the literature suggests that risky and bold individuals lack inhibitory control and are hence more predictable, while shy individuals react more sensitive to changes in the environment (Coppens et al., 2010), this does not seem to be the case in our study system. We suggest that in the wild, where risky behaviour may come at a realised cost of disturbance and mortality female bears trade-off riskier diurnal behaviour with greater flexibility to switch to an alternate safer (i.e. nocturnal) behaviour (Moiron et al., 2020). We, however, acknowledge that our evidence is limited to one study system and we are unable to conclusively disentangle the two alternative explanations of an incomplete model or an adaptive response. Additional models that accounted for differences habitat structure—including anthropogenic features enhancing human access within a bear's home range (i.e. road and housing density)—did not affect our estimates of predictability (Supporting Information S3, Figure S4). This suggests that unpredictability is not caused by stochastic encounters with humans but likely represent a true behavioural adaptation to elevated human

encounter risk. Environmental similarity among bear home ranges also failed to explain behavioural similarity (Figure S5). However, bears in our study area inhabit a relatively homogenous landscape. In populations with more pronounced environmental gradients, including for example predator density, variation in the environment could, however, explain variation in both average behaviour and predictability. Our results would therefore have to be contrasted across population with varying levels of environmental heterogeneity in order to conclude on the generality of patterns between behavioural types and behavioural predictability in risky behaviours in the wild.

Past studies have examined the ramifications and ecological importance of behavioural predictability as degree of specialisation on the among-species level for population survival and fitness. In these studies, behavioural generalist species have been frequently shown to be more successful under changing environmental conditions than specialist species. For example, bird species with more behavioural flexibility, have a higher invasion success (Sol et al., 2002), are more successful in coexisting with humans in urban environments (Sol et al., 2013), and persisting in fragmented landscapes (Devictor et al., 2008). In many cases, behavioural flexibility will also be a deciding factor whether a species can adapt to warming temperatures (Beever et al., 2017). On the other hand, specialist species tend to be more successful and have higher reproductive output under more constant conditions (Kassen, 2002). All these examples support the idea that intraspecific variation in behavioural predictability could have similar important consequences for population persistence, that is, that predictable individuals may fair better under static environmental conditions and vice versa. Several studies have convincingly shown that greater spatial flexibility is a more successful strategy in changing environmental conditions using measures of foraging specialisation (Abrahms et al., 2018; Harris et al., 2020; Wakefield et al., 2015). For example, in northern elephant seals, individuals specialised on low exploration and high foraging site fidelity coexist with individuals specialised on high exploration and low foraging site fidelity (Abrahms et al., 2018). These alternative strategies provided foraging benefits under contrasting environmental conditions with individuals showing high site fidelity outperforming individuals with low site fidelity under normal climatic conditions and the latter faring better under anomalous conditions. This is in line with studies showing that more exploratory and more active behavioural types are also more tolerant towards landscape fragmentation or urbanisation (Atwell et al., 2012; Breck et al., 2019; Lowry et al., 2013). Such challenging environments may also require greater behavioural flexibility because if individuals living in close proximity to humans were at the same time risky and predictable they could more readily come into conflict with humans and face higher mortality (Poessel et al., 2013) which is consistent with our findings.

Animal personalities are often treated as lifetime properties of individuals, for example when behavioural types are related to life-history traits (Biro & Stamps, 2008). Yet, repeatability estimates tend to decrease with longer time intervals between measures (Bell et al., 2009). Behavioural types may therefore change

within the lifetime of an individual as a result of learning (Stamps & Groothuis, 2010), epigenetic modification (Trillmich et al., 2018), responses to environmental conditions (Dingemanse et al., 2010), or ageing (Araya-Ajoy & Dingemanse, 2017). Partitioning behavioural variation into its short-term and long-term sources, in our case annual and multiannual monitoring scales, helps understand at which temporal scales behavioural variation is most strongly expressed (Araya-Ajoy & Dingemanse, 2017). We found that both the behavioural type and behavioural predictability were more pronounced within one monitoring year than across years for both behaviours. Nonetheless, diurnality was a stronger long-term individual trait than daily movement distance. Inter-annual fluctuations in food abundance (Hertel, Zedrosser, et al., 2019) or shifts in home range size from year to year (Frank et al., 2018) could explain the greater variance in movement than in diurnality. In line with our prediction, changing reproductive status between years drove changes in behavioural types and in behavioural predictability across monitoring years. Cubs restricted female movements, which resulted in lower average movement distances and higher predictability of movement. Conversely, females were more diurnal, most likely to avoid infanticidal males (Steyaert et al., 2013), but also more unpredictable in their diurnality when with cubs than when solitary.

Measures of residual intra-individual variability are particularly sensitive to unaccounted changes in behaviour (Westneat et al., 2015). It is therefore important to account for systematic changes in behaviour, that is, over the course of the study period or reproductive status, and to partition behavioural variance into short-term and long-term variability for a better understanding of drivers and temporal scales of behavioural predictability. Nevertheless, stochastic events in the environment, such as human encounters, may bias estimates of intra-individual variability because the resulting behavioural adjustments are pooled into the residual variance. We found no indication that anthropogenic features facilitating access of humans affect whether bears are predictable or unpredictable. Furthermore, the long monitoring time of 50 days should limit the effect of such stochastic events, in particular because behavioural predictability was conserved over multiple years. Although uncontrollable environmental effects are a limitation in field studies, we believe that studying behavioural predictability in the wild will offer a new aspect to the study of among-individual behavioural variation and might reveal trade-offs which are not present in the laboratory (Moiron et al., 2020).

5 | CONCLUSIONS

We here show that significant among-individual variation and among-reproductive class variation in predictability of routine movement and activity behaviours exist in a wild brown bear population, and that biologging data are a useful tool to reveal such variation. We document a syndrome where more diurnal individuals on average also moved longer daily distances and were less predictable in both of these behaviours than their nocturnal, sedentary and more predictable counterparts. This general syndrome

was disrupted in years when females had cubs of the year, most likely because cubs consistently constrain movement of females to shorter daily distances. At the same time females becoming more diurnal and unpredictable potentially trade-off risk of encountering infanticidal male bears with being disturbed by human. We propose that heightened behavioural unpredictability is an adaptation for individuals to maintain a diurnal and mobile behavioural type which increases the likelihood to encounter and be disturbed by humans. Behavioural predictability could therefore be a key trait facilitating how individuals cope with changing conditions in the Anthropocene. Our study highlights the power of biologging data as a key tool to reveal such variation.

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AUTHORS' CONTRIBUTIONS

A.G.H. and T.M. developed the work; A.G.H. performed the statistical analyses with input from R.R.; A.Z. provided the data; A.G.H. wrote the manuscript with help from T.M. and R.R. and input from all authors.

DATA AVAILABILITY STATEMENT

Data and R code to reproduce our results have been uploaded to the Open Science Framework and are publicly available under <https://doi.org/10.17605/OSF.IO/65DJR> (Hertel & Royauté, 2020).

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SUPPORTING INFORMATION

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