Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife

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Animal personality traits and the emergence of behavioural syndromes, i.e. between-individual correlation of behaviours, are commonly quantified from behavioural observations in controlled environments. Subjecting large and elusive wildlife to controlled test situations is, however, rarely possible, suggesting that ecologists should exploit alternative measures of behaviours for quantifying differences between individuals. Our goal was to test whether movement and space use data can be used to quantify behavioural syndromes in the wild. We quantified six behaviours from GPS and dual motion sensor tracking devices of 46 adult female brown bears followed in southcentral Sweden over the summer and early autumn. As well as daily travel distance, an indicator for activity, and daily displacement, an indicator for exploration, we quantified four behaviours that increase a bear's likelihood of encountering humans and could thus serve as indicators for boldness: diurnality, selection for roads and selection for two open habitat types, bogs and clearcuts, with low lateral cover. We tested (1) whether behaviours showed repeatable between-individual variation (animal personality) and (2) whether behaviours were correlated between individuals and thus formed a behavioural syndrome. Repeatability of behaviours ranged from 0.16 to 0.61 confirming between-individual variation in movement, activity and space use. A multivariate mixed model revealed significant positive correlations between travel distance, displacement and diurnality, suggesting the existence of an activity—exploration and potentially partial boldness syndrome in our bear population. Selection for exposed or human-frequented habitats were uncorrelated with the activity—exploration syndrome and with each other, albeit there was a trend for stronger road avoidance by bears that readily used clearcuts. We show that large tracking data sets can be used to quantify between-individual correlation in spatial behaviours. We suggest that delineating behavioural types from wildlife tracking data will be of increasing interest because of the importance of animal personality for ecological processes, wildlife conservation and human—wildlife coexistence.

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Animal personality, defined as repeatable between-individual variation in behaviour across context and time, is of growing interest in behavioural ecology and highlights that behaviours are not completely plastic because individuals are constrained to only express a limited range of the behavioural trait values present in the population (Dingemanse, Kazem, Réale, & Wright, 2010; Réale et al., 2010). Syndromes of repeatable behaviours, that is, between-individual covariation of behaviours, may thus constrain individuals to behave nonoptimally compared to others in some contexts, which can have important ecological and evolutionary implications because correlated behaviours cannot evolve independently (Dochtermann & Dingemanse, 2013; Sih, Bell, & Johnson, 2004). For example, repeatable between-individual variation in the propensity to take risks and to react proactively in risky situations,

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a personality trait termed boldness (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), has been linked to faster growth and increased reproductive success but reduced survival (Réale et al., 2007; Smith & Blumstein, 2008 and references therein). These relationships, however, can change in magnitude and direction depending on the environment (Boon, Réale, & Boutin, 2007) and thus call for a better understanding of behavioural syndromes of natural behaviours expressed in the wild. For example, individual variation in movement and space use behaviours facilitate spatial co-occurrence of behavioural types within wild populations and may thereby enhance their carrying capacity (Spiegel, Leu, Bull, & Sih, 2017; Wolf & Weissing, 2012).

Behavioural types are commonly determined by measuring behaviours in a set of standardized tests, such as the open-field test or the novel object test (Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Niemelä & Dingemanse, 2014; Sih et al., 2004). To study animal personality in wild populations, biologists therefore mostly adopt a two-step approach. First, wild animals are captured and tested multiple times to determine the repeatability of their behavioural responses. Second, animals are released and natural behaviours, life history traits or ecological processes are linked to their behavioural type (Niemelä & Dingemanse, 2014). A key limitation of this procedure is that it relies on the assumption that behaviour in a controlled test situation correlates with natural behaviours expressed in the wild (Archard & Braithwaite, 2010; Niemelä & Dingemanse, 2014). In addition, animals need to be manageable and conscious to be able to subject them to a test situation, which is challenging for studies of large and elusive wildlife (Patrick, Pinaud, & Weimerskirch, 2017). Most personality studies have therefore focused on small species or have been carried out in captivity (Bell, Hankison, & Laskowski, 2009; Haage, Bergvall, Maran, Kiik, & Angerbjörn, 2013). Researchers, therefore, need to exploit alternative measures of behaviour to assess personality traits in wild animals that cannot be subjected to controlled experiments. For example, Réale and Festa-Bianchet (2003) used a combination of trappability, behaviour during handling and behavioural observations in the natural environment as indices of personality traits in bighorn sheep, *Ovis canadensis*. Found and St. Clair (2016) used a combination of behavioural observations of natural behaviours, that is, location in the herd, social encounters and vigilance, and responses to novel stimuli to describe behavioural syndromes in elk, *Cervus canadensis*. Finding feasible and informative behavioural measures of personality may be even more challenging for elusive animals for which behavioural observations are rare or that live in inaccessible habitats. Especially in aquatic ecosystems, biologists have now started to use biotelemetry sensors to study personality-dependent spatial ecology in the wild (Finger et al., 2016; Harrison et al., 2015; Nakayama, Laskowski, Klefoth, & Arlinghaus, 2016; Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2017).

Even though animal personality and movement ecology are both fields in behavioural ecology, they have mostly developed in parallel and are still poorly intertwined (Spiegel et al., 2017). That is despite the fact that large data sets of GPS tracking data have accumulated over the last two decades (Cagnacci, Boitani, Powell, & Boyce, 2010), spanning numerous terrestrial, avian and aquatic taxa (Kranstauber et al., 2011). These data sets often feature simultaneous monitoring of many individuals in a population, over meaningful ecological time periods and environmental gradients. Under high temporal resolution of relocations, tracking data can be used to quantify spatial and movement behaviours with great detail (Cagnacci et al., 2010). It is therefore surprising that few studies have used tracking data to assess whether repeatable between-individual differences in space use and movement exist and whether spatial behaviours are correlated between individuals and

thus form behavioural syndromes (Leclerc et al., 2016; Patrick et al., 2017; Spiegel et al., 2017; Villegas-Ríos et al., 2017).

Here we quantified the degree of between-individual variation in a range of movement, timing of diel activity and habitat selection behaviours and further tested whether these behaviours are correlated and thus form a behavioural syndrome. We used a long-term GPS and activity monitoring data set of an elusive large carnivore, the European brown bear, *Ursus arctos*. For this population it has recently been shown that strength of selection for two open-canopy habitat types (bogs and clearcuts) differed between bears in a consistent fashion over 2–5 monitoring years (Leclerc et al., 2016). Also, Hertel, Swenson, and Bischof (2017) showed that bears differ in their diel activity pattern and that being nocturnal, diurnal or crepuscular was a repeatable behaviour over multiple years. Building on Leclerc et al. (2016) and Hertel et al. (2017) we here propose that behaviours quantified from tracking devices can not only inform repeatable between-individual variation in behaviours but may also reveal covariation between them and thus elucidate behavioural syndromes. Such a syndrome involving functionally distinct movement, activity and habitat selection behaviours would delineate behavioural types meaningful for ecological processes and bear–human interactions. We used data of solitary, adult females and quantified a set of six behaviours that are ecologically relevant to bears as they affect energy expenditure, forage intake and likelihood of bear–human encounters: daily travel distance, daily displacement, diurnality, selection for roads, selection for clearcuts and selection for bogs. We propose that these behaviours are indicative of some commonly quantified personality traits: activity, exploration and boldness. Daily travel distance, that is, the sum of hourly displacements, is a measure used to quantify individual variation in activity (Harrison et al., 2015; Nakayama et al., 2016). Individuals that travel over longer distances exploit local resources less thoroughly and use more energy for movement but potentially also encounter higher quality resource patches by moving more. Daily displacement distances, that is, the straight-line distance between the first and last position of the day, can be used to measure exploration for unpredictable food resources because individuals with greater displacement will encounter and cross more habitat patches per day than individuals with shorter displacement distances (Patrick et al., 2017; Réale et al., 2007). Diurnal activity is largely affected by the degree of human presence in many species (Gaynor, Hojnowski, Carter, & Brashares, 2018). Animals tend to shift their diel activity away from periods when their main predator is active (Lima & Dill, 1990), which in the case of bears are humans. Bears in our study area change their diel behaviour by becoming more nocturnal after human encounters (Ordiz et al., 2013). More diurnal, that is, day-active individuals, may therefore be regarded as bolder because they accept greater risks of encountering humans or human-related disturbances, such as traffic (Murray & St. Clair, 2015). Following the same rationale, selection for areas closer to roads may be indicative of individuals with a higher tolerance for encountering humans and traffic and can thus be regarded as boldness (Holtmann, Santos, Lara, & Nakagawa, 2017). Lastly, we investigated selection for two open-canopy habitat types: clearcuts and bogs. The selection of these habitat types can also be linked to bolder behaviour. First, less lateral cover should increase the risk of being detected by humans and could thus be regarded as boldness (Ciuti et al., 2012). Second, clearcuts are a high-risk–high-return habitat for bears foraging on berries. Berries are distributed unevenly in spatial clusters of high density on clearcuts, whereas they occur evenly but in lower densities in the surrounding forest matrix (Hertel et al., 2016). Bears that choose to forage on clearcuts should therefore be more exploratory in their foraging behaviour.

We predicted (1) that, while controlling for environmental drivers of behaviour, a significant part of the remaining variance would be attributed to repeatable between-individual variation in behaviour. If supported, this would suggest that, despite different ecological constraints during the active season, individual brown bears consistently express higher or lower values for a behaviour relative to other individuals. We further predicted (2) that the six behaviours will form an activity–exploration–boldness behavioural syndrome, where individuals that travel further, and have longer displacement distances, will also be more diurnal, more resilient towards roads and select more strongly for clearcuts and bogs. If supported, such a syndrome would mean that brown bears in central Sweden vary in their behavioural type along a gradient from movement-restricted individuals with more nocturnal activity patterns that spatially avoid detection by humans by selecting against roads and open habitats to active, exploratory and bold individuals that readily use open habitats and are more resilient towards roads.

METHODS

Study Area

We used data collected by the Scandinavian Brown Bear Research Project (SBBRP; www.bearproject.info) in southcentral Sweden (ca. 61°N, 15°E) as part of an ongoing, long-term, individual-based monitoring project. The population inhabits an intensely managed boreal forest composed of differently aged forest blocks, interspersed by open areas of recent clearcuts and bogs. Forest management leads to a dense network of forestry roads (1 ± 0.5 km/km^2, range 0–4.6 km/km^2, Ordiz, Kindberg, Sæbø, Swenson, & Støen, 2014). Human population density is low (4–7 inhabitants/km^2) and mainly concentrated in six settlement areas with recreational cabins scattered throughout the study area (Ordiz et al., 2014).

Data Collection

Bears were immobilized from a helicopter (Arnemo & Fahlman, 2011) and fitted with GPS–GSM neck collars with dual-axis motion sensors (Vectronics Aerospace GmbH, Berlin, Germany). 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 (Mattson's Inc., Milltown, MT, U.S.A.). We used data of a homogeneous demographic group of adult (≥ 4 years), solitary (i.e. without dependent offspring) female bears to avoid behavioural differences caused by, for example, dispersal (Støen, Zedrosser, Sæbø, & Swenson, 2006) or reproductive status (Steyaert, Kindberg, Swenson, & Zedrosser, 2013). We used GPS relocation data taken at 1 h intervals and acceleration data from dual-axis motion sensors averaged at 5 min intervals during six consecutive 10-day periods (P1–P6) during late summer: 21–30 June, 1–10 July, 11–20 July, 21–30 July, 31 July–9 August, 10–19 August 2007–2016, to repeatedly quantify movement and space use behaviours of the same bears within a year. The chosen time window starts after the bear mating season and ends before the bear hunting season which are both known to affect spatiotemporal movements of female bears (Ordiz et al., 2012; Steyaert, Swenson, & Zedrosser, 2014). The chosen behaviours are subject to known external drivers during these periods. For example, daylength is reduced by >4 h between 21 June and 19 August, and a gradient in berry abundance, an important food item for bears (Stenset et al., 2016), ranges from no berries at the end of June to a peak in berry production by mid-August (Frank et al., 2015; Hertel et al., 2016). For each bear in each period (P1–P6) we quantified six behaviours (see below) from

GPS relocation and activity data. We used these as response variables to calculate repeatability of behaviour and to explore the existence of a behavioural syndrome in which behaviours are correlated one to another. In the analyses, we only included data from individuals with at least 75% successful relocations and activity data, to get a complete set of all six behaviours, in at least three periods in a given year (Appendix Table A1).

Ethical Note

All animal captures and handling were performed in accordance with relevant guidelines and regulations and were approved by the Swedish authorities and ethical committee (Uppsala Djurförsöksetiska Nämnd: C40/3, C212/9, C47/9, C210/10, C7/12, C268/12, C18/15. Statens Veterinärmediciniska Anstalt, Jordbruksverket, Naturvårdsverket: Dnr 35-846/03, Dnr 412-7093-08 NV, Dnr 412-7327-09 Nv, Dnr 31-11102/12, NV-01758-14). The SBBRP follows a strict and tested capture protocol (Arnemo & Fahlman, 2011) which is approved by the Scandinavian authorities. The SBBRP has captured bears since 1984 and has carried out ca, 3000 captures and immobilizations. It has a capture-related mortality rate of <2% (Arnemo et al., 2006). All capture-related mortalities are reviewed by the State Veterinary Institute of Sweden to establish the cause of death and to improve capture techniques. The project is thus constantly working to refine existing techniques. Bears were darted from a helicopter in spring after den emergence (April–May). The time between first sighting of the bear until darting was usually around 15 min and should never exceed 30 min (Arnemo & Fahlman, 2011). After immobilization the bear's eyes were immediately covered to avoid stressful light stimuli and intranasal oxygen supplementation was routinely administered to avoid hypoxemia. Bears were constantly monitored during anaesthesia by an experienced team of wildlife veterinarians (Arnemo & Fahlman, 2011).

Behaviours

Mean daily travel distance and daily displacement

We calculated daily travel distances as the sum of Euclidian distances between consecutive GPS positions within a day. To not underestimate the cumulative daily travel distance, we only included days with at least 17 of 24 possible relocations. Failed GPS relocation attempts are mostly associated with dense canopy cover (Rempel, Rodgers, & Abraham, 1995) which is selected by bears for resting (i.e. no movement), and there was no systematic correlation between number of daily relocations and daily travel distance ($r = 0.04$). Daily displacement was calculated as the Euclidian distance between locations taken at 0000 at night. For each period we calculated the mean daily travel distance and mean daily displacement for bears with enough data on at least 7 days.

Diurnality

We estimated bear diurnality, corrected for daylight changes, using acceleration data. The diurnality index (from here on diurnality) was calculated according to Hoogenboom, Daan, Dallinga, and Schoenmakers (1984):

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

where AD and AN are the sums of the acceleration values during the day and night, respectively, and DD and DN are the durations of the day and night, respectively. The diurnality index varies between -1 (night active) and 1 (day active).

Road, clearcut and bog selection

We extracted habitat types from the Swedish Corine Land Cover (resolution 25 × 25 m) for all bear positions as well as 1000 random locations within a bear's annual home range.

We extracted the shortest Euclidian distance to the nearest road for all bear and random positions and calculated selection for roads as:

$$\text{road selection} = \frac{\text{mean distance to roads for random positions}}{\text{mean distance to roads for bear positions}} \quad (2)$$

We estimated selection ratios for bogs and clearcuts (<8 years since final felling) as:

$$\text{bog (or clearcut) selection} = \frac{\text{no. of bear positions in bogs(or clearcut)/total no. of bear positions}}{\text{no. of random positions in bogs(or clearcut)/total no. of random positions}} \quad (3)$$

Higher selection values of roads, clearcuts and bogs indicate stronger use of these habitats compared to random use. To control for habitat availability, we calculated road density as the total length (km) of roads intersecting each bear's annual home range, divided by its home range size. We calculated clearcut and bog availability in each bear's annual home range as the area covered by the respective habitat relative to the total home range size.

Statistical Analyses

Repeatability of behaviour

We first fitted univariate linear mixed models for each behaviour to evaluate whether bears show repeatable between-individual variation in movement and spatial behaviours. We used the R package lme4 (Bates, Maechler, Bolker, & Walker, 2014). We fitted bear identity (BearID) and study year (2007−2016) as random intercepts. We controlled for time period (P1−P6 continuous linear and quadratic effect) and age as fixed effects. We further controlled for linear functional responses in habitat selection by adding road density and availability of bogs and clearcuts within a bear's annual home range in models for road, clearcut and bog selection, respectively (Leclerc et al., 2016). This accounted for individual differences in behaviours that are caused by bears living in different landscapes (Leclerc et al., 2016). Because previous studies have found that road density restricts bear movement (Bischof, Steyaert, & Kindberg, 2017) and affects diel behaviour (Hertel et al., 2017; Ordiz et al., 2014), we controlled for road density within a bear's home range in models for travel distance, displacement and diurnality. We visually inspected the distribution of model residuals and square root-transformed road, clearcut and bog selection to normalize residuals. We assessed temporal autocorrelation remaining in the model residuals for each bear and year. There was no temporal autocorrelation present (Appendix Fig. A1). From the individual mixed-effect models, we estimated the population level adjusted between-individual repeatability (R) of each behaviour as:

$$R = \frac{s^2_{\text{BearID}}}{s^2_{\text{BearID}} + s^2_{\text{year}} + s^2_{\text{residual}}} \quad (4)$$

where R is the adjusted repeatability, s^2_{BearID} is the variance between individuals, s^2_{year} is the variance explained by consistent behavioural variation between study years and s^2_{residual} is the residual variance, i.e. the remaining variance within individuals. The sum of between-individual (BearID), interannual (year) and within-individual (residual) variation equals the total behavioural variation not explained by the fixed effects. We used the 'rptR' package in R (Schielzeth & Nakagawa, 2013) to calculate repeatability values, 95% confidence intervals (CI) and statistical significance of repeatability, assuming a significance level of $P < 0.05$.

Between-individual behavioural covariation

To explore whether behaviours are correlated between individuals, that is, whether they form a behavioural syndrome, we also fitted a multivariate mixed model with travel distance, displacement, diurnality and square root-transformed road, clearcut and bog selection as response variables using the R package 'MCMCglmm' (Hadfield, 2010). Response variables were scaled (mean = 0, SD = 1), facilitating model fitting. We controlled for the fixed effects of period (linear and quadratic) and age on all response variables, for the effects of clearcut and bog availability on clearcut and bog selection, respectively, and the effect of road density on road selection, travel distance, displacement and diurnality. Period, age, clearcut and bog availability and road density were scaled. We used the MCMCglmm default prior for the fixed effects, and an inverse-gamma prior for the residuals ($V = 1$, $\nu = 0.002$). We used an uninformative, parameter-expanded prior for the random effects BearID and year ($V = 1$, ν (nu) $= 2$, $\alpha\mu = 0$, $\alpha V = 625$) and ran the model for 840 000 MCMC iterations, with a burn-in of 40 000 and a thinning interval of 100. Estimated model coefficients and credible intervals were based on 8000 posterior samples. We inspected trace plots and calculated effective sample size using the R package coda (Plummer, Best, Cowles, & Vines, 2006) to ascertain mixing of chains and absence of autocorrelation between posterior samples. We calculated the mean for all pairwise correlations of behavioural variances following the approach of Houslay and Wilson (2017), by dividing the covariance between two behaviours by the product of the square roots of their variances. We performed an eigen decomposition on the between-individual covariance matrix revealing how much between-individual variation is explained by each eigenvector (principal component). We calculated the trait loadings of our six behaviours onto the first two eigenvectors. Credible intervals for correlations between eigenvector loadings were obtained from the MCMC chain by modifying bootstrap code from Houslay, Vierbuchen, Grimmer, Young, and Wilson (2017). All statistical analyses were performed in R 3.4.2 (R Core Team, 2018).

RESULTS

We used data from 42 adult females (age range 4−20 years, mean age: 8 years) followed for 1−6 monitoring years (a total of 87 monitoring years). Repeated measures, that is, the number of periods with enough data ranged from 4 to 27 per bear (mean = 10, median = 8; Appendix Table A1). The bears' annual home ranges featured road densities between 0.54 and 1.4 km/km² (average 1 km/km²), proportions of recent clearcuts between <1% and 8% (mean 4.5%) and proportions of bogs between 4.5% and 25% (mean

13%). Despite bears generally displaying a high home range fidelity over multiple monitoring years, we did detect home range shifts over time (Appendix Fig. A2; Frank et al., 2018). The average change in home range compositions over multiple years was an increase in road density of 0.05 km/km^2 (range 0−0.4 km/km^2), an increase in clearcut availability by 1.2% (range 0−7.7%) and an increase in bog availability by 2.6% (0−9.8%). In total, 4113 GPS days were included in the study with an average daily GPS fix success rate of 91% (17 positions: 124 GPS days; 18 positions: 262 GPS days; 19 positions: 236 GPS days; 20 positions: 522 GPS days; 21 positions: 330 GPS days; 22 positions: 1027 GPS days; 23 positions: 286 GPS days; 24 positions: 1308 GPS days).

Repeatability of Behaviours

We found significant between-individual variation for all movement and habitat selection behaviours (Table 1). Adjusted repeatabilities (i.e. conditional on the model's fixed effects) ranged from 0.16 to 0.61 for the six behaviours (Table 1). This means that 16−61% of the observed behavioural variation can be explained by consistent between-individual differences in behaviour (Fig. 1). Diurnality was the behaviour with the highest repeatability, while clearcut selection and road selection were least repeatable (Table 1). Displacement, travel distance and bog selection were intermediately repeatable (Table 1). We did not find that behaviours varied in a consistent fashion between study years (travel: $R = 0.03$ [95% confidence interval $= 0$, 0.07]; displacement: $R = 0.03$ [0, 0.09]; diurnality: $R = 0.05$ [0, 0.13]; road selection: $R = 0.08$ [0, 0.18]; clearcut selection: $R = 0.03$ [0, 0.09]; bog selection: $R = 0.04$ [0, 0.1]). Because we found significant between-individual variation in all six behaviours, we fitted a multivariate mixed model including all six behaviours as response variables to explore behavioural syndromes.

Behavioural Variation Explained by Population Level Fixed Effects

We here report extracted posterior mean estimates and credible intervals from the fixed-effect model structure of the multivariate mixed model. These estimates were qualitatively the same compared to estimates of the univariate mixed models (Appendix Table A2). The age of a bear had a weak effect on road selection (posterior mean $= 0.6$, 95% credible interval 0.01−0.31). Older bears used areas closer to roads than younger bears. No other behaviour was affected by age (95% credible interval of the variable age overlapped with 0) suggesting that adult female bears do not systematically change their movement and habitat selection behaviour with age. Bears avoided roads more strongly with increasing road density within their home range (posterior mean $= -0.31$, 95% credible interval −0.46−0.15; Fig. 2). We found no functional responses of habitat availability for clearcut or bog selection (Fig. 2). Finally, we found population level behavioural differences across the six time periods investigated (Fig. 3). Daily travel distance and

displacement decreased in a linear fashion over time (Fig. 3a and b). Individuals increased their diurnal activity as daylength decreased (Fig. 3c) and more strongly avoided areas close to roads later in autumn (Fig. 3d). They significantly increased their selection for clearcuts by the end of our study period and decreased their selection for bogs (Fig. 3e and f).

*Between-Individual Behavioural Correlation*

Because we found significant between-individual variation in all six behaviours, we fitted a multivariate mixed model including all six behaviours as response variables to explore behavioural syndromes. We found significant between-individual covariation and correlation between the behaviours travel distance, displacement and diurnality (Table 2, Appendix Fig. A3). Those individuals that moved over longer daily distances also had a greater displacement (correlation $= 0.83$, 95% credible interval $= 0.66-0.96$) and were more diurnal (correlation $= 0.40$, 95% credible interval $= 0.03-0.74$) than bears that travelled for shorter daily distances (Fig. 4). Longer daily displacement distances were likewise correlated with more diurnal activity (correlation $= 0.45$, 95% credible interval $= 0.09-0.75$; Fig. 4). There was a nonsignificant trend that those bears that selected for clearcuts more strongly had a less strong selection for roads (i.e. stronger road avoidance, correlation $= -0.40$, 95% credible interval $= -0.80-0.07$; Table 2 and Appendix Fig. A3). No other habitat selection behaviours were significantly correlated with either our movement−diurnality syndrome or with each other (Table 2). Adjusted repeatability values over the full range of behaviours calculated from the multivariate mixed model (Table 2) were similar to repeatability values from univariate mixed models (Table 1). The first three eigenvectors explained significant amounts of between-individual variation (eigenvector 1 $= 48\%$, 95% credible interval: 36−62%; eigenvector 2 $= 25\%$, 95% credible interval: 16−34%; eigenvector 3 $= 14\%$, 95% credible interval: 8−21%). Travel distance, displacement and diurnality were mainly reflected along the first eigenvector (Fig. 5). Road selection was reflected along the second eigenvector corroborating that it is uncorrelated with the existing syndrome. Clearcut and bog selection were not reflected along any of the first three axes (Fig. 5; eigenvector 3 not shown).

DISCUSSION

We have shown that relocation data from GPS tracking devices and activity sensors can be useful to detect behavioural syndromes in the wild without any human intervention. We were able to quantify personality traits (prediction 1) and detect correlations between those traits (prediction 2) from measures of natural movement and spatial behaviours. Movement and activity behaviours were moderately (0.26−0.28) to highly (0.61) repeatable, whereas repeatability of space use was lower (0.16−0.25; Bell et al., 2009). Specifically, we could identify an activity−exploration and partial boldness behavioural syndrome among three of the six behaviours evaluated: individuals that travelled over longer distances also had a further overall displacement and were more diurnal. However, other repeatable behaviours that we expected to correlate with this syndrome, such as selection for open areas of high potential human disturbance and perceived risk (roads, clearcuts and bogs; Stankowich & Blumstein, 2005), were uncorrelated. Moreover, bears that readily used open clearcuts tended to avoid roads more strongly, suggesting a potential trade-off between two risky behaviours. Our expectation that more active individuals should also be more exploratory and bolder, as expressed by a set of movement, diel activity and habitat selection behaviours, therefore did not entirely hold. Our results highlight that interpreting how spatial behaviours quantified in the wild reflect classical animal

Table 1
Repeatability estimates (R), 95% confidence intervals (CI) and P values of six movement and habitat selection behaviours extracted from wildlife tracking data of 42 female brown bears monitored in southcentral Sweden

Behaviour	R	95% CI	P
Travel distance	0.28	0.15−0.40	0.001
Displacement	0.26	0.14−0.38	0.001
Diurnality	0.61	0.46−0.72	0.001
Road selection	0.20	0.09−0.31	0.001
Clearcut selection	0.16	0.06−0.26	0.001
Bog selection	0.25	0.13−0.37	0.001
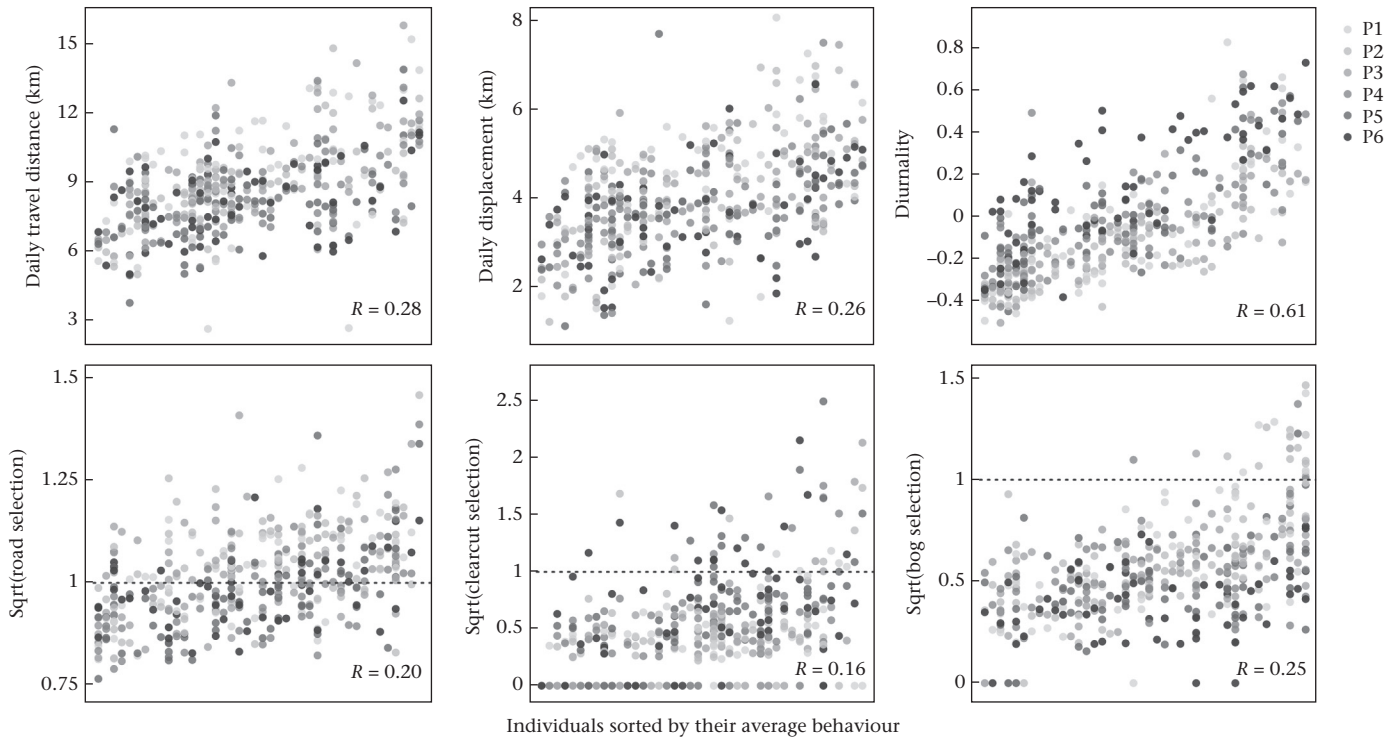
Figure 1. Observed values of six movement and habitat selection behaviours quantified from wildlife tracking data of 42 female brown bears during six consecutive 10-day periods (P1–P6 grey shaded) between 21 June and 19 August. Individuals are ordered by their average value for a given behaviour across all monitoring periods and years, showing that not all individuals express the full range of behavioural values present in the population. Repeatability values (*R*) accordingly indicate how much variance is explained by consistent between-individual differences. Road, clearcut and bog selection were square root transformed to normalize residuals. Values below the dotted lines indicate selection against, whereas values above indicate selection for a respective habitat.
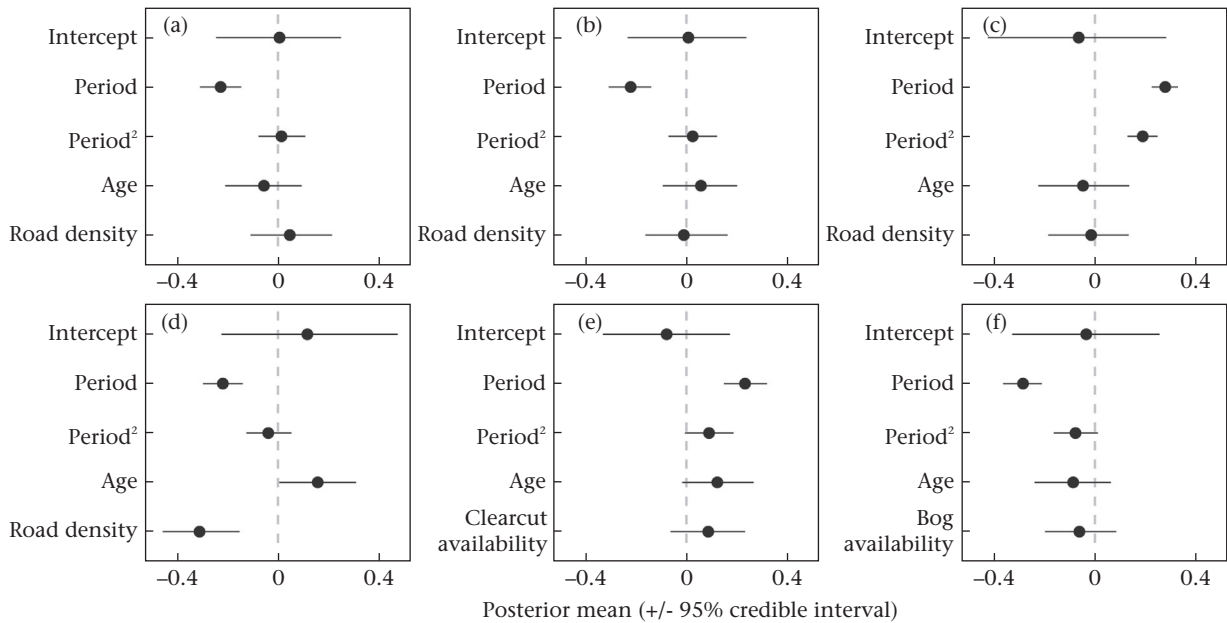
Figure 2. Posterior mean (± 95% credible interval) of fixed effects on brown bear behaviours based on estimates of a multivariate mixed model. (a) Travel distance (km), (b) displacement (km), (c) diurnality, (d) road selection, (e) clearcut selection, (f) bog selection.

personality traits may not be straightforward, especially as behaviours in the wild may be confounded by other environmental covariates, urging caution when drawing conclusions in relation to personality traits (Patrick et al., 2017). Given that large data sets of tracking data are available for numerous animal populations, we

call for further investigation as to whether movement and habitat selection behaviours that represent bold or exploratory behaviours also vary independently from one another in other species.

Population scale ecological effects provide an insight for why we did not find some of the relationships involving habitat selection
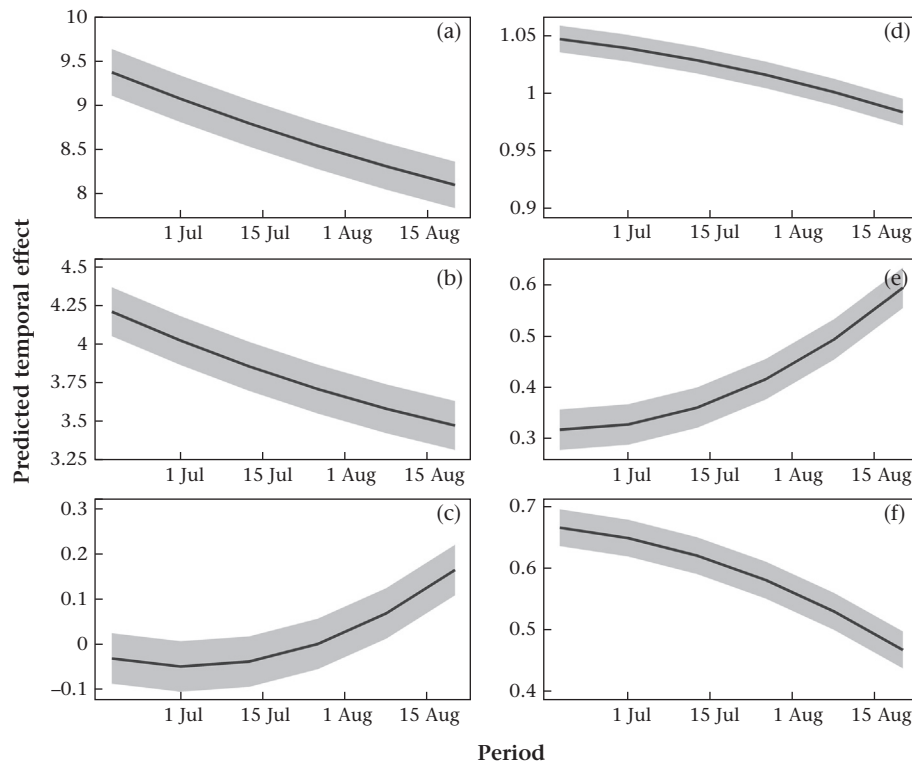
Figure 3. Temporal trends in brown bear behaviours over the course of the summer: predicted population level mean effect (± 95% confidence interval, grey shading) of time of year, measured as six continuous 10-day time periods from 21 June to 19 August, on bear behaviour. (a) Travel distance (km), (b) displacement (km), (c) diurnality, (d) road selection, (e) clearcut selection, (f) bog selection. Habitat selection ratios were square root transformed and values below 1 indicate selection against a habitat feature. Predictions are based on univariate models with unscaled response variables to facilitate interpretation.

behaviours that we expected from a behavioural syndrome framework. In late summer and autumn, Scandinavian brown bears should gear their behaviour towards one main objective: increasing their body mass in preparation for hibernation. Bears in our study area primarily feed on berries which start to ripen from mid-July on (Hertel et al., 2016). Accordingly, we observed a population level behavioural shift towards shorter daily movement distances and shorter displacement in response to the onset of the berry season which was expected given that bears engage in more area-restricted search behaviour when foraging on berries (Ordiz et al., 2012). Efficient berry foraging may, however, interact with bears trying to avoid humans because recreational and commercial berry pickers also frequent the Swedish forest as soon as berries start to ripen (Ordiz, Stoen, Delibes, & Swenson, 2011). Berry pickers use forest roads as access points and human disturbance is therefore highest close to roads. Bears reacted to that by increasingly avoiding roads later in the summer. Simultaneously, the later fruiting lingonberry, *Vaccinium vitis-idaea*, occurs in large quantities on clearcuts, which was reflected by a higher selection for clearcuts by bears later during our study (Hertel et al., 2016; Steyaert et al., 2016), but humans also use clearcuts close to roads for berry picking. Bears that readily use clearcuts may therefore choose areas further away from roads to offset their elevated risk of encountering humans. On the population scale, bears avoided all three habitat features, roads, clearcuts and bogs, suggesting that they indeed associate them with risk, thereby generally making stronger selection for these features an informative metric to infer individual differences in boldness. However, during autumn, only clearcuts are associated with both risk and resources and are therefore the ecologically most informative habitat selection measure of bold-ness. In summary, despite being repeatable, we did not find that

three habitat selection behaviours were correlated with one another or with the existing syndrome.

As we showed here, wildlife tracking devices can collect information at ecologically relevant temporal and spatial resolutions and produce large data sets that behavioural ecologists could exploit to study animal personality in the wild. This is especially true for elusive animals for which visual observations are difficult and rare. However, it is important to keep a number of methodological considerations in mind. To document behavioural variation in a population from captured and GPS-tagged animals it is important to maintain an unbiased capture regime (Merrick & Koprowski, 2017, and references therein). For example, if animals need to enter a trap, bolder individuals may have a higher likelihood of being captured (Biro, 2013; Biro & Dingemanse, 2009). In our population, bears are initially captured by snow tracking from a helicopter and offspring of female bears are systemically tagged over generations. This capture regime ensures that all behavioural types have the same likelihood of being captured. Further, finding informative behavioural metrics (Merrick & Koprowski, 2017; Smith & Blumstein, 2008) from tracking devices, while controlling for environmental factors known to affect these metrics, is a key component of success. Our results, for example, show that bears are more diurnal later in the year, which was a priori expected given the rapidly shortening daylength over the study period. By controlling for period, we found that individuals were consistent in their relative expression of the behaviour, despite changes in its absolute value. To better interpret tracking data, ecologists may seek inspiration from human psychologists who increasingly use GPS tracking to link repetitive spatial behaviours, such as use of green spaces (Bell, Phoenix, Lovell, & Wheeler, 2015), rates of revisiting preferred locations and exploratory tendency

Table 2
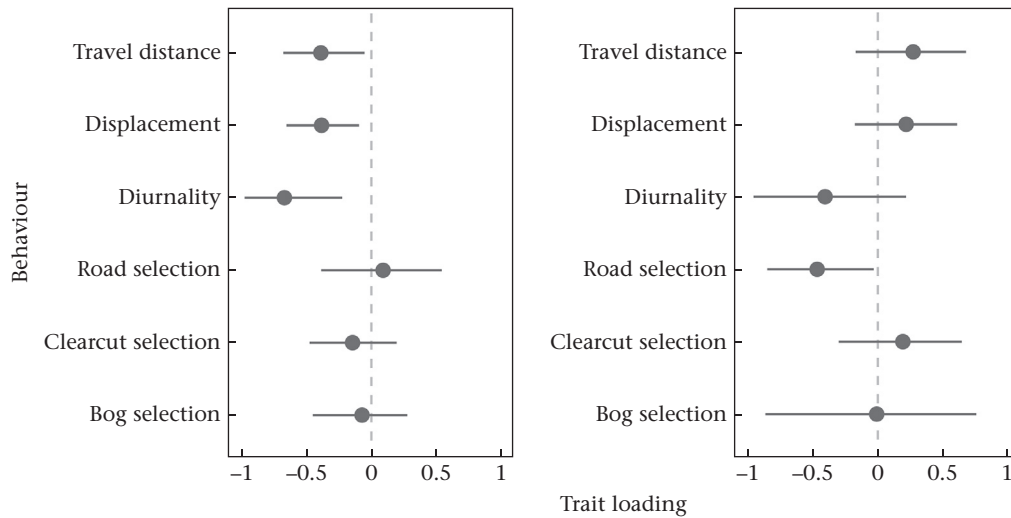Between-individual variance–covariance matrix

	Travel distance	Displacement	Diurnality	Road selection	Clearcut selection	Bog selection
Travel distance	*0.27 (0.14, 0.41)*	**0.83 (0.66, 0.96)**	**0.40 (0.03, 0.74)**	−0.38 (−0.75, 0.02)	0.34 (−0.18, 0.83)	−0.03 (−0.5, 0.40)
Displacement	**0.23 (0.07, 0.41)**	*0.24 (0.11, 0.39)*	**0.45 (0.09, 0.79)**	−0.35 (−0.74, 0.05)	0.26 (−0.28, 0.78)	0.13 (−0.29, 0.55)
Diurnality	**0.17 (0, 0.37)**	**0.18 (0.02, 0.38)**	*0.67 (0.55, 0.78)*	0.13 (−0.25, 0.51)	0.17 (−0.26, 0.61)	0.1 (−0.27, 0.47)
Road selection	−0.11 (−0.25, 0.02)	−0.1 (−0.23, 0.03)	0.05 (−0.12, 0.22)	*0.27 (0.15, 0.42)*	−0.40 (−0.80, 0.07)	−0.07 (−0.47, 0.36)
Clearcut selection	0.08 (−0.06, 0.22)	0.06 (−0.06, 0.19)	0.06 (−0.10, 0.24)	−0.09 (−0.22, 0.03)	*0.19 (0.06, 0.34)*	0.04 (−0.41, 0.5)
Bog selection	−0.01 (−0.15, 0.11)	0.03 (−0.09, 0.16)	0.05 (−0.11, 0.23)	−0.02 (−0.14, 0.10)	0.01 (−0.1, 0.13)	*0.29 (0.17, 0.43)*

Adjusted repeatability estimates (i.e. conditional on the model's fixed effects) are given in italics along the diagonal. Between-individual covariance between pairs of behaviours are given below and corresponding correlations are given above and underlined. The 95% credible intervals are based on 4000 models sampled from the MCMC chain at 1000-generation intervals. Significant covariances and correlations are shown in bold.
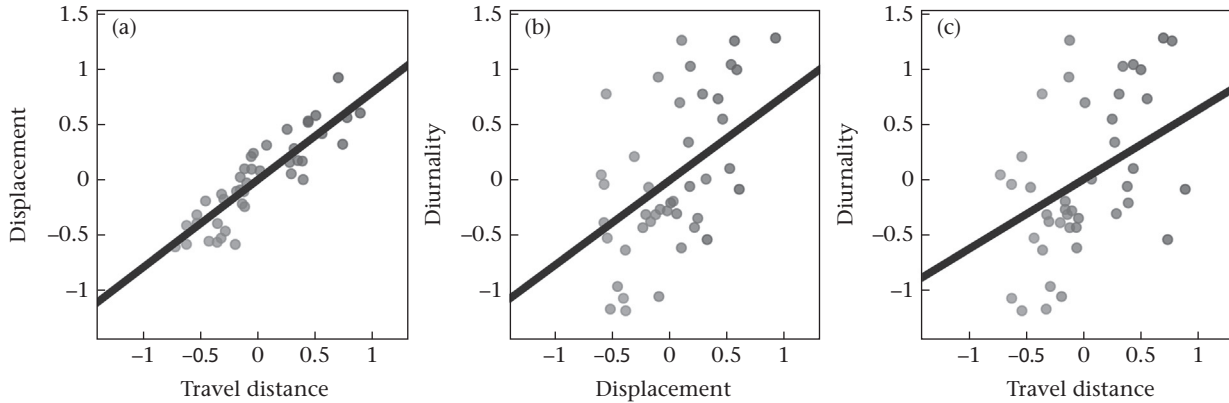
Figure 4. Association between (a) travel distance and displacement, (b) diurnality and displacement and (c) diurnality and travel distance in 42 adult female brown bears in southcentral Sweden between 2007 and 2016. Points are based on posterior modes of the individual random effect (bear ID) for the three behaviours extracted from the multivariate mixed model. Random effects grouped all behavioural observations taken by a bear across periods and study years. Regression lines between sets of behaviours are calculated by dividing the covariance between the two focal behaviours, by the variance of the behaviour shown on the x axis. Individuals are grey shaded uniquely across the three panels.

Figure 5. Trait loadings and 95% credible intervals of behaviours onto the (a) first and (b) second eigenvector of the between-individual covariance matrix.

(Alessandretti, Sapiezynski, Sekara, Lehmann, & Baronchelli, 2018) or speeding (Greaves & Ellison, 2011), with human personality traits, for example derived from self-assessment questionnaires. Greaves and Ellison (2011), for instance, found only a weak correlation between a risk-aversion metric and actual speeding behaviour and conclude that contextual differences and a combination of personality traits affects speeding behaviour in humans. Alessandretti et al. (2018) demonstrated that human exploration tendency, measured as the number of frequently visited locations, correlated with a person's number of social interactions. In behavioural ecological terms this mirrors a sociability–exploration behavioural syndrome.

Animal personalities may have important implications for the adaptability and persistence of animals in human-dominated environments. High boldness values, for example, have been associated with shorter flight initiation distances in response to

encounters with humans (Found & St. Clair, 2016). Bolder individuals seem to be more tolerant towards human encroachment and move more easily through human-modified landscapes (Holtmann et al., 2017; Lowry, Lill, & Wong, 2013; Sol, Lapiedra, & González-Lagos, 2013), which has implications for dispersal and population connectivity (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Bolder individuals may therefore generally be more resilient towards anthropogenic disturbances (Sih, 2013; Sol et al., 2013). The downside to this stronger resilience is that bolder individuals are also more likely to be involved in conflicts with humans (Found & St. Clair, 2016; Timm, Baker, Bennett, & Coolahan, 2004), and that they may be easier targets for hunters (Leclerc, Zedrosser, & Pelletier, 2017). Hunting is the single most important cause of mortality in our population and has recently been shown to select for slower life history traits (Van de Walle, Pigeon, Zedrosser, Swenson, & Pelletier, 2018). It would be interesting to test whether these slower life histories correlate with other behaviours, or even with the existing behavioural syndrome found in this study. Further, testing whether an activity–exploration–boldness syndrome can also be observed in other brown bear populations, particularly in populations with no or short persecution history, could help define whether the long-term persecution history could have eroded the personality gradient expressed by the Scandinavian brown bear population.

Conclusion

Behavioural ecologists should exploit existing large data sets of tracking data to delineate behavioural types from natural behaviours of elusive wildlife (Spiegel et al., 2017). Exploring behavioural syndromes in the wild using space use and movement behaviours has the potential to reveal the diversity of behavioural repertoires in the wild. This is important, given the increasing evidence that heritable personality traits affect the spatial distribution of individuals across the landscape, corroborating their implication for population resilience towards environmental change, conservation, ecological and evolutionary processes (e.g. Merrick & Koprowski, 2017; Sih, 2013; Smith & Blumstein, 2008; Wolf & Weissing, 2012).

Acknowledgments

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Appendix

Table A1
Overview of individual bears and their respective number of monitoring periods and monitoring years included in the study

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Number of repeats	Monitoring years
I_01	3			6	6		6				21	4
I_02	3				4	4			4		15	4
I_03	4	4									8	2
I_04	4		6								10	2
I_05	4				5						9	2
I_06	4										4	1
I_07	4										4	1
I_08		3	6								9	2
I_09		3		4		5		6	5	4	27	6
I_10		4									4	1
I_11		4									4	1
I_12		4									4	1
I_13		5	3								8	2
I_14		5	6								11	2
I_15		5									5	1
I_16		6	5		5		5	6			27	5
I_17		6									6	1
I_18		6									6	1
I_19			6	5	4	6		6			27	5
I_20			6	5					5		16	3
I_21			6	6	3	6			3		24	5
I_22			6		6						12	2
I_23			6								6	1
I_24				5	5						10	2
I_25				5							5	1
I_26				5							5	1
I_27				6	4						10	2
I_28				6							6	1
I_29					4	6	5				15	3
I_30					4	6					10	2
I_31					6	5	6			5	22	4
I_32					6	6		6			18	3
I_33					6						6	1
I_34						4					4	1
I_35						6					6	1
I_36							4				4	1
I_37							5				5	1
I_38							6				6	1
I_39								4	4		8	2
I_40								4			4	1
I_41								6	6	6	18	3
I_42									6		6	1

Table A2
Estimated fixed-effect sizes in individual univariate models and a multivariate model

	Univariate (unscaled)		Univariate (scaled)		Multivariate (scaled)		
	Estimate	SE	Estimate	SE	Mean	Lower credible interval	Upper credible interval
Travel distance							
(Intercept)	8724.678	247.292	0.002	0.119	0.009	−0.242	0.244
Period	−475.914	86.309	−0.229	0.042	−0.227	−0.313	−0.148
I(Period^2)	35.831	97.005	0.017	0.047	0.014	−0.080	0.107
Scale (roaddensity)	200.712	159.620	0.096	0.077	0.048	−0.106	0.217
Scale (age)	−121.539	167.075	−0.058	0.080	−0.055	−0.212	0.096
Displacement							
(Intercept)	3998.716	150.199	−0.006	0.121	0.009	−0.230	0.232
Period	−278.257	52.506	−0.224	0.042	−0.221	−0.304	−0.135
I(Period^2)	34.353	59.014	0.028	0.047	0.025	−0.071	0.119
Scale (roaddensity)	21.126	94.971	0.017	0.076	−0.010	−0.165	0.151
Scale (age)	98.141	99.424	0.079	0.08	0.058	−0.092	0.204
Diurnality							
(Intercept)	−0.058	0.036	−0.039	0.138	−0.064	−0.424	0.303
Period	0.073	0.007	0.280	0.027	0.280	0.228	0.338
I(Period^2)	0.050	0.008	0.191	0.031	0.190	0.128	0.251
Scale (roaddensity)	−0.0199	0.019	−0.076	0.073	−0.012	−0.169	0.150
Scale (age)	−0.0186	0.022	−0.071	0.084	−0.046	−0.222	0.130
Road selection							
(Intercept)	1.019	0.014	0.097	0.127	0.118	−0.218	0.477
Period	−0.024	0.005	−0.216	0.041	−0.220	−0.302	−0.144
I(Period^2)	−0.004	0.005	−0.035	0.046	−0.037	−0.127	0.052
Scale (roaddensity)	−0.032	0.008	−0.281	0.069	−0.314	−0.463	−0.156
Scale (age)	0.018	0.008	0.153	0.073	0.159	0.004	0.313
Clearcut selection							
(Intercept)	0.478	0.048	−0.092	0.108	−0.076	−0.319	0.192
Period	0.104	0.019	0.234	0.043	0.233	0.149	0.319
I(Period^2)	0.040	0.022	0.089	0.048	0.090	−0.008	0.187
Scale (Clearcut availability)	0.025	0.030	0.056	0.068	0.087	−0.056	0.245
Scale (age)	0.064	0.031	0.144	0.069	0.123	−0.024	0.261
Bog selection							
(Intercept)	0.545	0.029	0.023	0.114	−0.033	−0.342	0.258
Period	−0.074	0.074	−0.288	0.039	−0.286	−0.370	−0.211
I(Period^2)	−0.019	0.015	−0.077	0.044	−0.076	−0.163	0.013
Scale (Bog availability)	−0.015	0.017	−0.059	0.067	−0.063	−0.204	0.077
Scale (age)	0.025	0.019	−0.097	0.073	−0.083	−0.236	0.080

Comparison of estimates derived from univariate mixed models using either unscaled or scaled behaviours as response variables and mean posterior estimates and credible intervals extracted from a multivariate mixed model using scaled behaviours as response variables. Estimated effect sizes from univariate scaled models and the multivariate scaled model are similar.
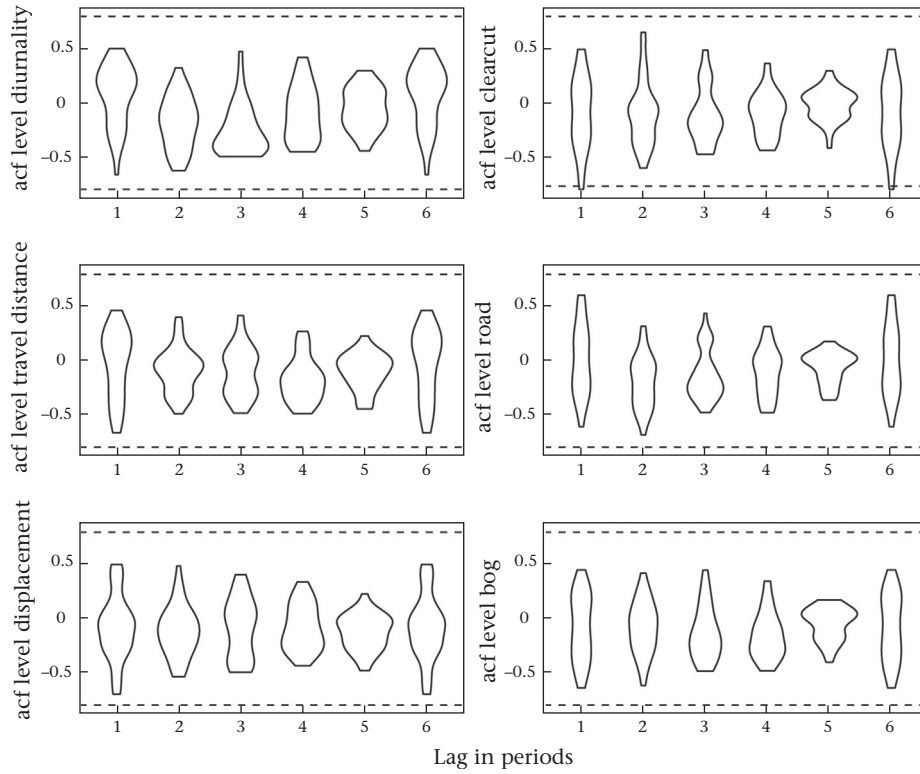
Figure A1. In our study we measured daily travel distance, daily displacement, diurnality, road selection, clearcut selection and bog selection between end of June and mid-August. Daily behaviours were averaged for six back to back 10-day periods. We extracted model residuals from univariate mixed models for each behaviour controlling for period as a linear and quadratic fixed effect. We expected no temporal autocorrelation in the model residuals. We assessed autocorrelation for each bear and year individually and present the density distribution of autocorrelation over 116 bear-years. Residuals are independent (i.e. not correlated because they were taken in consecutive periods) when the autocorrelation function (acf) levels are within the confidence intervals (black dotted lines).
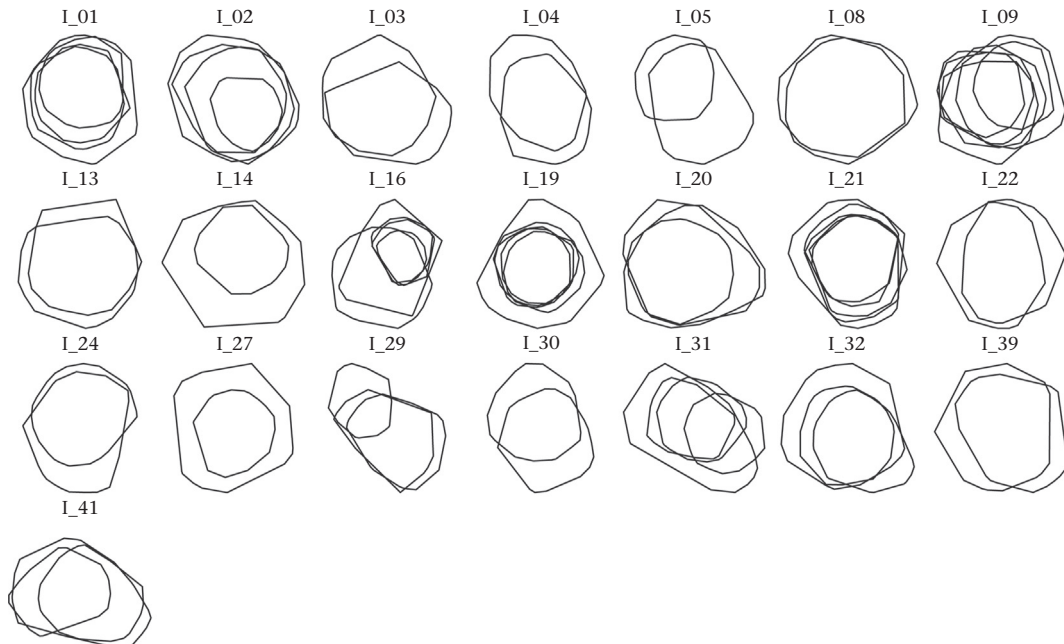
Figure A2. Overlap of annual home ranges of females included in this study with multiple monitoring years.
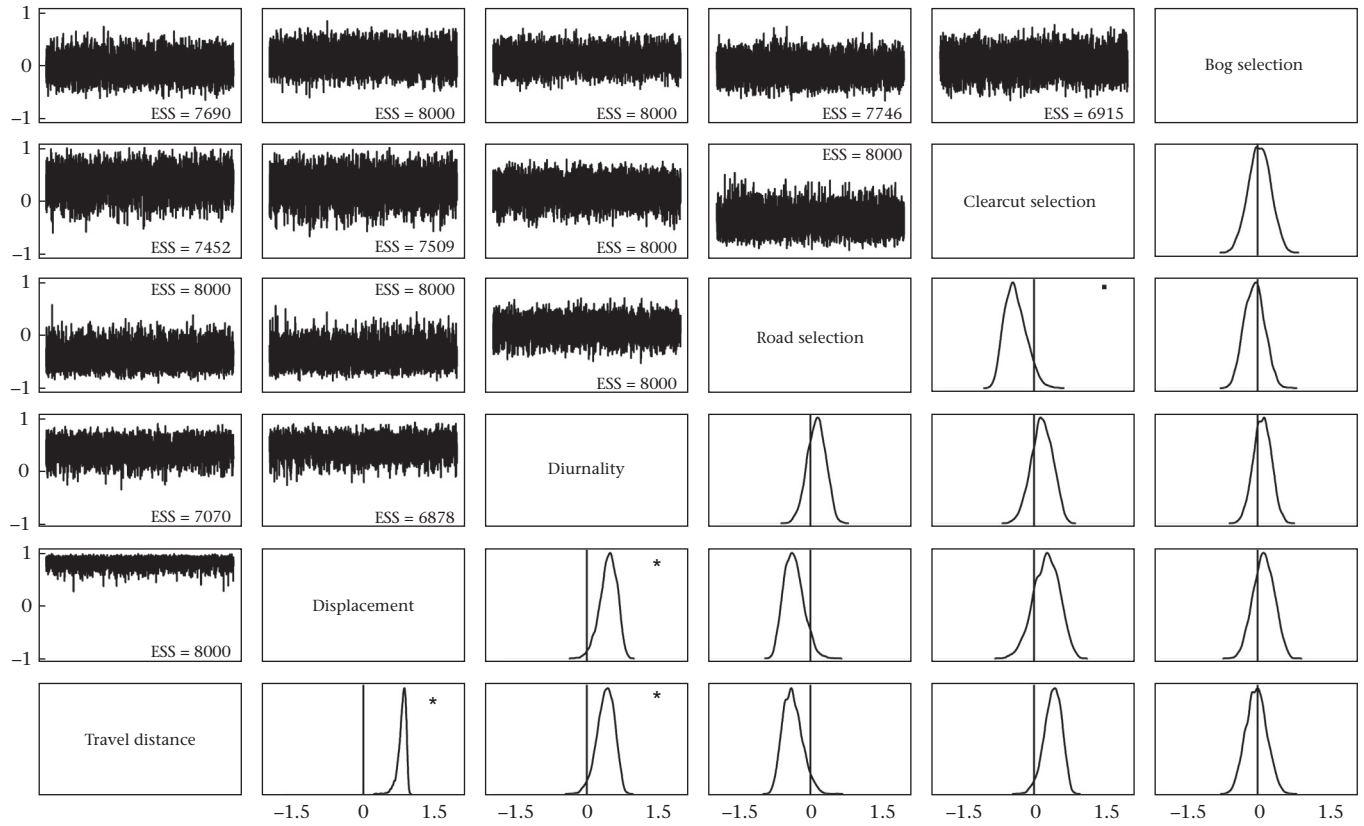
Figure A3. Between-individual correlation of behavioural traits. Trace and density plots of the posterior distribution are shown. Asterisks indicate significant correlations where the 95% credible intervals did not overlap 0; effective sample sizes (ESS) demonstrate the absence of autocorrelation between iterations.