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Animal personality: a comparison of standardized assays and focal observations in North American red squirrels

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As interest in animal personality research grows, methodologies for quantifying consistent among-individual differences in behaviour are expanding. Two of the most common methods for quantifying animal personality are standardized behavioural assays and focal animal sampling. We evaluated whether assays and focals provided similar animal personality measures in a wild population of free-ranging North American red squirrels, *Tamiasciurus hudsonicus*, by comparing the among-individual correlations of traits between methods. Assays described two behavioural axes—one associated with movement behaviours and another associated with antagonistic behaviours towards conspecifics. Focals described two additional behavioural axes—one associated with movement and territorial behaviours, and another associated with the trade-off between vigilant and feeding behaviours. Although we found evidence of high trait repeatability for behavioural axes measured with assays, both focal behavioural axes had low trait repeatability regardless of whether among-individual differences in the social environment were controlled for (i.e. to account for 'pseudopersonality'). We also found no among-individual correlations between assay and focal behavioural axes. The lack of correlation between methods may be because the dominant axes of variation differ between methods or because of the low trait repeatability of focals due to high behavioural plasticity. Given this, we conclude that assays will likely remain the mainstay for measuring consistent among-individual differences in behaviour given their ability to standardize for environmental conditions.

Animal personality (i.e. consistent differences in behaviour across time and context) has a broad range of ecological and evolutionary implications (reviewed in: Sih et al., 2015; Wolf & Weissing, 2012). For example, animal personality can be correlated with fitness (Boon et al., 2007; Nicolaus et al., 2012, 2016; Piquet et al., 2018; Rödel et al., 2015) and can alter the flow and spread of individuals, disease and information (Barber & Dingemanse, 2010; Cote et al., 2010; Duckworth, 2008; Duckworth & Badyaev, 2007; Krause et al., 2010). As such, researchers are continually employing new methodologies to measure animal personality. While many different approaches have been developed, there is little understanding of how (or if) these methodologies produce similar measures of animal personality.

Some of the more common approaches for assessing consistent among-individual differences in behaviour include standardized behavioural assays (hereafter assays; Beckmann et al., 2013; Carter et al., 2012; Stein & Bell, 2019; Tkaczynski et al., 2019; Žampachová et al., 2017) and focal animal sampling (Altmann, 1974; Araya-Ajoy & Dingemanse, 2013; Humphries & Boutin, 2000; Niemelä & Dingemanse, 2017; Seyfarth et al., 2012). Assays, such as open field and mirror-image stimulation trials, are widely used (Beckmann et al., 2013; Carter et al., 2012; Stein & Bell, 2019; Tkaczynski et al., 2019; Žampachová et al., 2017) due to their

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relative ease of implementation and because consistent among-individual differences using natural behaviours are often difficult to measure in the field owing to logistical limitations. While assays allow for standardization of environmental conditions across individuals, concerns about their use centre around ambiguity in defining what the measured traits represent given they are often not naturally occurring (Beckmann et al., 2013; Carter et al., 2012; McCormick & Holekamp, 2022) and that assays often measure variation along multiple axes (Perals et al., 2017). For example, mirror-image stimulation trials are assumed to measure how an individual interacts with conspecifics or themselves, either through aggression (i.e. antagonistic behaviours; Benus et al., 1992), sociability (i.e. amicable or avoidant behaviours; Budaev, 1997; Réale et al., 2007) or self-recognition (Suddendorf & Butler, 2013). Similarly, open field trials are thought to measure activity (i.e. locomotor actions; Smith, 1968), exploration (i.e. reaction to novelty; Montgomery, 1951) or boldness (i.e. vigilant behaviours; Clarke & Lindburg, 1993) if the environment is perceived as novel or risky (Réale et al., 2007).

Focal animal observation sessions (hereafter focals; Altmann, 1974) provide an alternative to assays for measuring behaviour in situ by allowing researchers to record a wide range of behaviours, including those that are rare, without removing an individual from their natural habitat (Araya-Ajoy & Dingemanse, 2013; Archibald et al., 2013; Niemelä & Dingemanse, 2017; Seyfarth et al., 2012). However, variable environmental conditions can influence behavioural expression (e.g. Niemelä et al., 2019), adding noise to the among- and within-individual variance components. This can make it difficult to differentiate ‘pseudopersonality’ (i.e. plastic responses to repeatable differences in the environment) from ‘true’ animal personality (Niemelä & Dingemanse, 2017). For example, an individual living in a high population density area may consistently exhibit one suite of behaviours compared with an individual living in a low population density area because of the environmental gradient, rather than intrinsic differences in behaviour. Considering this environmental variation, local conditions need to be accounted for when measuring consistent among-individual differences in behaviour using focals.

There have been few studies examining how consistent among-individual differences in behaviour compare between assays and focals conducted in the field (e.g. Tkaczynski et al., 2019). This comparison is important because it allows us to assess whether different methods capture similar behavioural axes and whether consistent among-individual differences in behaviour can be disentangled from environmental variation when using focals. Using long-term data from a population of North American red squirrels, *Tamiasciurus hudsonicus* (hereafter red squirrels) in Yukon, Canada, we asked whether assay and focal methods provide similar animal personality measures in this species after first quantifying trait repeatability. Red squirrels are ideal to study consistent among-individual differences in behaviour because they are easy to observe and trap due to their territoriality, site fidelity, conspicuousness and diurnal activity patterns (Anderson & Boutin, 2002; Smith, 1968).

In this population of red squirrels, we have used assays to describe two behavioural axes (Boon et al., 2007; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012). The first (assay behavioural axis 1) is associated with behaviours involving movement in an open field trial. This was previously interpreted to be a measure of activity (Boon et al., 2007; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012) because all behaviours involving movement load positively on this axis. The second (assay behavioural axis 2) is associated with antagonistic behaviour towards a simulated conspecific during a mirror-image stimulation trial. This was previously interpreted to measure aggression (Boon et al., 2007; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012) because some red squirrels attacked their mirror image. We refer to these axes as assay behavioural axis 1 and 2 to avoid subjective considerations when defining and interpreting what is being measured. Assay behavioural axes 1 and 2 are repeatable (0.37–0.51; Boon et al., 2007; Taylor et al., 2012) and, at least partially, heritable (0.08–0.12; Taylor et al., 2012) in red squirrels. Both traits develop over ontogeny (Kelley et al., 2015; Martinig et al., 2021), becoming more repeatable with age (Martinig et al., 2021), and are correlated with offspring recruitment (Cooper et al., 2017) and fitness (Boon et al., 2007, 2008; Taylor et al., 2014). Assay behavioural axis 1 is also positively correlated with trappability (Boon et al., 2008), and both assay behavioural axes are negatively correlated with physiological stress reactivity in juveniles (Westrick et al., 2021).

Focals have been used to assess plasticity in behaviour, which has been found to change in this population in response to population density (Dantzer et al., 2012) and the familiarity of the social environment (Siracusa et al., 2019). In this study, we used a principal component analysis to isolate two behavioural axes from focal data. The first behavioural axis (focal behavioural axis 1) is associated with increased travelling and territorial calling (i.e. rattling; Lair, 1990), and decreased time resting in the nest. This was previously interpreted as a trade-off between time spent in the nest versus time spent doing other behaviours (Dantzer et al., 2012), and may broadly capture activity, boldness or territoriality/aggression. The second behavioural axis (focal behavioural axis 2) is associated with increased feeding and decreased vigilance. This was previously interpreted as a trade-off between vigilance and feeding (Dantzer et al., 2012), and may broadly capture activity or boldness. Here too we refer to these axes as focal behavioural axis 1 and 2 to maintain objectivity.

We hypothesized that focals, like assays, would capture consistent among-individual differences in behaviour (as measured by behavioural repeatability). Next, we hypothesized that assays and focals would describe similar behavioural axes. We predicted a positive correlation between what we interpreted to be a measure of activity from assays (i.e. assay behavioural axis 1) and focal behavioural axes 1 or 2, given these traits are associated with locomotory behaviours. Additionally, we predicted a positive correlation between what we interpreted to be a measure of aggression from assays (i.e. assay behavioural axis 2) and focal behavioural axis 1, given it is also associated with territorial behaviour, and red squirrel rattles are a vocal expression of site ownership (Smith, 1978) that reduce the risk of intrusion by conspecifics (E. Siracusa et al., 2017). If focals do not capture consistent among-individual differences in behaviour and/or if assay and focal behavioural axes are not correlated, then this would suggest that, at least in our study, focals are limited in their ability to capture consistent among-individual differences in behaviour, assays and focals do not capture similar axes of variation and/or more data may be needed to adequately compare methods. This may have important implications for our broader understanding of the relationship between assays and focals but further research will be necessary to assess the generalizability of these findings.

METHODS

Study Area

We monitored red squirrels at three locations over 40 ha (two control (Kloo and Sulphur) and one experimental (Agnes) study grid) in southwestern Yukon, Canada (61°N, 138°W) within the traditional territory of the Champagne and Aishihik First Nations (more details can be found in Dantzer et al., 2020). The control grids are separated by the Alaska highway, a two-lane undivided paved highway with a large verge that acts as a barrier to regular (back and forth) movements in red squirrels (Martinig et al., 2020), while the experimental grid is roughly 8 km away from the control grids. Individuals with territories on the experimental grid were part of a food supplementation experiment between 2004 and 2017. Each autumn to spring they received peanut butter ad libitum on their territory (Boon et al., 2007; Dantzer et al., 2013, 2020).

The study area is dominated by mature white spruce, *Picea glauca*, with smaller pockets of aspen, *Populus tremuloides*, wetlands and meadows containing willow (*Salix* spp.) and birch, *Betula glandulosa* (Douglas, 1974). White spruce, whose seeds are the main food source for red squirrels in this area (Fletcher et al., 2013), are a masting species that produce variable numbers of cones each year, leading to variation in the food supply (Boutin et al., 2006; LaMontagne & Boutin, 2007; McAdam et al., 2019).

Study Species

Red squirrels are diurnal, territorial rodents commonly found throughout the boreal forest (Steele, 1998). They are relatively long-lived for a rodent; individuals that survive their first winter live 3–4 years on average, and can live up to 8 years (McAdam et al., 2007). Red squirrels are exclusively territorial, with natal dispersal occurring in the late summer and early autumn (Martinig, 2021). Territory acquisition is correlated with improved winter survival, and juveniles that do not secure a territory before their first winter have higher rates of mortality (Hendrix et al., 2020; Larsen & Boutin, 1994).

Data Collection

From 2005 to 2019, we intensively (6 days/week) monitored individuals between March and October using a combination of behavioural observations, telemetry monitoring and live traps (Tomahawk Live Trap, Hazelhurst, GA, U.S.A.) baited with peanut butter (see McAdam et al., 2007 for general trapping protocol). To reduce trapping stress, we checked traps every hour. We monitored offspring born in our population using a combination of behavioural observations and radiotelemetry (radiocollar model PD-2C, 4 g, Holohil Systems Ltd, Carp, ON, Canada) of pregnant females. Immediately after parturition, we located the nest and temporarily removed offspring to obtain weight measurements, sex and tissue samples. Red squirrel mothers do not desert offspring after handling; however, 83% of mothers do move their offspring to another nest afterwards (Westrick et al., 2020). To facilitate individual identification, we put alphanumeric eartags (0.25 g per tag; Model no. 1; 5 digits; National Band and Tag, Newport, KY, U.S.A.) on juveniles at approximately 25 days old, or on untagged individuals who were not locally born. We ensured eartags were secure enough that individuals were only tagged once during their lifetime. We affixed coloured discs or coloured wires, respectively, to juvenile or adult eartags to allow for identification from a distance. We changed colours yearly for surviving individuals. We separated individuals into different age classes by classifying them as juveniles if they were less than 1 year old at the time of data collection, as yearlings if they were approximately 1 year old, and as adults if they were older than 1 year. Similar to Martinig et al. (2020), we considered untagged fully grown individuals (>220 g) to be yearlings at time of first capture and verified whether they were immigrants or locally born individuals through tissue sampling (i.e. genetics).

Each May and August, we conducted a full population census and recorded territory ownership of all individuals. Because red squirrels are diurnal, defend exclusive territories year-round (Smith, 1968; Steele, 1998), exhibit stable territory ownership (i.e. after initial acquisition, adult dispersal is rare; Berteaux & Boutin, 2000) and have high recapture rates (recapture rates > 0.95; see Descamps, 2006), this allowed us to reliably record ownership of each midden and timing of change-over if an owner died. Due to the potential for the social environment to influence exhibited behaviours (i.e. pseudopersonality), we calculated local population density and average social familiarity (i.e. how long an individual has lived adjacent to the specific individuals that occupy neighbouring territories). To do this, we determined the number of individuals within 130 m of the focal individual and the pairwise familiarity of each to the focal individual (i.e. the estimated number of days that the focal individual and neighbour occupied their current territories). Pairwise familiarity measures were averaged to obtain a measure of familiarity for the social environment (detailed in E. Siracusa et al., 2017, 2021). The outer limit at which territorial vocalizations (rattles; Lair, 1990) are known to be detectable to the human ear is 130 m (Smith, 1978). Both density and familiarity at this scale have been shown to have detectable effects on behaviour and fitness (Dantzer et al., 2012; Fisher et al., 2017; Siracusa et al., 2019, 2021). Because turnover in red squirrel territory ownership between May and August is relatively low, we used the May census to calculate density and familiarity for observations conducted before July, and the August census for observations conducted in July or after unless there was a census available in the same month as the record. Juveniles and immigrants were given a familiarity score of zero for their first year. This is an appropriate approximation of familiarity as juveniles and immigrants would have only very recently established their territories and therefore would not be familiar with any of their neighbours. Note familiarity does not account for previous social associations between kin in the nest. Relatedness to neighbours has previously been shown not to affect red squirrel fitness (Siracusa et al., 2021) or behaviour (E. R. Siracusa, personal communication), and so was not included.

Standardized behavioural assays

We conducted 956 assays on 672 individuals over 15 years from 2005 to 2019. Of these, we assayed 351 adults, of which 154 females and 94 males were assayed once and 55 females and 48 males were assayed two to four times, 189 yearlings, of which 83 females and 59 males were assayed once and 20 females and 27 males were assayed twice, and 192 juveniles, of which 69 females and 61 males were assayed once and 36 females and 26 males were assayed two to three times. Note the sum of individuals across age classes is greater than the total number of individuals because individuals were sampled across multiple age classes. Subsets of these data have already been analysed in other papers (e.g. Boon et al., 2007; Cooper et al., 2017; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2014, 2012; Westrick et al., 2019) separate from this study.

We measured behavioural axes in a novel environment using an open field trial (Martin & Réale, 2008; Walsh & Cummins, 1976) and a mirror-image stimulation trial (Svendsen & Armitage, 1973). Following trapping, we transferred red squirrels to the testing arena: a 60 × 80 × 50 cm white plastic box with a clear acrylic lid. The testing arena also contained four blind holes in the floor to explore (Martin & Réale, 2008). We conducted all assays in a flat area without vegetation overhead within approximately 5vm of where the individual was trapped to minimize stress. The open field trial lasted 7.5 min and also served as habituation to the arena. We then uncovered a mirror (45 × 30 cm) in the testing arena and began the mirror-image stimulation trial, which lasted 5 min. Following the completion of the trial, we released the individual and cleaned the arena with 70% isopropyl alcohol and allowed it to evaporate before starting the next trial. Cleaning the arena helped minimize stress associated with smelling conspecifics and also reduced the risk of disease transmission. We recorded each trial with a camcorder (Sony Handycam, Sony of Canada Ltd., Toronto, ON, Canada) placed above the testing arena and later logged behaviours using JWatcher Video 1.0 (Blumstein & Daniel, 2007), Cowlog 2 software (Hänninen & Pastell, 2009) and Behavioral Observation Research Interactive Software (Friard & Gamba, 2016). Because eight different observers scored individual videos, we only included assay behaviours with high (>0.70) interobserver repeatability (Taylor et al., 2012; see Appendix, Table A1).

Behavioural focals

We conducted 5636 focal animal observation sessions on 333 individuals over 11 years from 2008 to 2019. Of these, we conducted focals on 223 adults, of which 26 females and 15 males were sampled once and 67 females and 118 males were sampled two to 105 times, 128 yearlings, of which 38 females and 17 males were sampled once and 28 females and 45 males were sampled two to 55 times, and 7 juveniles, of which 5 females and 1 male were sampled once and 1 male was sampled twice. Note that individuals are represented in multiple age classes, meaning the sum of individuals across the different age classes is greater than the number of individuals overall. Each red squirrel was sampled by 26 different observers ($N = 696$ average focals per observer, range 1–1429 focals) one to four times per day, for a maximum of 4 days of focals per week (range 1–4 days).

We located individuals using radiotelemetry (model PD-2C radiotransmitters, 4 g, Holohil Systems Limited, Carp, ON, Canada; the unit weighed <2 % of an adult red squirrel's body weight) and followed an instantaneous sampling protocol (Altmann, 1974), recording behaviour every 30 s until the end of the focal period (7 min). To minimize any effects on individual behaviour, we maintained at least 5 m of distance between the focal individual and observer. We recorded 16 different behaviours, of which 11 were commonly expressed across all individuals and the rest were rare events (e.g. social interactions, nest building, foot stomping, mating chase, etc.) that cumulatively represented 0.71% of observations during focals. For analysis, we removed these rare behaviours, leaving us with the following common behaviours: vocalizing (barking, squeaking and all occurrences of rattling; Smith, 1978), feeding, foraging, travelling, caching food items, self-grooming, resting, vigilant or in nest (see Appendix, Table A1; Dantzer et al., 2012; Humphries & Boutin, 2000; Siracusa et al., 2019). We differentiated vigilance from resting by the red squirrel being inactive but alert, as observed by standing on hindlimbs or sitting in an upright posture indicative of the former (Dantzer et al., 2012). Resting red squirrels often lay with their head down or eyes closed and so are not alert (Dantzer et al., 2012; Siracusa et al., 2019).

We removed any focals where the red squirrel was out of sight (i.e. location known or unknown, but not visible) for more than half of the focal duration ($N = 81$ focals). We excluded an additional 4271 out-of-sight observations from the remaining focals before calculating behavioural proportions. Due to this filtering, we only included focals that were 5–7 min long (after removing out-of-sight instances) to minimize the effects of differences in sampling durations. This yielded our final sample size of 5636 focals on 333 individuals. For each focal, we calculated the proportion of time each behaviour occurred by summing the total number of records for that behaviour and dividing that by the total number of behaviours recorded in the focal.

Principal component analysis

Because the raw behaviours were zero-inflated, non-independent from one another and correlated within methods (Appendix, Fig. A1), we instead grouped these behaviours using principal component analyses (PCA), which meant that the principal component (PC) scores used in all analyses had Gaussian distributions and allowed us to provide an overall assessment of behaviour. Using all individuals, we ran separate PCAs to extract behaviours from the assays ($N = 672$ individuals) and focals ($N = 333$ individuals), thereby assuming that repeated measures on the same individuals are independent (Budaev, 2010). We used the ‘prcomp’ function in the baseline ‘stats’ package, v.3.6.2 (R Core Team, 2019), which uses the singular value decomposition method (i.e. Q-mode) of the centred and scaled data matrix (not eigenvectors from a covariance matrix). We isolated the first PC from each assay similar to earlier studies (Boon et al., 2007; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012), generating a score for the open field trial and another for the mirror-image stimulation trial. We considered a behaviour to be heavily loaded if it had a loading of ≥0.40 (Budaev, 2010). We identified walk (positively loaded), jump (positively loaded) and still (negatively loaded) as heavily loaded for PC1 from the open field trial (Table 1). PC1 explained 34.21% of the variance (Table 1). We refer to this as ‘assay behavioural axis 1’. We identified front of arena (positively loaded), back of arena (negatively loaded), attack latency (negatively loaded) and approach latency (negatively loaded) as heavily loaded for PC1 from the mirror-image stimulation trial (Table 1). PC1 explained 52.61% of the variance (Table 1). We refer to this as ‘assay behavioural axis 2’. The loadings for both assays were consistent with those reported from previous studies (e.g. Boon et al., 2007; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012).

For the focals, we present all PCs in the Appendix (Table A2), but only discuss the first two PCs (Table 2) following Dantzer et al. (2012) and based on the proportion of variance explained relative to the number of variables. We identified travel (positively loaded), rattle (positively loaded) and in nest (negatively loaded) as heavily loaded for focal PC1 (Table 2). Focal PC1

Table 1
Principal component analyses of behaviours measured in standardized behavioural assays using open field and mirror-image stimulation trials ($N = 672$ individuals)

Open field trial		Mirror-image stimulation trial	
Behaviours	Loadings	Behaviours	Loadings
Chew	0.30	Approach latency	−**0.51**
Hang	<−0.01	Attack	0.26
Hole	0.30	Attack latency	−**0.47**
Jump	**0.51**	Back of arena	−**0.45**
Self-groom	−0.08	Front of arena	**0.51**
Still	−**0.55**		
Walk	**0.50**		
Standard deviation	1.55	**Standard deviation**	1.62
Proportion of variance	0.342	**Proportion of variance**	0.526

Values are reported for the first principal component. Bolded values indicate heavy loading (score ≥0.40). Proportion of variance is the variance captured by that specific PC.

Table 2
Principal component analyses of focal behaviours for the first two principal components (PC; $N = 333$ individuals)

Behaviour	PC1	PC2
Bark	0.05	−0.21
Caching	0.18	0.28
Feeding	0.13	**0.63**
Forage	0.38	0.11
In Nest	−**0.61**	−0.01
Rattle	**0.44**	−0.15
Resting	−0.10	−0.39
Self-grooming	0.15	−0.16
Squeak	0.04	−0.15
Travel	**0.45**	−0.17
Vigilant	0.07	−**0.48**
Standard deviation	1.38	1.16
Proportion of variance	0.17	0.12
Cumulative proportion	0.17	0.30

All behaviours with observations were included. Bolded values indicate behaviours that are heavily loaded (score ≥ 0.40). Proportion of variance is the variance captured by that specific PC, while the cumulative proportion is the variance captured by that specific PC in addition to earlier PCs.

explained 17.36% of the variance (Table 2). We refer to this as ‘focal behavioural axis 1’. The focal PC2 behaviours that we identified as heavily loaded included feeding (positively loaded) and vigilance (negatively loaded; Table 2). Focal PC2 explained 12.27% of the variance (Table 2). We refer to this as ‘focal behavioural axis 2’.

Estimating behavioural repeatability

We estimated assay repeatabilities ($N = 672$ individuals) for assay behavioural axes 1 and 2 for 351 adults ($N = 465$ assays), 189 yearlings ($N = 236$ assays) and 192 juveniles ($N = 255$ assays) separately, and focal repeatability ($N = 333$ individuals) for focal behavioural axes 1 and 2 for 223 adults ($N = 4542$ focals) and 128 yearlings ($N = 1086$ focals) separately. We did not calculate repeatability for the focals conducted on juveniles because of insufficient sample size ($N = 8$ focals). We retained individuals that were sampled once because these data points increase our precision in estimating among-individual variation (Nakagawa & Schielzeth, 2010). Repeatability estimates for assays are qualitatively the same as estimates calculated using only individuals with repeated measures (i.e. two or more measures per individual; Table 3, Appendix, Table A3).

We first measured repeatabilities that were not corrected for methodological and environmental effects on behaviour (nonadjusted repeatabilities) using the ‘lmer’ function in the package ‘lme4’, v.1.1−21 (Bates et al., 2015) and visually inspected and verified that model residuals met the assumptions of normality and homoscedasticity. We then added trial number (discrete variable), among-individual local population density (continuous variable), among-individual average social familiarity (continuous variable, excluded for juvenile estimates), study grid (categorical variable) and sex (categorical variable) as fixed effects to estimate adjusted repeatabilities. Before calculating adjusted repeatabilities, we mean-centred and standardized all numerical variables to one standard deviation within birth year and study grid (Schielzeth, 2010). We included individual identity, year and observer identity (focal models only) as random effects in all models. To simulate values of the posterior distributions of the model parameters, we used the ‘sim’ function of the ‘arm’ package, v.1.10−1 (Gelman & Su, 2018). Based on 1000 simulations, we extracted the mode (β) of the estimated effect using the ‘posterior.mode’ function of the ‘MCMCglmm’ package, v.2.29 (Hadfield, 2010) and 95% credible intervals (CrI) using the ‘HPDinterval’ function of the ‘coda’ package, v.0.19−3 (Plummer et al., 2006). We calculated nonadjusted and adjusted repeatabilities as the among-individual variance/(among-individual variance + residual variance) (Lessells & Boag, 1987).

Evaluating correlations between assays and focals

We analysed the correlations between assays and focals using all individuals (956 assays on 672 individuals and 5636 focal sessions on 333 individuals for a total of 917 unique individuals, 88 of which were sampled across methods), and also present Bonferroni-corrected Pearson's correlations between the raw behaviours (Appendix, Table A4). We estimated among-individual correlations by fitting the assay behavioural axes and focal behavioural axes as four response variables in a single Bayesian multivariate generalized linear model using the ‘MCMCglmm’ function from in the ‘MCMCglmm’ package, v.2.29 (Hadfield, 2010). An important advance of these multivariate Bayesian techniques is that they quantify uncertainty around the estimate of each individual's mean dependent trait value and then carry that uncertainty forward in the test of among-individual correlations (Hadfield, 2010; Houslay & Wilson, 2017). We included individuals that only had measures for one behavioural method because the model uses these measures to improve estimation of the error around individual variation in dependent traits. We included sex (categorical variable), a linear and quadratic term for age (continuous variables), Julian date (continuous variable), local population density (continuous

Table 3
Nonadjusted and adjusted repeatabilities (R) for assay behavioural axes 1 and 2 for adults ($N = 351$ individuals), yearlings ($N = 189$ individuals) and juveniles ($N = 192$ individuals) using the full assay data set ($N = 672$ individuals) and for focal behavioural axes 1 and 2 for adults ($N = 219$) and yearlings ($N = 128$) using the full focal data set ($N = 333$ individuals)

Behavioural axis	Age class	Nonadjusted			Adjusted		
		R (95% CrI)	Among-individual variance (95% CrI)	Within-individual variance (95% CrI)	*R* (95% CrI)	Among-individual variance (95% CrI)	Within-individual variance (95% CrI)
Assay behavioural axis 1	Adult	0.39 (0.36, 0.42)	0.78 (0.65, 0.89)	1.22 (1.05, 1.35)	0.38 (0.34, 0.41)	0.66 (0.56, 0.76)	1.11 (0.97, 1.25)
	Yearling	0.47 (0.42, 0.52)	0.80 (0.71, 1.05)	0.96 (0.80, 1.16)	0.51 (0.45, 0.54)	0.77 (0.67, 1.01)	0.80 (0.69, 1.00)
	Juvenile	0.09 (0.07, 0.10)	0.18 (0.15, 0.24)	1.87 (1.64, 2.31)	0.09 (0.07, 0.11)	0.20 (0.15, 0.24)	1.94 (1.64, 2.34)
Assay behavioural axis 2	Adult	0.23 (0.21, 0.26)	0.58 (0.49, 0.69)	1.88 (1.69, 2.17)	0.24 (0.21, 0.26)	0.60 (0.49, 0.68)	1.92 (1.67, 2.15)
	Yearling	0.56 (0.51, 0.61)	1.53 (1.32, 1.91)	1.29 (1.02, 1.48)	0.52 (0.47, 0.57)	1.33 (1.09, 1.65)	1.29 (1.06, 1.54)
	Juvenile	0.17 (0.14, 0.20)	0.36 (0.26, 0.43)	1.68 (1.43, 2.05)	0.17 (0.14, 0.19)	0.34 (0.27, 0.44)	1.80 (1.46, 2.06)
Focal behavioural axis 1	Adult	0.11 (0.09, 0.12)	0.19 (0.15, 0.21)	1.53 (1.49, 1.61)	0.09 (0.08, 0.11)	0.16 (0.13, 0.19)	1.54 (1.47, 1.60)
	Yearling	0.06 (0.04, 0.07)	0.08 (0.08, 0.10)	1.32 (1.21, 1.44)	0.05 (0.04, 0.06)	0.06 (0.05, 0.08)	1.31 (1.20, 1.42)
Focal behavioural axis 2	Adult	0.12 (0.10, 0.13)	0.14 (0.12, 0.17)	1.10 (1.06, 1.15)	0.11 (0.09, 0.12)	0.13 (0.11, 0.16)	1.10 (1.05, 1.14)
	Yearling	0.13 (0.10, 0.15)	0.17 (0.12, 0.20)	1.12 (1.02, 1.20)	0.11 (0.09, 0.14)	0.15 (0.11, 0.18)	1.11 (1.02, 1.20)

Values are reported along with 95% credible intervals (CrI).

variable) and average social familiarity (continuous variable) as fixed effects. We included individual identity and year as random effects.

Our multivariate model was fitted using Monte Carlo Markov chains, which provide 95% CrI around the mode. We used a parameter-expanded prior (alpha.mu = 0, alpha.V = diag(4) × 1000) with a Cauchy distribution (nu = 1) and an identity matrix (V = diag(4)) (Hadfield, 2010). We fixed the within-individual covariance between behavioural axes at zero (rcov = ~idh (trait):units). We set our burn-in period to 3000 iterations, the thinning interval to 300 and the total number of iterations to 30 3000, resulting in a total sample of 1000 retained estimates. We assessed convergence visually and with the Gelman–Rubin statistic (1.05). As above, we mean-centred and standardized all numerical variables to one standard deviation within birth year and study grid to allow for the direct comparison of effect sizes (Schielzeth, 2010). We performed all analysis in the statistical software R, v.3.6.2 (R Core Team, 2019).

Ethical Note

This project was approved by the University of Alberta (Animal Care Permit AUP000000028) and the Yukon Government's Department of Tourism and Culture (Yukon Science and Explorers Permit 19-06S&E, 18-08S&E, 17-13S&E, 16-09S&E, 15-07S&E, 14-07S&E, 13-09S&E, 12-09S&E, 11-04S&E, 10-06S&E, 09-09S&E, 08-03S&E) and Department of Environment (Wildlife Research Permit 303).

RESULTS

Repeatability of Behavioural Axes

Comparable with the estimates presented in Martinig et al. (2021), we found that the adjusted and nonadjusted repeatabilities for the assay behavioural axes were highest for yearlings, followed by adults and juveniles (Table 3). While assay repeatabilities were moderate to high, especially for yearlings and adults (range 0.23–0.56; Table 3), focal repeatabilities were low overall (Table 3). For both focal behavioural axes, we detected low adjusted and nonadjusted repeatabilities for adults and yearlings (range 0.06–0.13; Table 3). Nonadjusted and adjusted repeatability estimates for both assays and focals were not significantly different across age classes (Table 3).

Evaluating Correlations between Assays and Focals

Assay behavioural axis 1 exhibited a strong positive among-individual correlation with assay behavioural axis 2 ($r^2 = 0.94$, 95% CrI = 0.83, 1.00; Fig. 1, Appendix, Table A5). Between assay and focal behavioural axes, we detected no among-individual correlations (Fig. 1, Appendix, Table A5); however, we found weak but significant correlations between certain assay and focal behaviours (Appendix, Table A4). We also found that behavioural expression was influenced by other variables for assay behavioural axis 1 and focal behavioural axis 1. All individuals had lower assay behavioural axis 1 scores (β = −0.12, 95% CrI = −0.22, −0.02) and higher focal behavioural axis 1 scores later in the season (β = 0.18, 95% CrI = 0.13, 0.23; Fig. 2, Appendix, Table A6) and higher focal behavioural axis 1 scores when local familiarity was higher (β = 0.08, 95% CrI = 0.01, 0.14). Males had lower focal behavioural axis 1 scores than females (β = −0.15, 95% CrI = −0.29, −0.02; Fig. 2, Appendix, Table A1). None of the other variables had a significant effect on behavioural expression.

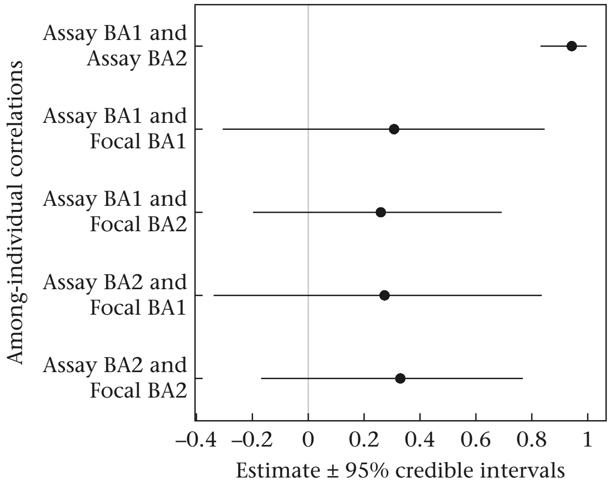

Figure 1. Among-individual correlations (± 95% credible intervals) observed for behavioural axes (BA).

DISCUSSION

As a result of the wide-reaching ecological and evolutionary consequences of consistent among-individual differences in behaviour (i.e. animal personality; Wolf & Weissing, 2012), behavioural ecology has seen a surge in methodologies used to capture this variation with little assessment of whether different methodologies capture similar behavioural axes in the same species. We used a tractable model system with a well-characterized ethogram where consistent among-individual differences in behaviour have been established (Boon et al., 2007; Cooper et al., 2017; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012, 2014; Westrick et al., 2019) to evaluate whether two commonly used methods, standardized behavioural assays and focal animal observations, provide similar measures of animal personality in a wild mammal. Our results align with previous studies in this system, demonstrating that when measured using assays, red squirrels show consistent among-individual variation that develops over ontogeny along two behavioural axes, which have been interpreted as ‘activity’ and ‘aggression’ (Boon et al., 2007; Cooper et al., 2017; Haines et al., 2020; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012, 2014; Westrick et al., 2019). However, counter to our a priori expectation, we did not detect strong among-individual correlations between the behavioural axes measured by assays and focals. Specifically, we expected a positive correlation between assay behavioural axis 1 and focal behavioural axes 1 or 2 and assay behavioural axis 2 and focal behavioural axis 1, given these composite measures were broadly associated with locomotion and territorial behaviour, respectively. This lack of correlation likely stems from the low repeatabilities of the behavioural axes measured through focal observation, or because the behaviours and dominant axes of variation were not conserved across methods. Our results suggest that the use of different methods may produce distinct measures of animal personality.

The low repeatabilities of the focal traits could be caused by a lack of trait stability across time or context (Biro & Stamps, 2015; Boake, 1989) or behavioural plasticity. If individuals respond differently to even slight environmental deviations (e.g. Martin & Réale, 2008; Niemelä et al., 2019; Nussey et al., 2007) or if focal traits also develop over ontogeny similar to traits measured with assays in this population (Kelley et al., 2015; Martinig et al., 2021), our precision in estimating among- and within-individual variance (and trait repeatability) will decrease. While we were not able to

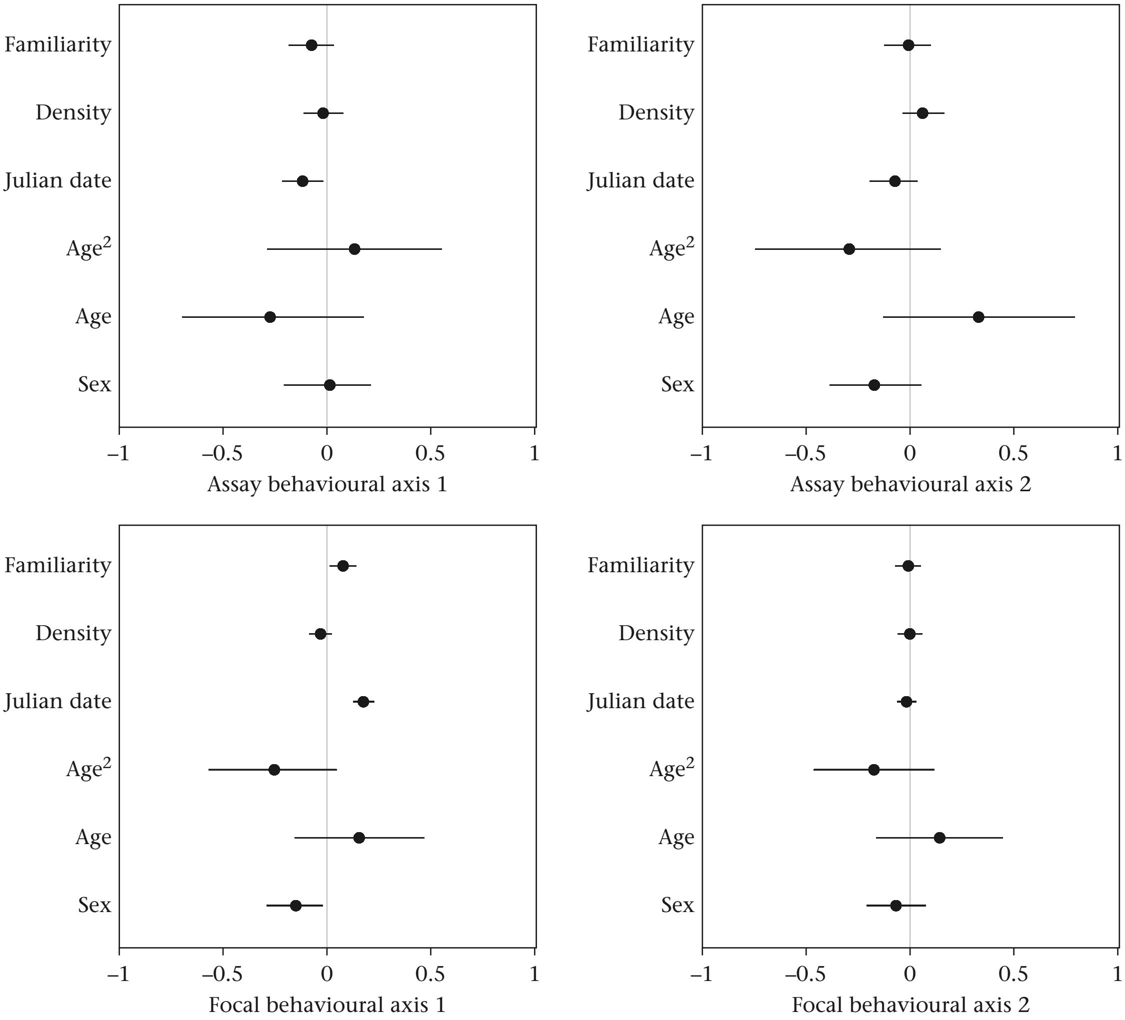

Figure 2. Coefficient plots (estimated means ± 95% credible intervals) for all behavioural axes.

account for all possible sources of environmental variability (e.g. breeding season, temperature, caching season, etc.), we did account for differences in the social environment that are known to affect behaviour in this population (e.g. population density: Dantzer et al., 2012; social familiarity: Siracusa et al., 2019). Despite this, our repeatability estimates were low, but bounded away from zero, suggesting that red squirrels exhibit consistent individual differences in a suite of behaviours (Boon et al., 2007; Cooper et al., 2017; Kelley et al., 2015; Martinig et al., 2021; Taylor et al., 2012, 2014; Westrick et al., 2019), including those measured using focal data. However, due to the low repeatabilities of focal behavioural axes relative to behavioural axes measured with assays, the latter may remain a more viable option to adequately control for the environment.

Another possibility for why we found no relationship between assay and focal measures is that the inherent differences between assays and focals indicate that behaviours were not interchangeable across methods. For example, mirror-image stimulation trials can be used to measure antagonistic behaviours in reaction to a conspecific by recording behaviours that are not naturally occurring (e.g. position relative to a mirror, or forced engagement with their reflection), whereas focals document naturally occurring behaviours like territorial calls, vigilance and interactions with conspecifics, which are behaviours that were not, or could not, be recorded during assays. These built-in differences between assays and focals may have contributed to the lack of correlation between behavioural axes across methods and is exemplified by the behaviours themselves being weakly correlated across methods. While we did detect weak correlations between the behaviours themselves, the relationships were difficult to interpret and not in the directions that would be expected, suggesting that assays capture behaviours we may not be measuring during focals. Despite measuring different behaviours from those measured using focals, consistent individual differences in behaviours as measured with assays do capture something of biological relevance in this population (e.g. fitness, offspring recruitment and physiological stress reactivity; Boon et al., 2007, 2008; Cooper et al., 2017; Martinig et al., 2021; Taylor et al., 2014; Westrick et al., 2021).

While we did not detect strong among-individual correlations between assay and focal behavioural axes, we did detect a strong positive among-individual correlation between the two assay behavioural axes. Building on earlier studies (Boon et al., 2007; Haines et al., 2020; Kelley et al., 2015; Taylor et al., 2012), we parsed out the within- and among-individual components, allowing us to better understand the link between these two behavioural axes. One potential explanation for the strong positive phenotypic correlation between assay behavioural axes is early life hormone exposure, as being subject to androgens or glucocorticoids can affect offspring development and behaviour (e.g. Brummelte et al., 2012; Eising et al., 2006; Müller et al., 2009); however, previous research in this system found that increased exposure to maternal glucocorticoids during lactation did not impact the correlation between assay behavioral axes (Westrick et al., 2021), suggesting involvement of some other mechanism.

While we have tried to use more objective labelling of each behavioural axis, the ambiguity in defining and interpreting what is being measured is a major problem in animal personality research (Beckmann et al., 2013; Carter et al., 2012). How we interpret each axis of variation is subjective and mislabelling of behavioural axes is not uncommon (Cabrera et al., 2021; Carter et al., 2012). For example, because all behaviours involving movement positively loaded on assay behavioural axis 1, we interpret this axis to be a measure of activity, although earlier work in this species (Boon et al., 2007) and in a similar taxonomic group (e.g. eastern chipmunks, *Tamias striatus*; Martin & Réale, 2008) used the term exploration. However, individuals that exhibit locomotory behaviours during the open field trial (e.g. walking and jumping) could also be exhibiting a stress response to their environment (Koolhaas et al., 1999). Likewise, we interpret focal behavioural axis 2, similar to Dantzer et al. (2012), as capturing a trade-off between vigilance and feeding (referred to as boldness elsewhere; Réale et al., 2007; Sih et al., 2004; Silva et al., 2008) and focal behavioural axis 1 as a measure of territoriality (i.e. loaded positively on travelling and rattling, and negatively on nest use); but it is possible that the focal behavioural axes are composite measures of assay behavioural axis 1 (e.g. activity), with focal behavioural axis 2 being orthogonal to focal behavioural axis 1. If we consider focal behavioural axis 1 to be indicative of whether an individual is inside or outside of the nest, then focal behavioural axis 2 may be a measure of what the individual is doing when outside of the nest (i.e. whether they are active or inactive). Even if measuring ecologically relevant or naturally occurring behaviours may improve our ability to label these behaviours more accurately, we are still making a subjective judgement about how to label these traits. Where possible, avoiding the use of subjective labelling of behavioural axes and instead letting the behaviours speak for themselves appears warranted.

Conclusion

Our study highlights that assays and focals are not interchangeable and instead appear to capture unique dominant axes of behavioural variation. While measuring ‘real world’ behaviours with focals may improve our ability to understand what is being measured, our focal measures exhibited low repeatability, possibly due to behavioural plasticity. Indeed, this may explain why the prevailing view of individual behaviour shifted over time from being highly plastic (reviewed in Wilson, 1998) to potentially repeatable and indicative of animal personality (Carere & Maestripieri, 2013) as studies began to measure the behaviour of wild animals under standardized conditions, rather than in natural contexts. Future studies should be aware of the challenges that environmental variation poses when trying to measure animal personality using naturally occurring behaviours and recognize that such measures may differ substantially from those measures obtained in controlled trials. Therefore, where possible, standardized behavioural assays are likely to continue to be widely used to quantify consistent among-individual differences in behaviour. Connecting measurements from controlled trials to natural behaviours to better understand what behaviours measured in standardized assays represent remains a difficult task for future studies.

Data Availability

All data will be archived on figshare and available from https://doi.org/10.6084/m9.figshare.14988579.v1 after 1 August 2023 to allow for future publications. During this embargo period, we will respect any reasonable request regarding data accessibility.

Author Contributions

A.R.M.: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original draft, review, and editing. **H.J.K.**: Formal analysis; funding acquisition; visualization; writing – original draft, review, and editing. **E.R.S.**: Formal analysis; funding acquisition; investigation; methodology; validation; writing – review and editing. **E.K.S.**: Funding acquisition; investigation; writing – review and editing. **P.P.**: Investigation; writing – review. **A.G.M.**: Data curation; funding acquisition; project administration; methodology; resources; writing – review and editing. **B.D.**: Funding acquisition; investigation; methodology; project administration; resources; writing – review and editing. **D.M.D.**: Methodology; writing – review. **J.E.L.**: Funding acquisition; project administration; methodology; resources; writing – review. **S.B.**: Funding acquisition; project administration; methodology; resources; writing – review.

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Appendix

Table A1
Ethogram of behaviours measured in the open field trial assay, mirror-image stimulation assay and behavioural focals

Behaviour	Definition
Open field trial	
Chew/scratch	Individual chews or scratches surface of testing arena
Hang	Individual holds top edge of arena or mirror with at least one limb
Hole	Individual pauses and dips head in holes on arena floor
Jump	Individual leaves ground and reaches top of testing arena
Self-grooming	Individual touches any part of body with mouth/hands
Still	Individual is motionless for 2 s
Walk	Individual moves forward with both back feet
Mirror-image stimulation	
Approach latency	Begins when individual orients head towards mirror
Attack latency	Begins at same time as approach latency. Ends with first attack
Attack rate	Individual strikes mirror with one or both paws; each discrete contact is recorded as a separate attack
Back of arena	Individual is located in the back third of the testing arena, farthest from the mirror
Front of arena	Individual is located in the front third of the testing arena, closest to the mirror
Focal	
Bark	Vocal call signifying presence of predator (Smith, 1978). Call consists of a repeated low-amplitude, high-frequency ‘peep’
Caching	Individual stores food (e.g. spruce cones, fungi) in environment
Feeding	Individual handles and ingests food
Foraging	Individual actively looks for food
In nest	Individual is located in its nest
Rattle	Territorial vocal call, consists of medium-pitched notes repeated at a consistent interval
Resting	Individual has head tucked or resting on a branch, eyes are often closed
Self-grooming	Individual touches any part of body with mouth/hands
Squeak	Call consisting of short, quiet high-pitched notes repeated at high frequency. Call function currently unknown
Travelling	Moving across ground or trees
Vigilant	Individual is stationary and crouching on hindlimbs in a tree, chin is off the branch and eyes are open and alert

Behaviours listed are those used here.

Table A2
Principal component analyses of focal behaviours for all principal components (PC; $N = 333$ individuals)

Focal behaviour	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Bark	0.05	−0.21	0.13	**−0.60**	−0.05	−0.11	−0.23	**0.72**	0.01	−0.01	0.12
Caching	0.18	0.28	−0.22	−0.07	**0.67**	−0.22	**0.49**	−0.09	0.01	−0.20	0.23
Feeding	0.13	**0.63**	**0.56**	−0.03	−0.16	−0.03	−0.09	−0.03	0.08	0.13	**0.46**
Forage	0.38	0.11	−0.36	0.07	−0.10	0.13	−0.25	0.14	**−0.73**	−0.07	0.25
In nest	**−0.61**	−0.01	**−0.44**	−0.07	−0.20	−0.03	0.02	−0.03	0.10	0.06	**0.61**
Rattle	**0.44**	−0.15	−0.26	0.02	0.03	0.03	0.03	−0.03	0.29	**0.78**	0.13
Resting	−0.10	−0.39	0.31	**0.51**	0.35	**0.47**	0.08	0.14	−0.07	0.02	0.33
Self-grooming	0.15	−0.16	0.11	0.21	**−0.54**	−0.19	**0.73**	−0.01	−0.17	−0.03	0.06
Squeak	0.04	−0.15	0.09	**−0.53**	−0.02	**0.52**	0.17	**−0.60**	−0.16	≤0.01	0.04
Travel	**0.45**	−0.17	−0.15	0.04	−0.20	0.11	−0.17	−0.05	**0.52**	**−0.57**	0.25
Vigilant	0.07	**−0.48**	0.31	−0.14	0.12	**−0.62**	−0.26	−0.25	−0.19	0.01	0.30
Standard deviation	1.38	1.16	1.10	1.05	1.01	1.00	0.97	0.96	0.91	0.85	0.08
Proportion of variance	0.17	0.12	0.11	0.10	0.09	0.09	0.09	0.08	0.07	0.07	0.00
Cumulative proportion	0.17	0.30	0.41	0.51	0.60	0.69	0.78	0.86	0.93	1.00	1.00

All behaviours with observations were included. Bolded values are heavily loaded (score ≥ 0.40). Proportion of variance is the variance captured by that specific PC, while the cumulative proportion is the variance captured by that specific PC in addition to earlier PCs.

Table A3
Nonadjusted and adjusted repeatabilities (*R*) for assay behavioural axes 1 and 2 only for individuals with repeated measures (in the same age class) for 103 adults ($N = 217$ assays), 47 yearlings ($N = 94$ assays) and 62 juveniles ($N = 125$ assays)

Behavioural axis	Age class	Nonadjusted			Adjusted		
		R (95% CrI)	Among-individual variance (95% CrI)	Within-individual variance (95% CrI)	*R* (95% CrI)	Among-individual variance (95% CrI)	Within-individual variance (95% CrI)
Assay behavioural axis 1	Adult	0.43 (0.36, 0.48)	0.85 (0.64, 1.01)	1.09 (0.91, 1.33)	0.40 (0.33, 0.45)	0.62 (0.53, 0.85)	1.01 (0.86, 1.25)
	Yearling	0.41 (0.35, 0.52)	0.75 (0.49, 1.03)	0.99 (0.71, 1.27)	0.47 (0.36, 0.55)	0.69 (0.645 1.00)	0.81 (0.61, 1.11)
	Juvenile	0.10 (0.07, 0.13)	0.21 (0.14, 0.30)	1.92 (1.50, 2.47)	0.10 (0.07, 0.14)	0.24 (0.14, 0.32)	1.99 (1.53, 2.45)
Assay behavioural axis 2	Adult	0.20 (0.17, 0.26)	0.48 (0.36, 0.63)	1.78 (1.47, 2.18)	0.20 (0.18, 0.27)	0.50 (0.39, 0.68)	1.90 (1.54, 2.21)
	Yearling	0.49 (0.40, 0.60)	1.17 (0.74, 1.48)	1.17 (0.86, 1.53)	0.47 (0.36, 0.55)	0.96 (0.68, 1.38)	1.14 (0.88, 1.59)
	Juvenile	0.17 (0.12, 0.21)	0.34 (0.23, 0.48)	1.77 (1.37, 2.23)	0.16 (0.11, 0.20)	0.34 (0.20, 0.47)	1.79 (1.36, 2.30)

Values are reported along with 95% credible intervals (CrI).

Table A4
Pearson's correlations across methods for individuals with both assays and focals ($N = 88$ individuals)

Focal behaviour	Assay behaviour											
	Walk	Jump	Hole	Hang	Chew	Self-groom	Still	Front of arena	Back of arena	Attack	Attack latency	Approach latency
Bark	0.05	0.01	−0.03	−0.01	−0.02	−0.04	−0.01	−0.07	**−0.09**	−0.05	0.03	0.07
Caching	−0.03	−0.05	−0.08	−0.10	**−0.14**	0.06	0.04	0.04	−0.03	−0.05	0.01	−0.08
Feeding	0.07	0.002	0.06	−0.01	0.004	0.06	−0.05	0.05	−0.03	0.004	−0.06	−0.07
Forage	−0.06	0.01	0.04	**0.09**	0.09	−0.05	−0.02	0.08	**−0.11**	−0.02	−0.03	−0.04
In nest	−0.03	−0.002	0.03	0.005	0.02	−0.01	0.04	0.004	0.04	0.04	0.02	0.05
Rattle	−0.07	−0.06	−0.08	0.01	−0.05	−0.002	0.01	0.01	−0.05	−0.05	−0.02	0.02
Resting	−0.03	0.03	−0.01	0.04	0.03	0.004	−0.02	−0.03	0.05	0.05	0.04	0.03
Self-grooming	−0.03	−0.02	0.01	0.01	−0.02	0.04	−0.03	0.004	−0.06	0.02	−0.02	0.03
Squeak	0.02	0.03	0.03	0.07	0.03	−0.02	−0.03	0.02	0.003	−0.003	0.01	−0.03
Travel	0.04	0.02	−0.001	0.05	0.09	−0.07	−0.003	−0.03	0.05	−0.06	0.02	0.003
Vigilant	0.02	0.01	−0.07	−0.07	−0.06	−0.02	0.01	**−0.09**	−0.01	−0.003	0.03	0.04

Bolded values indicate significance after correcting for multiple comparisons ($P < 0.00379$).

Table A5
Among-individual correlations observed for all behavioural axes

Among-individual correlations	Assay behavioural axis 1	Assay behavioural axis 2
Assay behavioural axis 2	**0.94 (0.83, 1.00)**	
Focal behavioural axis 1	0.31 (−0.31, 0.85)	0.27 (−0.34, 0.84)
Focal behavioural axis 2	0.26 (−0.20, 0.69)	0.33 (−0.17, 0.77)

Values in parentheses represent 95% credible intervals (CrI).

Table A6
Bayesian linear mixed models with behavioural axes as both the response variable and the fixed effects ($N = 917$ individuals)

	Response variable			
	Assay behavioural axis 1	Assay behavioural axis 2	Focal behavioural axis 1	Focal behavioural axis 2
Fixed effect	**β (95% CrI)**	**β (95% CrI)**	**β (95% CrI)**	**β (95% CrI)**
Age	−0.27 (−0.70, 0.18)	−0.33 (−0.13, 0.79)	0.16 (−0.15, 0.47)	0.14 (−0.16, 0.45)
Age^2	0.13 (−0.29, 0.55)	−0.29 (−0.75, 0.15)	−0.26 (−0.57, 0.05)	−0.17 (−0.46, 0.12)
Average familiarity	−0.07 (−0.18, 0.03)	−0.01 (−0.12, 0.10)	**0.08 (0.01, 0.14)**	−0.01 (−0.07, 0.05)
Julian date	**−0.12 (−0.22, −0.02)**	0.07 (−0.20, 0.04)	**0.18 (0.13, 0.23)**	−0.02 (−0.06, 0.03)
Local density	−0.02 (−0.11, 0.08)	0.06 (−0.04, 0.17)	−0.03 (−0.09, 0.02)	−0.001 (−0.06, 0.06)
Sex[a]	0.01 (−0.21, 0.21)	0.17 (−0.39, 0.05)	**−0.15 (−0.29, −0.02)**	−0.07 (−0.21, 0.08)
Random effects				
Individual identity	0.83 (0.61, 1.06)	0.70 (0.46, 0.94)	0.11 (0.07, 0.14)	0.13 (0.10, 0.19)
Year	0.47 (0.09, 2.01)	0.17 (0.04, 0.77)	0.39 (0.10, 2.06)	0.40 (0.10, 1.89)
Residual variance	1.32 (1.10, 1.47)	1.81 (1.58, 2.05)	1.50 (1.44, 1.55)	1.13 (1.09, 1.17)

Values represent the effect mode (β). Bold values indicate strong (no 95% credible interval (CrI) overlap with zero) support for an effect.

[a] Reference category for ‘sex’ was set to ‘female’.

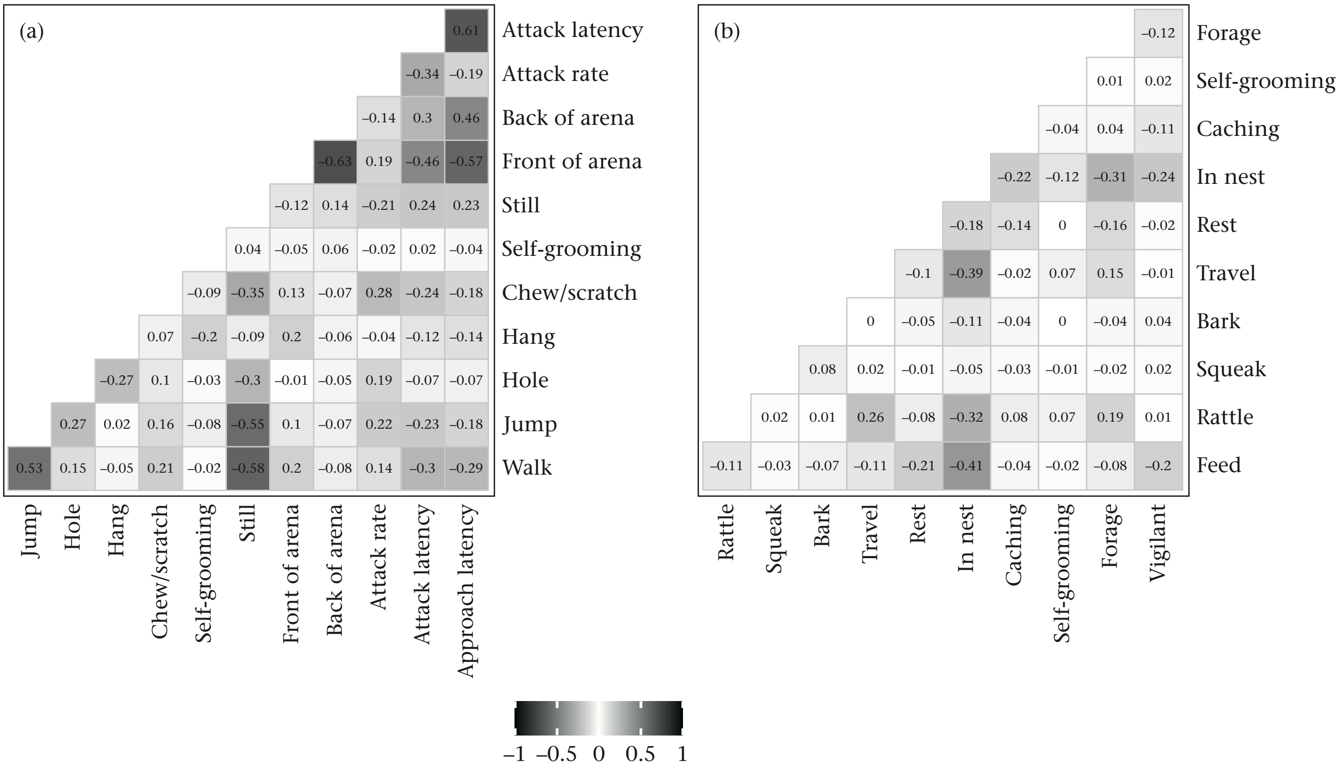

Figure A1. Pearson’s correlations for behaviours measured in (a) assays and (b) focals.