Moose on the loose: personality-driven space use and activity in a large, free-roaming cervid

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Abstract

Background

Animal personality (i.e., consistent inter-individual behavioural and physiological differences that are repeatable over time and across contexts) has important implications for ecological processes, yet remains poorly studied in large herbivores such as cervids.

Methods

In this study, we investigated personality and the occurrence of a behavioural syndrome in 33 free-ranging female moose (*Alces alces*) inhabiting a human-dominated boreal landscape in central Sweden, using long-term GPS tracking data. We quantified three movement-based behavioural traits (movement rate as a proxy of activity, intensity of space as a proxy of exploration, and distance from forest edge as a proxy of boldness) and assessed their repeatability and covariance using linear mixed models and Bayesian multivariate approaches.

Results

We found strong and repeatable inter-individual variation across all traits (repeatability: 0.40–0.61), demonstrating clear evidence of personality in moose. Trait expression was significantly

influenced by both intrinsic factors (e.g., age) and extrinsic environmental drivers (e.g., daylength, proximity to human infrastructure), indicating that personality is expressed within a context of environmental modulation. However, despite pronounced individual differences, we found no evidence for consistent correlations among traits, and thus no support for a behavioural syndrome.

Conclusions

The absence of a behavioural syndrome likely reflects the complex and heterogeneous conditions of human-dominated, multi-predator landscapes, where individuals must respond flexibly to multiple, and sometimes conflicting, selective pressures. This may favour independent adjustment of behavioural traits rather than covariation of multiple traits.

Our findings highlight that, although personality is present in moose, behavioural traits may remain weakly integrated in complex environments, emphasizing the role of behavioural plasticity in shaping individual strategies. These results provide a valuable baseline for future studies investigating how personality varies across environmental gradients and influences ecological processes, population dynamics, and management outcomes in large herbivores.

Keywords: Behavioural syndrome; Movement ecology; Ungulates; Behavioural plasticity; Repeatability;

Background

Over the past 30 years, the study of personality (i.e., consistent inter-individual behavioural and physiological differences that are repeatable over time and across contexts [1]) in animals has increasingly gained attention. More specifically, research reveals that within-individual variation previously dismissed as measurement error or non-adaptive variation around an

adaptive mean [2] can instead provide critical insights into consistent inter-individual differences [3] expressed in ecologically relevant contexts [foraging: 4, e.g., dispersal: 5, acquisition of dominance rank: 6, group joining preferences: 7]. Accordingly, there is increasing consensus that, apart from variation due to individual characteristics (e.g., age, sex), internal state or motivation, and external environmental factors [8], consistent inter-individual variation in the mean expression of behaviour is an intrinsic characteristic of individuals reflecting, among others, both their genetic make-up and developmental history [9]. For example, in sleepy lizards (*Tiliqua rugosa*), variation over a continuum from resident to explorers reflected variation in life-history tactics, varying the degree of interactions with their surroundings [10]. Within this context, explorative lizards were more likely to interact with more conspecifics, including potential mates, and find new resources than resident lizards, who would rely on monopolizing smaller but more profitable areas that reproductive partners regularly visit. Importantly, behavioural consistency does not preclude behavioural plasticity, as animals must still adjust their behaviour to varying environmental conditions [6, 11, 12]. The degree of plasticity will, however, differ among behavioural types and bear different consequences. For example, in male tree swallows (*Tachycineta bicolour*), individuals displaying high levels of a trait (i.e., aggressiveness) do not need to adjust their behaviour across contexts, because its expression was sufficient to ensure high fitness. Instead, greater cross-context plasticity would be expected of less aggressive individuals to achieve high fitness [13]. Interestingly, such a difference did not apply to female tree swallows, whose reproductive success was neither predicted by personality nor plasticity. Notably, today there is consensus on the existence and extent of persistent among-individual differences, commonly quantified as repeatability, which are thought to explain approximately 35% of behavioural variation in both wild and captive settings [14].

Within the existing literature, movement ecology [15, 16] is the field in which investigations of the relationship between individual variation and movement have produced some of the strongest empirical support for the relevance of personality. Movement data as part of biologging data typically consist of spatial positions recorded at discrete timestamps using animal-borne devices [17, 18]. Quantifying inter-individual variation requires large sample sizes (i.e., many different individuals) and many repeated measurements [19]. Recent advances in the accuracy of tracking technologies have enabled the remote acquisition and study of high-resolution data, revealing the potential to unravel aspects of animal movement and both their response to the surrounding environment as well as implications for animal ecology, behaviour, and ecosystem functions, even for elusive species living in remote places [20]. In this light, extracted movement-based metrics such as distance travelled, use of open habitats, and intensity of use can be considered as proxies of commonly assessed behavioural traits, such as activity, boldness, and exploration [21]. These proxies show moderate-to-high repeatability and are often correlated, creating what is known as a "behavioural syndrome" [22]. Because movement decisions integrate risk-taking, habitat selection, energetic trade-offs, and learning over long temporal scales [23-25], movement trajectories are particularly informative for detecting personality in long-lived wild and free-roaming animals, for which traditional experimental assays are often impractical, if not impossible to use [8, 19, 26].

As a result of these methodological developments, evidence of personality has been found in several taxa [27]. However, research remains limited in many ecologically and economically important groups, such as cervids (family Cervidae, commonly known as "deer"). Co-occurring with humans across all types of anthropogenic landscapes [28], deer have a long history of interacting with humans, providing important services and recreational benefits (e.g., hunting

activities and aesthetic value, seed dispersal, and meat [29]). They are also responsible for significant economic loss in human land use and interests through damages to crops [30], forests [31, 32], and economically valuable species [33, 34], as well as through wildlife-vehicle collisions [35-37]. Their longevity (up to 15-20 years of age [38]), and learning capacity affect movement and space use [39, 40], making them particularly attractive for exploring different personality types. Yet, despite the diverse impacts these species have on both ecosystems and society, and their worldwide distribution, studies exploring their personality are extremely limited [41]. This gap likely reflects a historical focus on population-level management metrics, assumptions of behavioural homogeneity, and the logistical difficulty of applying experimental personality assays to forest-dwelling, free-ranging species.

Within the deer family, moose (*Alces alces*) is the largest representative and one of the most iconic species of the temperate-boreal megafauna [42], deeply intertwined with society [43]. With a lifespan of up to 20 years [44], this long-lived large herbivore holds an important cultural, practical, and traditional role for many Indigenous cultures [45-47], and it is the source of economic benefit, sustenance, and recreational opportunities. In managed forests, moose are directly responsible for forest damage due to selective browsing on economically valuable trees [48]. Across its European range, it possesses a multifaceted ecology, encompassing partially migrating populations [49, 50] and diverse responses to different predators [51, 52] and human harvest [53], all of which may be shaped by individual personalities [54, 55]. However, as highlighted by Esattore, Masilkova [41], most studies have only indirectly acknowledged possible implications of personality. For example, Johnsen [56] discussed individual consistency in anti-human movement responses in moose, showing that females exhibited strong among-individual variation in escape behaviour when disturbed by humans, particularly in flight distance and use of alternative tactics (running vs. sneaking).

These behavioural differences were independent of hunting-season survival, indicating that variation in movement responses reflects stable behavioural tendencies rather than short-term plasticity. Rolandsen, Solberg [57] and Bunnefeld, Börger [58] showed consistent inter-individual differences in migratory strategy in female moose, and Rolandsen, Solberg [57] emphasized how it correlated with different fitness outcomes (i.e., better body conditions and higher twinning rate in migratory animals). Similarly, Van Moorter, Singh [59] explored how individual heterogeneity affected migration decisions within Fennoscandia**,** concluding that behavioural predispositions operating along environmental drivers could not be excluded. Finally, Ofstad, Markussen [60] pinpointed the high repeatability in the use of risky, food-rich open grasslands both across years and seasonal contexts, highlighting the trade-off between gaining higher reproductive benefits (e.g., heavier calves, higher twinning rate) and suffering lower survival during hunting.

Regardless of suggestions on individual-specific behaviours, an in-depth characterization of personality in this long-lived species is still lacking. Such knowledge could be crucial for understanding responses to rapidly changing ecosystems under anthropogenic pressure, e.g., in Fennoscandian moose, a resource of high hunting value but with partially declining populations (Artfakta (Swedish Species Database); artfakta.se). To fill this gap, this study aims to characterize inter-individual variability in moose based on long-term data from GPS collars. Following an approach already applied to another ungulate species (e.g., wild boar (*Sus scrofa)* [21]), we hypothesize that I) moose will exhibit repeatable inter-individual variability in three behavioural traits (i.e., movement rate, intensity of space use, distance from forest edge) and that II) these traits will covary, creating a movement syndrome.

Material and methods

Study area

Our study was conducted in central Sweden, in an area within Gävleborg, Jämtland, and Västernorrland counties (Fig.1). The vegetation is characterized by intensively managed boreal forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with an understory of heather (*Calluna vulgaris*), berry-producing shrubs, and grasses. The region experiences strong seasonality in photoperiod, with marked variation in daylength across the year, and the natural landscape is interspersed with human infrastructure. Local moose density averages between 4 and 9 moose per 10 km^2 [61]. Alongside moose, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are present in the area, together with predators including brown bears (*Ursus arctos*), wolves (*Canis lupus*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*), and golden eagle (*Aquila chrysaetos*).

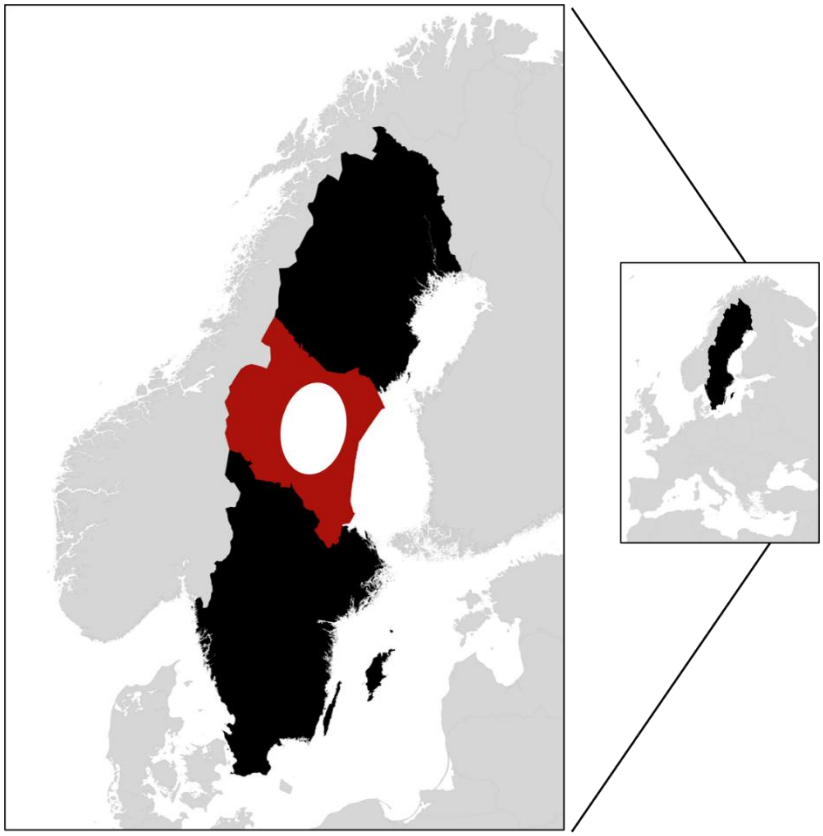

Figure 1: Map of the study area (in white) within the Gävleborg, Jämtland, and Västernorrland counties highlighted in red (Sweden, 2026).

158

159 **GPS data**

160 Moose were immobilized from a helicopter during winter (February–March, 2020–2025) using
161 a CO_2-powered dart rifle (DANiNJECT, Kolding, Denmark) administering a mixture containing
162 50 mg xylazine (Xylased® 500 mg, Bioveta, Ivanovice na Hané, Czech Republic) and 4.45 mg
163 etorphine hydrochloride (Captivon® 98 Etorphine HCl, 9.8 mg ml^{-1}, Wildlife Pharmaceuticals
164 (Pty) Ltd, White River, South Africa). Immobilization was reversed with 50–100 mg naltrexone
165 and 5–6 mg atipamezole. Age was estimated based on tooth wear. Each individual was
166 equipped with a GPS neck collar (Vectronic Aerospace GmbH, Berlin, Germany), and capture
167 and handling followed established protocols described in detail by Græsli, Thiel [62]. All animal
168 marking and handling had been approved by the Animal Care Committees in Umeå, Sweden
169 (DNR A14-15, A11-20, A6-25). The collars were programmed to record locations at 3-hour
170 intervals throughout the year, switching to a finer scale (30 minutes) during the calving period
171 (May-June). All location data were stored and managed in the Wireless Remote Animal
172 Monitoring (WRAM) database system at the Swedish University of Agricultural Sciences,
173 ensuring standardized data handling and long-term data security [63]. To minimize the effects
174 of capture, anesthesia, and post-handling stress, we excluded the first month of tracking
175 following collar deployment for each individual [62, 64]. We removed duplicates and
176 subsampled the data to 3-hour intervals to ensure consistency throughout the year and across
177 years. Finally, we retained individuals for whom we had at least three consecutive years of
178 data. Our final dataset included 431.629 observations for 39 individuals (33 females, 6 males).
179 Due to the skewed sample size and to avoid the confounding effects of sex-specific movement
180 behaviour, we focused only on females, resulting in 374.807 observations.

181

Land use data processing and spatial metrics

We downloaded land use data for the three counties included in the study (Gävleborg, Jämtland, and Västernorrland) from the Swedish National Land Cover Database (NMD, naturvardsverket.se), and processed it using ArcGIS Pro (Esri, Redlands, CA). Although the most recent national land use inventory was updated in 2023, part of these counties were not included in that release. Because our analyses focused on human-generated open areas (e.g., clearcuts) to quantify boldness-related metrics, we therefore used the NMD land use layer updated to 2018, and manually added spatial information on forest clearcuts using national forestry records obtained from the Swedish Forest Agency (skogsstyrelsen.se). Then, we derived three thematic layers from the resulting land use raster: forest, clearcuts, and human infrastructure. Clearcut polygons corresponding to the period 2018–2025 were erased from the forest polygon layer using a pairwise erase procedure, yielding a forest structure that more closely reflects the contemporary spatial configuration of open and closed habitats. We imported GPS locations of moose as point features and projected them to match the coordinate reference system of the land-use layers. For each GPS fix, we calculated Euclidean distances to the nearest forest edge, excluding clearcuts, and the nearest human infrastructure. The resulting distance metrics were exported for subsequent statistical analyses.

Movement traits

We selected three commonly used metrics of animal movement as proxies of different behavioural traits, following the approach described in Masilkova, Ciuti [21] for wild boar. Therefore, we used movement rate as a proxy of Activity, and intensity of space use as a proxy of Exploration. However, as in our case “diurnality” used by Masilkova and colleagues would

not have represented a valid indicator of Boldness in our setting due to a different species activity pattern [i.e., bimodal instead of nocturnal as in wild boar, 44], and strong seasonality in daylength across the year characteristic of our study area, we opted for "distance from forest edge" as a proxy of Boldness. Following the approach by Masilkova, Ciuti [21], all metrics were calculated as weekly means to reduce short-term noise from climatic and other unmeasured local factors [19]. Specifically:

- *Movement rate*: calculated as Euclidean distance (in meters) covered by a moose between two consecutive fixes. It represents general activity in a given week, with more active individuals covering longer distances than less active ones [65].
- *Intensity of space use*: computed by dividing the total movement distance in a week by the square root of the area of the weekly area of movement (i.e., 95% of the minimum convex polygon of all locations). It reflects exploration, with individuals with a lower intensity of use moving in a linear and more explorative way (i.e., crossing more habitat patches and exploring new food resources) compared to those scoring higher, who would move in restricted, familiar areas [66].
- *Distance from forest*: calculated as Euclidean distance (in meters) between the moose position and the edge of the nearest forest polygon. It indicates boldness, with larger values interpreted as increased exposure within open and potentially risky habitats [60].

Statistical analyses

All analyses were conducted in R (ver. 4.3.3, R Core Team, 2024). To explore the effect of different factors on our response variables, we built a series of linear mixed models (summarized in Table 1) using the package *lme4* [67]. When needed, we log-transformed the

response variable to ensure normality and applied 'female ID' and 'year' as random effects in all univariate mixed models to account for repeated measures and autocorrelation [67]. For all models, we checked collinearity among predictors using variance inflation factors (VIF), and proceeded with predictors with a value below 5, indicating no problematic multicollinearity. We used model diagnostics (R packages *DHARMa* and *performance* [68, 69]) to assess deviations from the assumptions of normality, homoscedasticity, and independence.

Individual movement trajectories were constructed using the *ltraj* function from the *adehabitatHR* package [70]. From each trajectory, we calculated step length (i.e., the Euclidean distance between consecutive fixes, in meters) and step rate (i.e., step length standardized by the time interval between fixes, in meters/hour). Visual investigation of yearly trajectories was used to infer moose's migratory status, and each individual was consequently labelled as "migratory" or "resident" based on their seasonal movement patterns [49, 50]. Weeks were defined using ISO calendar weeks, and daylength was calculated for each GPS location using the *suncalc* R package [71]. As moose respond sensitively to roads [72], in our models we also accounted for the influence of roads on movement patterns. Consequently, daylength and distance from human infrastructure were included in the model as weekly means, as were all response variables. We also added the time of day, or 'hour', as a covariate to account for the bimodal daily activity patterns in moose (i.e., activity peaks during twilight [44]). All continuous covariates were centered and scaled before modeling. Quadratic terms were included where exploratory analyses suggested non-linear relationships (i.e., distance from human infrastructure). Following Masilkova's approach [21], we estimated the adjusted repeatability (*sensu* Nakagawa & Schielzeth) using the *rptR* package [73], partitioning variance into between-individual, between-year, and residual components.

To test for correlated among-individual variation (behavioural syndrome), we fitted a Bayesian multivariate mixed-effects model using the *brms* package [74]. The three behavioural traits (movement rate, intensity of space use, and distance from forest) were modeled jointly with Gaussian error distributions. The model included fixed effects for age, distance to human infrastructure (linear and quadratic), daylength, and hour of day. Female ID was modeled as a correlated random intercept across traits, while year was excluded from the multivariate model to improve convergence and computational efficiency, following previous studies and given that our primary focus was on among-individual covariation rather than temporal variance partitioning [e.g., 21].

Models were fitted using the *cmdstanr* function, and posterior convergence was assessed using trace plots, effective sample sizes, and posterior predictive checks. Posterior samples were used to estimate pairwise correlations among individual traits. Best Linear Unbiased Predictors (BLUPs [75]) were extracted from individual random effects (i.e., posterior means of individual-level random intercepts, referred to here as BLUPs for visualization purposes) to place each moose along the behavioural continuum. Models were fitted with multiple Markov chain Monte Carlo chains, random initialization, and default weakly informative priors. We ran the model using eight chains with 2000 iterations each, including 800 warm-up iterations. The total variance explained (R^2) by the model for each trait was obtained using the *bayesRsquare* function [74]. Model fit was evaluated using posterior predictive checks implemented via the *pp_check* function, which indicated good predictive performance for all response variables. The proportion of variance explained (Bayesian R^2) was calculated from posterior draws. From the posterior distributions, we extracted the among-individual variance–covariance matrix to estimate pairwise correlations among behavioural traits. BLUPs were obtained from individual-level random intercepts to characterize each female's relative position along the

behavioural continua. Posterior means and 95% credible intervals were calculated, and BLUPs were visualized using pairwise scatterplots, density plots, and correlation matrices to illustrate the structure and strength of the behavioural syndrome.

*Table 1: Structure of the three linear mixed models to test the effects of individual, environmental and methodological factors on our response variables. [a]Categorical variable (Migratory/Resident); [b]Age of the moose in years; [c] Weekly mean distance of each moose's position from the nearest human infrastructure (i.e., buildings, roads, railway, artificial surfaces): [d]Weekly daylength, calculated as number of hours from sunrise to sunset; [e]Hour of the day; ●denotes variables that were log-transformed; * denotes variables that were added to the models as linear and quadratic effects. All numerical variables were scaled and centered.*

Response variable	Fixed effects	Random effects
Movement rate●	Migratory status[a] Age[b] Distance from human infrastructure[c]* Daylength[d] Hour[e]	Female ID Year
Intensity of use●	Migratory status[a] Age[b] Mean distance human infrastructure[c]* Daylength[d] Hour[e]	Female ID Year
Distance from forest edge●	Migratory status[a] Age[b]	Female ID Year

	Mean distance human infrastructure[c]* Daylength[d] Hour[e]	

Results

Univariate linear mixed models

Over the annual cycle, moose displayed movement rates averaging (mean ± SD) 60.88 m/h ± 38.22, an average intensity of space use of 2.55 ± 1.01, and a distance from forest edge of 31.64 ± 25.32 m (Figure S1). All three models revealed substantial inter-individual variability, supporting our metrics as good proxies of behavioural traits in moose (Figure 2). Fixed effects accounted for ~46% of the variation for movement rate, ~33% for intensity of use, and ~41% for distance from forest edge (Table 2). In addition, long-term inter-individual differences and inter-annual differences (i.e., random effects) explained ~34% of the variability in movement rate, ~37% of intensity of use, and ~49% in distance from forest edge (Table 3). Adjusted repeatability was 0.40 for intensity of use, 0.46 for movement rate, and 0.61 for distance from forest edge, confirming the latter as both our strongest and most repeatable personality proxy (Table 3).

Movement rate (i.e., a proxy of activity) was significantly predicted by all the effects included in the linear mixed model, except for hour, although their effect sizes differed considerably. Migratory status had a small negative effect (Fig. S2d), indicating that the residents' weekly activity was slightly lower than migrants'. Age also had a strong negative effect on activity (Fig. S2b), with activity declining as individuals' age increased. Distance from human infrastructure had a strong, non-linear effect on activity (Fig. S2c), with activity increasing with distance up

306 to an intermediate level and declining at greater distances. Finally, daylength also had a
307 strong, positive effect on activity (Fig. S2a), which increased with increasing hours of light.

308 Intensity of use (i.e., a proxy of exploration) was also significantly predicted by all effects
309 included in the model. As for the previous proxy, migratory status had a weakly significant
310 effect: residents were more exploratory than migrants (Fig. S3d), with the effect size being
311 stronger than for movement rate. As for movement rate, exploration also decreased with
312 increasing age (Fig. S3b). Instead, distance from human infrastructure showed the very
313 opposite trend than for movement rate, with individuals being more explorative at very low
314 or very high distances from human infrastructure but minimally explorative at intermediate
315 distances (Fig. S3c). Finally, animals' exploration increased with increasing daylight (Fig. S3a),
316 and there was also a small and barely significant positive effect of hour.

317 Finally, the distance from the forest edge (i.e., a proxy of boldness) was significantly predicted
318 by most of the effects included in the model. While there seemed to be no significant
319 difference between resident and migratory moose, nor connected to the hour of the day, once
320 again age had a substantial and strongly positive effect (Fig. S4b), with older animals keeping
321 a larger distance from the forest edge compared to young ones. The variation of boldness in
322 function of human infrastructure followed the same pattern as for activity (Fig. S4c), with
323 boldness being higher at intermediate distance from infrastructure. Finally, daylength had a
324 strong negative effect on boldness (Fig. S4a), with individuals keeping closer proximity to the
325 nearest forest edge on longer days. Inter-individual variability for each movement trait is
326 shown in Figure 2.

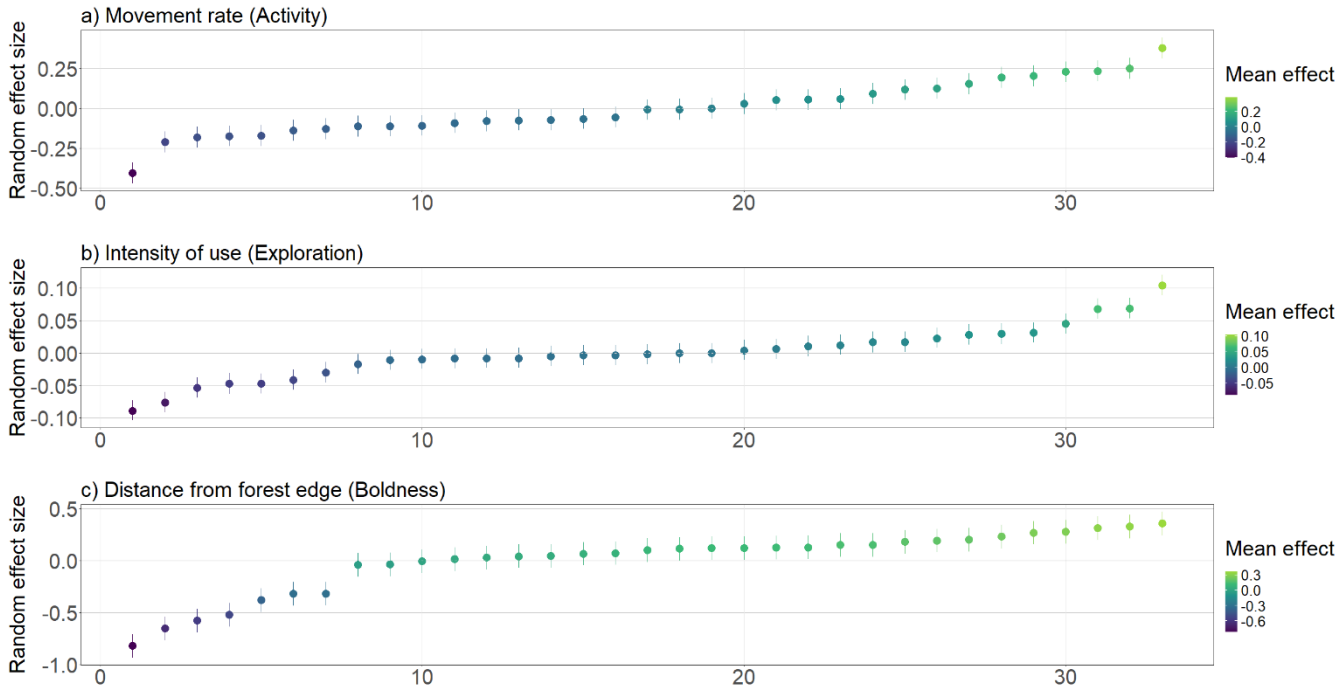

Figure 2: Inter-individual variability depicting behavioural types for three movement traits (a. movement rate, b. intensity of use, c. distance from forest edge), as obtained from the random intercepts of the mixed effect models explaining traits' variability. The horizontal line represents the median behaviour of the population, and each dot corresponds to one of the 33 individual female moose. The values in the y-axis represent the size of the individual random effect, with colour reflecting the mean size and error bars representing the standard deviation. The order of the individuals on the x-axis is different across the three plots (Sweden, 2020-2025).

Behavioural syndrome

Using the covariance structure among our three metrics (movement rate, intensity of use, distance from forest edge) in a multivariate Bayesian mixed-effects model, we found no clear evidence for the presence of a movement syndrome in moose, because the consistency in among-individual correlations among all three traits was low.

Posterior mean correlations were weak and highly uncertain (movement rate–intensity of use: r = -0.13 [-0.45, 0.21]; movement rate–distance from forest edge: r = 0.25 [-0.09, 0.56]; intensity of use–distance from forest edge: r = 0.01 [-0.33, 0.36]). In all cases, credible intervals overlapped zero, indicating a lack of robust covariance among traits. The broad posterior

distributions and the absence of clear relationships between individual-level estimates (BLUPs) further supported this pattern. Pairwise relationships between individual-level behavioural traits revealed weak trends among traits, but with substantial uncertainty (Fig. S5). Movement rate showed a slight positive association with distance from forest edge, while a weak negative trend emerged between intensity of use and movement rate. However, these relationships were highly variable, with wide confidence intervals and strong overlap around zero (Fig. 3). Overall, our results did not indicate consistent covariation among traits and therefore did not support the presence of a movement syndrome in the studied population of moose.

Behavioural composition of the population

The examination of inter-individual variability in behavioural traits to assess the behavioural composition of the population (Fig. 2) showed that distance from forest edge was the metric showing the highest asymmetry, with 48.5% of individuals (n = 16) having values significantly above the population mean (i.e., presumably being bolder), 21.2% (n = 7) being below the mean, and 30.3% (n = 10) overlapping the population mean. The opposite was true for movement rate, for which only 30.3% of individuals (n = 10) displayed values significantly above the population mean, while most of our study population (42.4%; n = 14) showed significantly lower values (i.e., less activity). However, this was the trait with the highest diversification within the population, considering that only a few individuals (27.3%; n = 9) did not differ from the population mean. Finally, for intensity of use, a larger proportion of individuals overlapped the population means (45.5%, n = 15), with 30.3% (n = 10) and 24.2% (n = 8) exhibiting significantly higher and lower values, respectively.

Overall, the fact that a substantial proportion of individuals exhibited values significantly different from the population mean indicates marked inter-individual variability in movement traits. However, despite this pronounced inter-individual variability, these differences were not structured consistently across traits (i.e., suggesting no behavioural syndrome), indicating that behavioural types were not organized along a common behavioural axis.

Table 2: Parameters estimated from the models. All numerical covariates are scaled. Significant effects are in bold.

Response variable	Predictor	β	SE	df	t	p
Movement rate	Intercept	3.889	0.156	11.33	24802	<.001
Number of observations = 374807	**Migratory status (Resident)**	**-0.028**	**0.004**	**374100**	**-6.123**	**<.001**
Number of Female IDs = 33	**Age**	**-0.635**	**0.008**	**231000**	**-78.176**	**<.001**
Number of years= 6	**Distance from human infrastructure**	**0.4351**	**0.003**	**374800**	**142.702**	**<.001**
Random effects						
FemaleID variance= 0.285						
SD = 0.534	**Distance from human infrastructure^2**	**-0.432**	**0.003**	**374800**	**-143.583**	**<.001**
Year variance=0.095						
SD=0.309						
Residual variance = 0.237	**Daylength**	**0.270**	**0.000**	**367700**	**302.730**	**<.001**
SD = 0.487	Hour	0.000	0.000	374800	0.471	0.637

Intensity of use **Number of observations = 374807** **Number of Female IDs = 33** **Number of years = 6** **Random effects** **FemaleID variance= 0.045** **SD = 0.212** **Year variance=0.015** **SD=0.126** **Residual variance = 0.051** **SD = 0.226**	Intercept	1.209	0.063	10.97	19045	<.001
	Migratory status (Resident)	**0.039**	**0.002**	**373300**	**18.308**	**<.001**
	Age	**-0.224**	**0.003**	**174800**	**-59.350**	**<.001**
	Distance from human infrastructure	**-0.091**	**0.001**	**374800**	**-64.983**	**<.001**
	Distance from human infrastructure^2	**0.095**	**0.001**	**374800**	**68.444**	**<.001**
	Daylength	**0.047**	**0.000**	**361600**	**114.679**	**<.001**
	Hour	**0.000**	**0.000**	**378400**	**2.475**	**0.0133**
Distance from forest edge **Number of observations = 374807** **Number of Female IDs = 33** **Number of years= 6** **Random effects** **FemaleID variance= 2.072**	Intercept	3.289	0.421	11.12	7.802	<.001
	Migratory status (Resident)	0.005	0.007	374800	0.772	0.440
	Age	**1.505**	**0.013**	**348400**	**114.706**	**<.001**
	Distance from human infrastructure	**0.196**	**0.004**	**374800**	**39.975**	**<.001**

SD = 1.439 **Year variance=0.689** **SD=0.830** **Residual variance = 0.614** **SD = 0.784**	**Distance from human infrastructure^2**	**-0.130**	**0.004**	**374800**	**-26.888**	**<.001**
	Daylength	**-0.103**	**0.001**	**374100**	**-71.846**	**<.001**
	Hour	-0.000	0.001	374800	-0.104	0.917

374

375 *Table 3: Variance explained by fixed effects (R^2marginal) and both fixed and random effects (R^2 conditional) as predicted by*
376 *mixed effect models explaining the variability and the repeatability of movement traits in our 33 female moose monitored*
377 *between 2020 and 2025 in Sweden.*

Movement trait	**Explained variance**		**Adjusted repeatability**		
	R^2 marginal	R^2 conditional	Estimate	95% CI	P value
Movement rate	0.455	0.791	0.461	0.30-0.61	0.001
Intensity of use	0.327	0.693	0.402	0.27-0.53	0.001
Distance from forest edge	0.405	0.892	0.614	0.42-0.77	0.001

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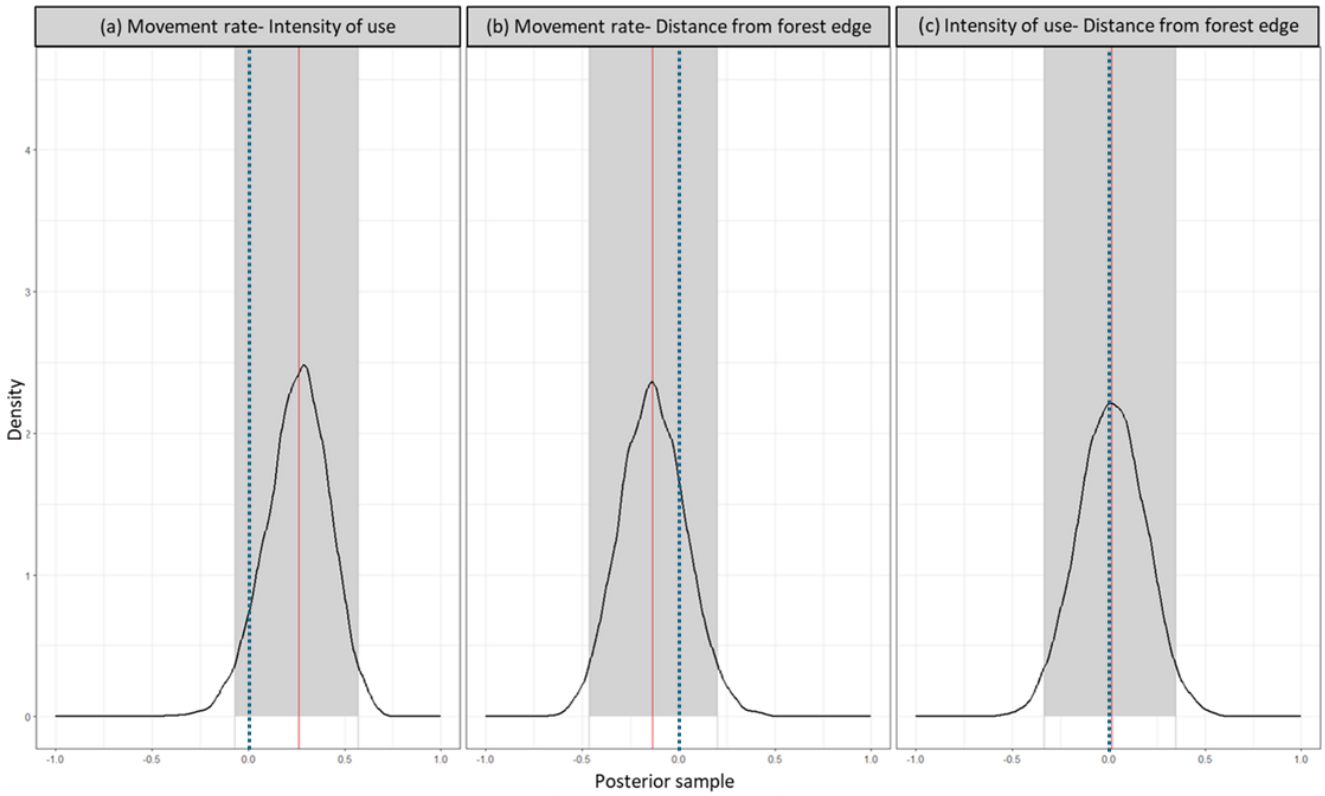

Figure 3: Posterior density of the covariance for all pairs of response variables. The red line represents the median value, the shaded area represents the high posterior density (HPD) region, and the dashed blue line indicates 0.

Discussion

In this study, we tested for behavioural traits in free-ranging female moose inhabiting a human-dominated landscape using long-term GPS tracking data to address a major knowledge gap on cervid personality. Our work generated two main findings: first, moose exhibited strong and repeatable inter-individual variation in all three movement-based traits, indicating that this variation could be interpreted as an expression of personality [1]. Second, despite this pronounced variation, we found no evidence for a behavioural syndrome, suggesting that behavioural traits in moose vary independently rather than covary within individuals.

Consistent with our first hypothesis, the moderate-to-high repeatability estimates observed across traits (0.402-0.614) indicate that a substantial proportion of behavioural variation

394 reflects stable differences among individuals rather than short-term plasticity or
395 environmental noise [14, 76]. These findings contribute to a rapidly growing body of
396 literature demonstrating the invaluable contribution of GPS-based movement data to
397 capture meaningful inter-individual behavioural variation [77] in elusive, free-ranging species
398 [78-80], while reducing biases associated with captivity [77].
399 In addition to identifying consistent inter-individual differences, our results also highlight
400 how environmental and individual factors shape the expression of each behavioural trait in
401 this long-lived cervid.
402 All three traits were influenced by a combination of intrinsic (e.g., age) and extrinsic drivers
403 (e.g., proximity to human infrastructure, daylength), suggesting that personality is expressed
404 within a framework of strong biological and environmental modulation rather than as fixed
405 behavioural outputs in moose. This is in line with previous research on moose, where
406 authors have shown that these factors strongly shape movement behaviour and habitat
407 selection [49, 50]. In our case, age emerged as one of the most consistent predictors across
408 traits, with activity and exploration declining with increasing age, while boldness increased.
409 In moose, age-related variation in habitat use and movement behaviour has been linked to
410 differences in experience and risk sensitivity, with older individuals often showing distinct
411 spatial strategies compared to younger animals [49]. The pattern shown in our results likely
412 reflects ontogenetic shifts in risk-taking and energy allocation among individuals, with older
413 ones adopting more conservative movement strategies while simultaneously tolerating
414 more open or exposed habitats. Distance from human infrastructure, an integrated part of
415 most wildlife habitats [81, 82], also played a key role in shaping behavioural expression,
416 although its effect differed among traits.

417 Complex and non-linear responses to human presence have already been documented in
418 moose, where individuals adjust habitat use and movement patterns to balance foraging
419 opportunities with risk avoidance [72], but also how linear objects affect movement
420 decisions in the natural environment [83]. These contrasting responses suggest that
421 different behavioural dimensions are shaped by different drivers in this long-lived herbivore,
422 often acting at different temporal scales. Similarly, daylength exerted strong effects across
423 all traits, likely reflecting seasonal changes in resource availability and risk exposure. In
424 moose, diel and seasonal changes in movement and habitat use are well documented [44]
425 and frequently associated with variation in daylength, temperature, and predation risk [84].
426 Moreover, ungulates are known to modulate their behavioural responses to environmental
427 factors, further emphasizing that behaviour is dynamically adjusted in response to changing
428 ecological conditions [85].
429 Finally, the weak differences between resident and migratory individuals suggest that life-
430 history strategies may also contribute to behavioural variation. In moose, partial migration
431 has been associated with differences in resource use and risk exposure, with individuals
432 adopting alternative strategies depending on environmental conditions to improve fitness
433 [49]. Given that personality research has already helped clarify some mechanisms underlying
434 partial migration in other cervids (e.g., wapiti (*Cervus canadensis*) [86]), extending this
435 approach to moose could further improve our understanding of how the expression of
436 different traits modulates this crucial aspect of their biology.
437 Despite clear evidence of personality, we found no support for our second hypothesis. Thus,
438 our results provide no evidence for a behavioural syndrome (i.e., suites of correlated
439 behaviours across situations [87]) in moose, indicating that behavioural traits vary
440 independently within individuals rather than covary. Even though they are in contrast with

findings from other authors [e.g., 21, 55], our results are not surprising. One likely explanation for the absence of a behavioural syndrome in our system is that we investigated it in a species inhabiting a human-dominated landscape in a multi-carnivore species setting (with particularly high densities of brown bears [88]), which exposes animals to multiple, often conflicting selective pressures (e.g., predation risk, human avoidance, resource availability, and habitat fragmentation [89]). In prey species, including ungulates, behavioural responses to risk are highly flexible and context-dependent, with individuals adjusting movement, habitat selection, and activity patterns to balance foraging opportunities against perceived danger [90, 91]. In such environments, different behavioural traits may respond to different drivers, thus weakening correlations among traits. Humans can also elicit behavioural responses that are equal to or stronger than those triggered by natural predators, leading to rapid shifts in movement and space use strategies [92, 93]. Such multidimensional and often conflicting pressures may decouple behavioural traits, preventing the emergence of consistent syndromes. For example, poison frog tadpoles (*Allobates femoralis*) under predation risk showed a weaker or non-existent behavioural syndrome between novel environment exploration and shelter emergence than their naïve counterpart, supporting the idea that environmental stressors can disrupt behavioural syndromes [94]. Similarly, rabbits (*Oryctolagus cuniculus*) responded to spatial and temporal variation in predation risk by domestic cat (*Felis catus*), adjusting multiple, complementary behaviours independently [95]. Finally, a study on coyotes (*Canis latrans*) across an urban gradient has shown that the expression of different behavioural traits (i.e., boldness, exploration, and detection) varied in function of the degree of anthropogenic pressure (e.g., human density, pollution), showing the adaptivity of separating rather than covarying behavioural traits in a complex system [96].

Another aspect that likely further contributes to our results is behavioural plasticity (i.e., the ability of individuals to modify their behaviour in response to changing environmental conditions or internal states; Komers 1997). In heterogeneous environments with fluctuating resource availability, individuals need to adjust different behavioural traits independently in response to environmental variation. Recent work has highlighted that behavioural syndromes are often context-dependent and can be weakened or disrupted by variation in individual plasticity [97]. In movement ecology, individual behavioural variation can be decomposed not only into consistent differences among individuals, but also into reversible behavioural plasticity and differences in predictability, all of which may vary independently. Because individuals can differ in how strongly they respond to environmental gradients, correlations among traits at the population level may be reduced even when traits are individually repeatable [19].

In large herbivores, including ungulates, movement decisions integrate multiple processes that may operate on different spatial and temporal scales. For example, in African elephants (*Loxodonta africana)*, individuals vary not only in their average movement strategies but also in how strongly they adjust movement behaviour across seasonal gradients, leading to substantial variation in behavioural plasticity among individuals [19]. Moreover, individuals located near the centre of a behavioural continuum are believed to rely more heavily on behavioural plasticity to achieve sufficient fitness, whereas individuals at the extremes can adopt more consistent strategies [98, 99]. For example, in sticklebacks (*Gasterosteus aculeatus*), bolder individuals show more consistent and predictable behaviour, whereas less extreme individuals exhibit greater behavioural plasticity in response to environmental variation [100]. Similarly, in wild perch (*Perca fluviatilis*), individuals differ not only in their average behavioural expression but also in how strongly they adjust behaviour across

environmental gradients, indicating substantial variation in plasticity among individuals [101]. In large herbivores, bold individuals consistently exploit riskier habitats, while other individuals adjust their habitat use more flexibly in response to changing risk-reward trade-offs [102]. For example, in roe deer, some individuals consistently select safer habitats while others adjust habitat use plastically in response to variation in predation risk and resource availability, resulting in differing levels of behavioural consistency [103]. Likewise, in red deer, individuals modify habitat use and activity patterns in response to hunting risk, but the magnitude of these adjustments varies among individuals, indicating substantial variation in behavioural plasticity [104]. In this context, the relatively high proportion of individuals with intermediate behavioural expressions observed in our study animals (27.3-45.5% of the study population, depending on the considered trait) may have contributed to the separation of traits, as these individuals adjust their behaviour flexibly across contexts rather than consistently expressing correlated trait combinations.

Finally, our findings are of particular interest given moose's solitary nature (but see [105]for seasonal changes in aggregation patterns, and [106] for modulation of grouping behaviour in function of perceived predation risk). Thus, in gregarious animals, the social environment plays a major role in shaping behavioural expression. Consequently, individuals within groups of the social species may have more similar personalities [107] or the behaviour of a single individual measured in isolation may not reflect that individual's expression in a social group [108]. In contrast, solitary species make decisions largely independently of conspecifics, and their behavioural variation is more likely to reflect intrinsic factors, which allow traits to respond more flexibly and independently to environmental conditions. This further emphasizes the importance of advancing our understanding of personality in moose

to better elucidate its role in shaping key aspects of the biology and ecology of this long-lived, large, and solitary species.

Conclusions

Our study demonstrates that females of a long-lived cervid, like moose, exhibit strong and repeatable individual differences in movement-based behaviours that can be attributed to personality. The absence of consistent correlations among traits indicates that these behaviours are not organized into a behavioural syndrome, in contrast with patterns reported in other species, including ungulates (e.g., wild boar [21], wapiti [86]). This separation of behavioural traits suggests that, in anthropogenic and heterogeneous landscapes such as our setting, behavioural variation may be widespread in individuals but only weakly integrated across dimensions (i.e., different metrics). Moreover, in a population where the mean expression of a trait overlaps with the population mean for 27.3–45.5% of individuals, the behavioural plasticity of these individuals becomes an important factor to consider in future research and management.

In a long-term perspective, our findings provide a valuable baseline for investigations into how personality varies across environmental gradients (such as latitude or differing levels of human disturbance), and how it shapes key ecological processes and ecosystem function.

Personality-mediated differences can influence anti-predator responses and interactions with the environment, including habitat selection [109], movement decisions, and herbivore–plant dynamics arising from trade-offs between foraging and risk [110]. By linking consistent individual behavioural variation to these processes, future work will improve our

534 understanding of the fitness consequences of personality and its role in shaping population
535 dynamics and ecosystem processes in large herbivores such as deer and other ungulates [111].

536 Finally, from an applied perspective, personality is known to influence how animals respond
537 or not to management interventions, but this aspect has seldom been considered in deer (e.g.,
538 in wapiti [86], sika deer (*Cervus nippon*) [112-114], moose [115]). Therefore, incorporating
539 personality into management frameworks may improve predictions of animal responses to
540 environmental change and enhance the effectiveness of interventions, particularly in
541 increasingly human-modified ecosystems that are prone to conflicts. This, in turn, will deepen
542 our understanding of aspects of deer biology in the Anthropocene that have so far been
543 neglected or only partially understood.

544 **Declarations**

545 **Ethics statement**

546 All personnel handling the moose were certified according to the standards of the Swedish
547 Animal Welfare Agency and the Swedish Board of Agriculture. The marking of moose has
548 been approved by the Animal Care Committee in Umeå, Sweden (A-14-15, A11-20, A6-25).

549 **Availability of data**

550 The datasets analysed during the current study are not publicly available, but are available
551 from the corresponding author on reasonable request.

552 **Competing interests**

553 The authors declare no competing interests.

554 **Funding statement**

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Authors' contributions

Conceptualization: BE, WN; Methodology: BE; Data curation: BE; Formal analysis: BE; Visualization: BE; Writing – original draft: BE, WN; Writing – review & editing: All authors; Supervision: WN

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Microsoft Copilot to improve the clarity and readability of the English language. After using this tool, the authors reviewed and edited the content as needed, and take full responsibility for the publication's content.

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