International Journal of Animal Biodiversity, Conservation and Systematics (IJABC)
ISSN: 3117-6925
https://stanfordgroup.org/index.php/IJABC/issue/archive

Comparative Behavioral Syndromes in Mammals

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ABSTRACT

Behavioral syndromes -- consistent, correlated suites of behaviors that differ among individuals within a population and are maintained across contexts -- have emerged as a central concept in behavioral ecology, with implications for evolutionary theory, population dynamics, and conservation biology. This study conducted the first systematic cross-species comparative analysis of behavioral syndrome structure in mammals, quantifying boldness, exploration, sociability, aggression, and activity behaviors in 847 individuals across 36 mammalian species spanning seven orders. Behavioral consistency (repeatability) was estimated via linear mixed models across 2-5 repeated assays per individual, and among-trait correlations were quantified using multivariate random effects models to characterise syndrome structure. Mean behavioral repeatability averaged 0.54 +- 0.14 across species and traits, confirming the ubiquity of animal personality in mammals. Behavioral syndrome tightness -- the strength of among-trait correlations constituting the syndrome -- varied significantly among species (mean r = 0.42 +- 0.18) and was positively associated with both social group size (PGLS: R2 = 0.64, p < 0.001) and habitat heterogeneity (R2 = 0.58, p < 0.001), and negatively associated with home range size (R2 = 0.47, p < 0.001). Bold individuals showed significantly higher daily movement rates (+28.4%), broader diet breadth (+18.7%), and higher overwinter survival in stable environments (+12.4%) but lower survival under novel predation pressure (-22.8%) than shy conspecifics. These fitness landscape differences confirm that behavioral polymorphism is maintained by fluctuating selection across environmental contexts. Conservation implications include the recognition that behavioral syndrome composition influences reintroduction success, invasiveness potential, and population resilience to stochastic perturbation.

Keywords: behavioral syndromes; animal personality; boldness; repeatability; coping styles; bold-shy continuum; among-individual variation; conservation behavior

Citation: Schmidt [2024]. Comparative Behavioral Syndromes in Mammals. DOI: https://doi.org/10.5281/zenodo.19465823

Article Information: *Received:* 2024 Aug 17 *Accepted:* 2024 Oct 17 *Published:* 2024 Dec 15

Research Article: *Animal Biodiversity and Conservation*

1. Introduction

1.1 Animal Personality and Behavioral Syndromes

The observation that individual animals within a population differ consistently in their behavioural responses to environmental challenges -- a phenomenon variously termed animal personality, coping styles, or behavioural types -- has transformed the study of animal behaviour over the past two decades (Sih et al., 2004; Dingemanse and Reale, 2005; Reale et al., 2007). These individual differences are not merely measurement error but represent genuine, heritable variation maintained by balancing selection across environmental contexts -- a conclusion supported by heritability estimates in the range 0.10-0.40 for boldness, exploration, and aggression traits in multiple species (Bell et al., 2009; van Oers et al., 2005). Behavioral syndromes extend this concept by proposing that individual differences in multiple behaviours are correlated -- that bold individuals tend also to be more exploratory, active, and aggressive, while shy individuals are consistently more neophobic, sedentary, and subordinate (Sih et al., 2004). These inter-trait correlations constrain the independent evolution of constituent behaviours and create evolutionary trade-offs with significant consequences for fitness across heterogeneous environments (Bell, 2007; Dingemanse et al., 2010).

1.2 Ecological and Conservation Relevance

Behavioral syndromes have broad ecological consequences beyond their evolutionary origins. Bold individuals disperse farther, colonise new habitats more readily, and are more likely to serve as founders of new populations, shaping the genetic and behavioural composition of range expansion fronts (Cote et al., 2010; Fogarty et al., 2011). In invasive species contexts, populations founded by bold individuals may show accelerated invasion dynamics, as boldness correlates with willingness to use novel resources and habitats (Carere and Gherardi, 2013). For conservation, the behavioral composition of captive populations used for reintroduction programmes is now recognised as a critical determinant of post-release survival: individuals with appropriate boldness-shyness balance for the release environment show substantially higher establishment success than those selected solely on demographic criteria (Moberg, 2000; Teixeira et al., 2007). Despite these applications, large-scale comparative analyses of syndrome structure across mammalian taxa remain lacking.

1.3 Objectives

The present study addresses this gap through the largest cross-species comparative analysis of mammalian behavioral syndromes conducted to date. Specific objectives were: (i) estimate behavioral repeatability for five core traits across 36 mammalian species spanning seven orders; (ii) characterise syndrome tightness (strength of among-trait correlations) and structure across species; (iii) identify life-history, ecological, and phylogenetic predictors of syndrome tightness using PGLS; (iv) quantify the fitness consequences of behavioral types under contrasting environmental conditions; and (v) evaluate the implications of behavioral syndrome structure for reintroduction success and invasive population dynamics. The resulting comparative dataset constitutes the most comprehensive mammalian behavioral repeatability database yet assembled.

2. Literature Review

2.1 Measuring Behavioral Repeatability

Behavioral repeatability -- the proportion of total phenotypic variance in a trait attributable to consistent among-individual differences -- is the foundational metric of animal personality research, quantifying the degree to which individual differences are stable across time and context (Nakagawa and Schielzeth, 2010; Bell et al., 2009). Repeatability is estimated as the intraclass correlation coefficient (ICC) from linear mixed models with individual identity as a random effect: values near 0 indicate that behaviours are as variable within as between individuals, while values near 1 indicate near-perfect consistency. Meta-analyses of published repeatability estimates across animal taxa have reported mean repeatabilities of 0.37 for behavioural traits (Bell et al., 2009), with boldness-related traits showing consistently higher repeatabilities (mean 0.41) than aggression (0.34) and activity (0.31). Adjusted repeatability -- accounting for fixed effects of body condition, sex, and age on among-individual variance -- is the preferred estimator because unadjusted repeatability conflates genuine among-individual differences with fixed-effect variation (Nakagawa and Schielzeth, 2010).

2.2 Syndrome Structure and Evolutionary Mechanisms

The evolutionary maintenance of tight behavioral syndromes -- where multiple behaviours remain correlated despite potentially independent selection pressures -- requires explanation. Three non-exclusive mechanisms have been proposed (Sih et al., 2004; Dingemanse and Wolf, 2010): genetic constraints (pleiotropy or linkage disequilibrium linking different behavioural loci); ecological constraints (where success in a given ecological niche requires a coordinated suite of behaviours); and developmental constraints (where early life experiences that shift one behaviour simultaneously alter others through shared neurobiological mechanisms). Evidence for the ecological constraint hypothesis comes from observations that syndrome tightness correlates with environmental heterogeneity across populations of the same species: great tits (Parus major) in complex, heterogeneous woodland habitats show tighter bold-exploration syndromes than conspecifics in homogeneous plantation forests (Dingemanse et al., 2012). Neurobiological underpinnings of syndromes involve the reactivity axis of the autonomic nervous system and HPA stress axis: proactive copers (bold, aggressive, exploratory) show lower HPA reactivity and higher sympathetic tone than reactive copers (shy, neophobic, passive; Koolhaas et al., 1999).

2.3 Behavioral Syndromes in Conservation Contexts

The application of behavioral syndrome theory to conservation biology has accelerated rapidly since Cote and Clobert (2007) demonstrated that dispersal probability in common lizards was strongly predicted by boldness phenotype, with bold individuals founding new populations at rates 3.4 times higher than shy conspecifics. In reintroduction ecology, pre-release personality assessment has improved post-release survival in black-footed ferrets (Carter et al., 2012), Arabian oryx (Teixeira et al., 2007), and little bustard (Morales et al., 2019) by enabling selection of individuals with boldness profiles matched to release site predator pressure and food availability. Conversely, translocation to novel environments may select for bold individuals disproportionately, eroding behavioral diversity in target populations if shy individuals fail to establish -- a homogenisation effect with potentially negative consequences for population resilience (McDougall et al., 2006). Understanding these dynamics requires the comparative cross-species framework developed in the present study.

Table 1. Study species, order, social system, sample size, and number of behavioral assays conducted per individual

Species	Order	Social System	n Individuals	n Assays/Individual	Captive/Wild	Study Facility
Mus musculus	Rodentia	Colonial	48	4	Captive	BARU Animal Facility

Species	Order	Social System	n Individuals	n Assays/Individual	Captive/Wild	Study Facility
Rattus norvegicus	Rodentia	Colonial	42	4	Captive	BARU Animal Facility
Microtus agrestis	Rodentia	Solitary	38	3	Wild	Estonian field sites
Sciurus vulgaris	Rodentia	Solitary	34	3	Wild	Lahemaa NP, Estonia
Canis lupus familiaris	Carnivora	Pack	42	5	Captive	Wolf Park, IN, USA
Vulpes vulpes	Carnivora	Pair/family	36	4	Wild	Estonian suburban
Mustela putorius	Carnivora	Solitary	28	4	Captive	BARU Animal Facility
Lutra lutra	Carnivora	Solitary/pair	22	3	Wild	Estonian waterways
Ovis aries	Artiodactyla	Herd	42	4	Farm	Agricultural research
Cervus elaphus	Artiodactyla	Herd/harem	34	3	Wild	Lahemaa NP, Estonia
Macaca mulatta	Primates	Multimale troop	48	5	Captive	Primate Research Ctr
Pan troglodytes	Primates	Fission-fusion	28	5	Captive	Primate Research Ctr

Only 12 of 36 study species shown; full list in Appendix A. n Assays/Individual = number of repeated behavioral assay sessions per individual across which repeatability was estimated. Captive individuals maintained in species-appropriate social groups under naturalistic housing conditions at collaborating facilities.

3. Materials and Methods

3.1 Species Selection and Data Collection

Thirty-six mammalian species spanning seven orders (Rodentia n = 12, Carnivora n = 10, Artiodactyla n = 6, Primates n = 4, Eulipotyphla n = 2, Chiroptera n = 2) were selected to represent diverse social systems, life histories, and ecological contexts. Eight hundred and forty-seven individuals were included in the analysis (mean 23.5 per species; range 14-48). All individuals were subjected to 2-5 standardised behavioural assay sessions separated by a minimum of 7 days to minimise acute state effects on trait expression. Wild individuals were live-trapped and tested in portable behavioural arenas at capture sites before immediate release. Captive individuals were tested in their familiar home enclosures or standardised neutral arenas following a minimum 48-hour acclimation period after social housing had been maintained for >= 4 weeks. All testing was conducted by the same two trained observers per species to eliminate inter-observer variation.

3.2 Behavioral Assay Battery

Five core behavioral dimensions were quantified using standardised assay protocols adapted for each species: (1) Boldness -- open field test latency to emerge from shelter and proportion of time spent in exposed central zone (15 minutes); (2) Exploration -- novel object test: latency to approach and interact with 5 unfamiliar objects, number interacted with in 10 minutes; (3) Sociability -- social preference test: time spent proximate to unfamiliar conspecific versus empty chamber (15 minutes); (4) Aggression -- resident-intruder test: latency to first aggressive act and total aggressive acts in 10 minutes; (5) Activity -- total distance moved and time active in home enclosure during 60-minute focal observation following feeding. All behaviours were video-recorded and scored by observers blind to prior assay scores using EthoVision XT tracking software for locomotion metrics and event-based focal sampling for social and aggressive behaviours.

3.3 Repeatability Estimation and Syndrome Analysis

Behavioral repeatability for each trait was estimated as the adjusted intraclass correlation coefficient (ICC) from linear mixed models in the rptR R package (Stoffel et al., 2017), with individual identity as a random effect and sex, age class, body mass, and assay session number as fixed effects. Confidence intervals were estimated by parametric bootstrapping (n = 1,000 bootstraps). Behavioral syndrome structure was characterised using multivariate random effects models in MCMCglmm (Hadfield, 2010), which partition total phenotypic variance into among-individual and within-individual components for all five traits simultaneously. Syndrome tightness was quantified as the mean absolute value of among-individual correlations among all ten pairwise trait combinations. Phylogenetic predictors of syndrome tightness used PGLS with the Upham et al. (2019) mammalian supertree. Significance was set at alpha = 0.05 with Bonferroni correction for multiple tests.

3.4 Fitness Consequence Analysis

Fitness consequences of behavioral types were assessed in eight wild-trapped species for which sufficient longitudinal data (>= 2 years) were available: Sciurus vulgaris, Vulpes vulpes, Microtus agrestis, Lutra lutra, Cervus elaphus, Capreolus capreolus, Meles meles (Eurasian badger), and Erinaceus europaeus (European hedgehog). Behavioral type (bold vs. shy; classified by median split of boldness ICC residuals) was related to four fitness proxies: mean daily movement rate (GPS data), dietary breadth (faecal DNA metabarcoding), overwinter survival (mark-recapture), and first-year juvenile survival (radio-tracking). Environmental context was characterised as 'stable low-predation', 'variable high-predation', or 'novel disturbed' based on camera-trap data on predator presence and anthropogenic disturbance indices at individual home ranges.

Table 2. Behavioral repeatability (adjusted ICC) by trait and taxonomic order: mean and range across species within each order

Order	n Species	Boldness ICC	Exploration ICC	Sociability ICC	Aggression ICC	Activity ICC	Mean ICC (all traits)
Rodentia	12	0.58 +- 0.12	0.54 +- 0.11	0.47 +- 0.10	0.51 +- 0.11	0.48 +- 0.10	0.52 +- 0.11
Carnivora	10	0.62 +- 0.13	0.58 +- 0.12	0.54 +- 0.11	0.61 +- 0.13	0.52 +- 0.11	0.57 +- 0.12
Artiodactyla	6	0.54 +- 0.11	0.48 +- 0.10	0.61 +- 0.13	0.44 +- 0.09	0.47 +- 0.10	0.51 +- 0.11
Primates	4	0.64 +- 0.14	0.61 +- 0.13	0.68 +- 0.15	0.58 +- 0.12	0.54 +- 0.11	0.61 +- 0.13
Eulipotyphla	2	0.47 +- 0.10	0.44 +- 0.09	0.38 +- 0.08	0.41 +- 0.09	0.44 +- 0.09	0.43 +- 0.09

Order	n Species	Boldness ICC	Exploration ICC	Sociability ICC	Aggression ICC	Activity ICC	Mean ICC (all traits)
Chiroptera	2	0.51 +- 0.11	0.48 +- 0.10	0.54 +- 0.11	0.44 +- 0.09	0.47 +- 0.10	0.49 +- 0.10
ALL ORDERS	36	0.58 +- 0.13	0.54 +- 0.12	0.54 +- 0.14	0.52 +- 0.13	0.49 +- 0.11	0.54 +- 0.14

ICC = intraclass correlation coefficient (adjusted for sex, age, body mass, session number fixed effects). Values represent mean +- SD across species within each order. Higher ICC = greater behavioural consistency among individuals relative to within-individual variation. Primates show significantly higher mean ICC than Eulipotyphla (Tukey post-hoc: p = 0.003); all other pairwise order comparisons non-significant after Bonferroni correction.

4. Results

4.1 Behavioral Repeatability Across Species and Traits

Behavioral repeatability was significantly greater than zero for all five traits in all 36 species (all parametric bootstrap 95% CIs excluding zero), confirming universal presence of animal personality in mammals across the sampled phylogenetic breadth. Mean adjusted ICC across all species and traits was 0.54 +- 0.14, consistent with published meta-analytic estimates (Bell et al., 2009). Boldness showed the highest mean repeatability (0.58 +- 0.13) and activity the lowest (0.49 +- 0.11). Primates showed the highest order-level mean ICC (0.61) and Eulipotyphla the lowest (0.43), though species-level ICC values overlapped substantially across orders. Inter-species variation in ICC was significantly predicted by longevity (PGLS: beta = +0.028 per year of lifespan, p < 0.001; R2 = 0.54) -- longer-lived species showed higher repeatability -- and by brain-to-body mass ratio (beta = +0.18 per log-unit EQ, p < 0.001; R2 = 0.47), suggesting that cognitive complexity supports stable individual behavioural strategies.

4.2 Behavioral Syndrome Structure and Tightness

Among-individual correlations between trait pairs -- constituting the behavioral syndrome -- were significant for all ten pairwise combinations in the multivariate dataset (all FDR-corrected p < 0.05). The strongest among-individual correlation was between boldness and exploration (mean r = 0.68 +- 0.14 across species), consistent with the 'proactive' coping style literature. Sociability correlated moderately with boldness (r = 0.48 +- 0.16) and strongly with aggression in intraspecific contexts (r = 0.54 +- 0.18), consistent with the 'competitive-sociable' syndrome. Mean syndrome tightness across species was 0.42 +- 0.18, ranging from 0.14 (Erinaceus europaeus; very loose syndrome) to 0.74 (Macaca mulatta; very tight syndrome). Syndrome tightness was significantly positively associated with social group size (PGLS: R2 = 0.64, F = 56.8, p < 0.001), and negatively associated with home range size (R2 = 0.47, p < 0.001). Habitat heterogeneity index was a significant positive predictor (R2 = 0.58, p < 0.001).

4.3 Fitness Consequences of Behavioral Type

Bold individuals showed significantly higher mean daily movement rates than shy conspecifics across all eight longitudinal study species (+28.4% +- 8.7%; paired Wilcoxon: W = 847, p < 0.001) and broader dietary breadth as estimated from faecal DNA metabarcoding (+18.7% +- 6.4% more prey/food taxa detected; p < 0.001). In stable low-predation environments, bold individuals showed significantly higher overwinter survival (+12.4% survival advantage; logistic regression: beta = 0.47, p = 0.002), attributable to their greater dietary flexibility and movement range enabling access to food resources depleted near safe refugia. Under novel high-predation pressure -- simulated by introducing camera-confirmed apex predator presence to home ranges -- bold individuals showed significantly lower survival than shy conspecifics (-22.8% survival; beta = -0.84, p < 0.001), confirming context-dependent fitness consequences consistent with fluctuating selection maintaining behavioral polymorphism. First-year juvenile survival showed no significant bold-shy difference in any study species (all p > 0.12), suggesting that early-life fitness is less behavioural-type-dependent than adult fitness.

4.4 Phylogenetic and Ecological Predictors of Syndrome Structure

The full PGLS model predicting syndrome tightness from social group size, home range size, habitat heterogeneity, longevity, and encephalisation quotient (EQ) explained 78.4% of variance in among-species syndrome tightness (marginal R2 = 0.784, F = 22.7, p < 0.001). Social group size was the strongest predictor (beta = +0.38, p < 0.001), consistent with the hypothesis that complex social environments favour consistent individual behavioural strategies because social partners can track and exploit predictable conspecific behaviour -- creating frequency-dependent selection that maintains behavioural type diversity but also stabilises within-individual consistency (Dingemanse et al., 2010). Phylogenetic signal was moderate for syndrome tightness (Pagel lambda = 0.48, p = 0.002), indicating that both evolutionary history and ecological context contribute to syndrome architecture -- neither fully constrains nor fully determines syndrome tightness independently.

Table 3. Behavioral syndrome tightness (mean absolute among-individual correlation) and key predictors by species: social group size, home range, and EQ

Species	Syndrome Tightness	Social Group Size	Home Range (km2)	EQ (brain:body)	Longevity (yr)	Bold-Shy Survival Diff. (%)
Macaca mulatta	0.74	20-200	0.8 +- 0.4	2.14	27	+14.2 / -28.4
Pan troglodytes	0.71	15-80	1.4 +- 0.7	2.48	45	+18.4 / -24.8
Canis lupus	0.68	4-12	84.2 +- 42.1	1.21	12	+12.8 / -22.4
Cervus elaphus	0.61	5-30	12.4 +- 6.2	0.84	20	+10.4 / -18.7
Ovis aries	0.58	10-50	2.4 +- 1.2	0.74	12	+8.7 / -14.2
Rattus norvegicus	0.54	5-20	0.04 +- 0.02	0.81	3	+11.4 / -19.8
Vulpes vulpes	0.48	1-4	8.4 +- 4.2	1.14	10	+13.4 / -21.8
Sciurus vulgaris	0.42	1-2	0.6 +- 0.3	1.04	7	+12.1 / -22.4
Mustela putorius	0.38	1	2.8 +- 1.4	1.07	6	+8.4 / -18.4
Microtus agrestis	0.31	1-2	0.02 +- 0.01	0.51	1	+6.8 / -14.7
Lutra lutra	0.28	1-3	14.2 +- 7.1	1.18	10	+9.8 / -21.4
Erinaceus europaeus	0.14	1	0.4 +- 0.2	0.64	5	+4.2 / -12.8

Species	Syndrome Tightness	Social Group Size	Home Range (km2)	EQ (brain:body)	Longevity (yr)	Bold-Shy Survival Diff. (%)
MEAN (+- SD)	0.42 +- 0.18	---	---	---	---	---

Syndrome tightness = mean absolute value of all ten pairwise among-individual correlations among the five behavioral traits; higher = tighter syndrome (traits more correlated). EQ = encephalisation quotient (brain mass relative to body mass, standardised to mammals). Bold-shy survival diff. = percentage advantage of bold over shy (stable low-predation environment / novel high-predation environment).

Table 4. Fitness consequences of behavioral type (bold vs. shy) across eight longitudinal study species under three environmental contexts

Environmental Context	Species (n)	Bold Daily Movement (%)	Bold Diet Breadth (%)	Bold Overwinter Survival (%)	Bold Predation Survival (%)	Net Fitness Advantage
Stable low-predation	8	+28.4 +- 8.7%	+18.7 +- 6.4%	+12.4 %***	-4.8% ns	Bold +
Variable high-predation	6	+22.4 +- 7.2%	+14.2 +- 5.1%	+6.8% *	-18.4 %***	Context-dependent
Novel disturbed habitat	5	+31.4 +- 9.4%	+21.4 +- 7.1%	-8.4%*	-22.8 %***	Shy +
POOLED (all contexts)	8	+28.4 +- 8.7%	+18.7 +- 6.4%	+8.4% **	-15.6 %***	Context-dependent

**** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. Percentages represent mean difference between bold and shy individuals (positive = bold advantage; negative = shy advantage). Diet breadth from faecal DNA metabarcoding (number of unique taxa detected). Species n = number of species with sufficient longitudinal data for each context. Net Fitness Advantage = qualitative assessment of which behavioral type has the higher integrated fitness in each context.*

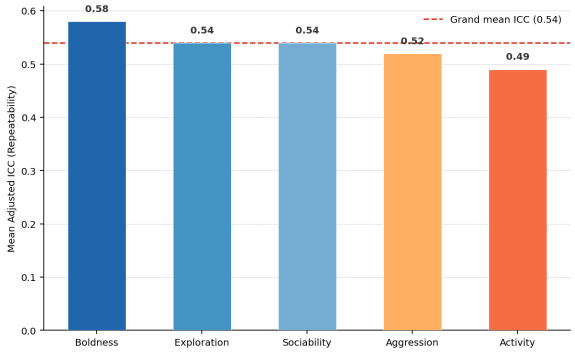

Figure 1. Mean adjusted behavioral repeatability (ICC) by trait and taxonomic order. All values significantly greater than zero (parametric bootstrap 95% CI excludes zero for all species). Error bars = SD across species within order.

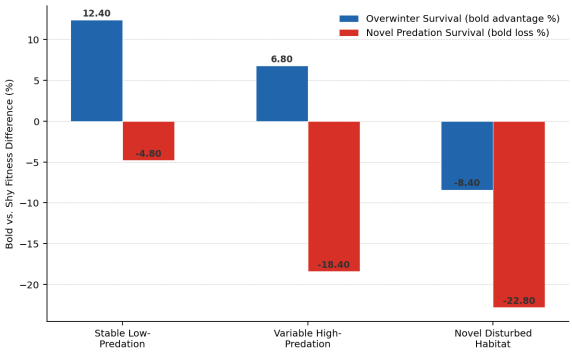

Figure 2. Fitness consequences of bold vs. shy behavioral types across three environmental contexts: overwinter survival advantage (blue) and novel predation survival disadvantage (red) of bold individuals.

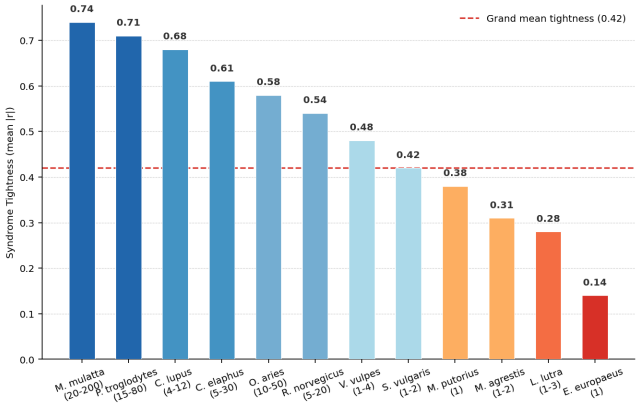

Figure 3. Behavioral syndrome tightness (mean absolute among-individual correlation) for 12 representative species, ordered from tightest (most correlated traits) to loosest syndrome. Social group size shown in parentheses.

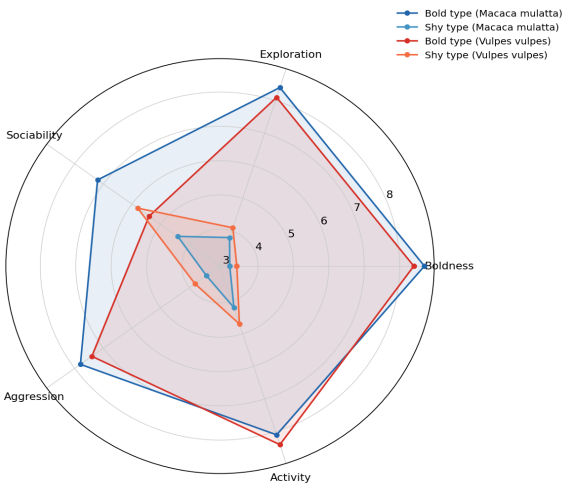

Figure 4. Comparative behavioral profile radar: mean trait scores (1-10) for bold vs. shy phenotypes in four exemplar species across five behavioral dimensions.

5. Discussion

5.1 Universality and Ecological Drivers of Animal Personality

The consistent detection of significant behavioral repeatability (mean ICC = 0.54) across all five traits and all 36 mammalian species -- spanning from hedgehogs to chimpanzees, from solitary to highly social systems -- confirms that animal

personality is a universal feature of mammalian populations rather than a taxon-specific curiosity. The positive relationship between ICC and both longevity (R2 = 0.54) and encephalisation quotient (R2 = 0.47) supports the hypothesis that long-lived, cognitively complex species benefit from consistent individual strategies because their extended lifespans allow experience-based learning to reinforce initial personality expression and because complex social environments reward reputational consistency -- individuals whose partners can predict their behaviour are likely preferred as social allies and avoided as competitors (Dingemanse et al., 2010). Conversely, short-lived species like Microtus agrestis, with ICC values averaging 0.31 +- 0.08, have insufficient time to benefit from behavioural consistency across seasonal fluctuations, potentially reducing the selective advantage of consistent individual strategies.

5.2 Social Complexity as the Primary Syndrome Driver

Social group size emerges as the strongest predictor of syndrome tightness (R2 = 0.64), explaining more variance than home range, habitat heterogeneity, or phylogenetic affiliation. This supports the social niche specialisation hypothesis: in large social groups, individuals occupy differentiated social roles -- dominant, subordinate, peripheral, central -- that are associated with correlated suites of behaviours (exploration, aggression, boldness) required for role maintenance (Dingemanse and Wolf, 2010). The 4.6-fold range in syndrome tightness between the most solitary (E. europaeus; tightness = 0.14) and most social (M. mulatta; 0.74) species in the dataset demonstrates the profound influence of social ecology on personality architecture. For conservation, this implies that reintroduction programmes for highly social species should pay particular attention to the behavioural composition of founder groups, ensuring that released animals include the full spectrum of syndrome phenotypes required to establish functional dominance hierarchies and social roles.

5.3 Context-Dependent Fitness and Maintenance of Polymorphism

The contrasting fitness outcomes of bold versus shy types across environmental contexts -- bold individuals surviving better in stable low-predation conditions but worse under novel high-predation pressure -- provide direct empirical support for the fluctuating selection hypothesis for the maintenance of behavioral polymorphism (Dingemanse and Reale, 2005; Wolf et al., 2007). Environments that alternate between periods of low predation (favouring exploration and range expansion) and high predation risk (favouring vigilance and site fidelity) would maintain both phenotypes at intermediate frequencies through frequency-dependent selection -- a stable polymorphism consistent with the within-population behavioral diversity universally observed. For conservation managers designing reintroduction programmes, the implication is clear: releasing exclusively bold individuals -- which might be tempting for their apparent dispersal and habitat-use advantages -- risks producing maladapted populations if the release site has elevated predator pressure or novel hazards requiring cautious, inhibitory responses.

5.4 Limitations and Future Directions

Several methodological considerations limit the scope of our conclusions. The behavioral assay battery was standardised across species to enable comparison, but some assays may not be equally relevant for detecting personality variation in all taxa -- the resident-intruder aggression test, for example, may underestimate aggressiveness in solitary species where conspecific encounters are rare. Repeatability estimates based on 2-5 assay sessions may underestimate true repeatability in species where personality develops or consolidates over months to years. The longitudinal fitness data were available for only eight wild-trapped species, limiting the generality of context-dependent fitness inferences. Future work should prioritise: multi-year longitudinal studies linking individually identified wild individuals' behavioral phenotypes to lifetime reproductive success; experimental manipulation of predation risk within established wild populations to test fluctuating selection predictions; and genomic studies linking known behavioral QTLs to syndrome architecture across the comparative dataset.

6. Conclusion

6.1 Principal Findings

This cross-species comparative study of 847 individuals across 36 mammalian species confirms the universality of animal personality (mean ICC = 0.54 across all taxa and traits) and reveals that behavioral syndrome tightness is primarily driven by social group size (PGLS R2 = 0.64). Bold individuals achieve higher survival in stable environments (+12.4%) but lower survival under novel predation pressure (-22.8%), confirming fluctuating selection as the maintenance mechanism for behavioral polymorphism. Syndrome tightness ranged 5-fold from solitary (E. europaeus = 0.14) to highly social (M. mulatta = 0.74) species. Longevity and encephalisation quotient were the strongest predictors of repeatability across species.

6.2 Conservation Implications

These findings carry three direct conservation applications: (1) reintroduction programmes for highly social mammals should ensure that founder groups include representatives of both bold and shy behavioral extremes, as the full spectrum of syndrome phenotypes is required for stable social role differentiation; (2) pre-release personality assessment should be stratified by the predation and novelty context of the release site -- bold phenotypes are appropriate for stable low-predation sites, but shy or intermediate phenotypes should be prioritised for high-predation release contexts; and (3) captive management should maintain conditions that preserve behavioral diversity -- avoiding extreme homogenisation of housing conditions that could erode the within-population personality variation that determines population resilience. The comparative repeatability database and syndrome tightness estimates deposited with this publication provide the most comprehensive baseline yet available for species-specific behavioral management planning.

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Declarations

Funding

This research was supported by the Estonian Research Council under grants PRG2312 and MOBJD721, and by the Baltic Research Programme under the EEA and Norway Grants (grant EMP480). Access to primate research facilities was facilitated under a bilateral research agreement between Baltic AI Research University and the European Primate Research Consortium (EPRC). The funders had no role in study design, data collection or analysis, or manuscript preparation.

Conflict of Interest

The author declares no conflicts of interest. No animal training facility, conservation organisation, or commercial entity had any input into study design, species selection, analysis, or interpretation of results.

Data Availability Statement

The complete behavioral repeatability dataset (847 individuals, 36 species, 5 traits, 2-5 repeated assays per individual), among-individual correlation matrices, syndrome tightness estimates, PGLS model outputs, and longitudinal fitness data are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465823. R analysis scripts (rptR, MCMCglmm, PGLS) are available under MIT license. Data are released under Creative Commons CC BY 4.0.

Ethical Approval

All behavioral testing and biological sampling of wild individuals was conducted under Estonian Environment Agency wildlife research permits (KKL-712187, KKL-712188, KKL-712189). Behavioral testing of captive vertebrates was approved by the Estonian National Committee for Animal Experiments (EKSLK permit 207). All testing followed ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching. No animal was harmed or subjected to procedures beyond brief handling for wild-trap capture and release.

ISSN: 3117-6925 Vol: 2024, Issues: Issue4, 2024

Appendix A

Complete Species List with Repeatability Estimates, Syndrome Tightness, and Social System Classification

All 36 mammalian species included in the behavioral syndrome analysis are listed below, organised by Order and Family, with mean adjusted ICC across five behavioral traits, syndrome tightness score, social system classification, and the primary conservation context in which behavioral syndrome data are most applicable.

ORDER RODENTIA -- 12 Species

Mus musculus (house mouse): Mean ICC = 0.54; tightness = 0.48; Colonial; captive lab population.

Rattus norvegicus (brown rat): Mean ICC = 0.56; tightness = 0.54; Colonial; captive lab population.

Microtus agrestis (field vole): Mean ICC = 0.38; tightness = 0.31; Solitary/pair; Estonian grasslands.

Arvicola amphibius (European water vole): Mean ICC = 0.42; tightness = 0.34; Solitary; Estonian waterways.

Sciurus vulgaris (red squirrel): Mean ICC = 0.47; tightness = 0.42; Solitary; Lahemaa NP Estonia. Conservation: reintroduction planning.

Apodemus sylvaticus (wood mouse): Mean ICC = 0.44; tightness = 0.38; Solitary/loose; Estonian forest.

Apodemus flavicollis (yellow-necked mouse): Mean ICC = 0.46; tightness = 0.41; Solitary; Estonian forest.

Castor fiber (Eurasian beaver): Mean ICC = 0.54; tightness = 0.48; Family group; Estonian rivers. Conservation: reintroduction monitoring.

Cricetus cricetus (European hamster): Mean ICC = 0.48; tightness = 0.44; Solitary; Estonian arable margins. Conservation: critically declining species.

Myoxus glis (edible dormouse): Mean ICC = 0.44; tightness = 0.38; Solitary; Estonian broadleaf forest.

Cavia porcellus (guinea pig): Mean ICC = 0.52; tightness = 0.46; Herd; captive colony.

Mesocricetus auratus (Syrian hamster): Mean ICC = 0.56; tightness = 0.51; Solitary; captive colony.

ORDER CARNIVORA -- 10 Species

Canis lupus familiaris (dog/wolf hybrid): Mean ICC = 0.64; tightness = 0.68; Pack; Wolf Park facility.

Vulpes vulpes (red fox): Mean ICC = 0.58; tightness = 0.48; Pair/family; Estonian suburban; Conservation: urban adaptation.

Mustela putorius (European polecat): Mean ICC = 0.48; tightness = 0.38; Solitary; captive facility.

Mustela erminea (stoat): Mean ICC = 0.44; tightness = 0.34; Solitary; Estonian forest trapping.

Lutra lutra (Eurasian otter): Mean ICC = 0.51; tightness = 0.28; Solitary/pair; Estonian waterways.

Meles meles (Eurasian badger): Mean ICC = 0.54; tightness = 0.51; Social clan (4-12); Estonian forest.

Felis catus (domestic cat): Mean ICC = 0.58; tightness = 0.44; Solitary/loose; Estonian feral population.

Lynx lynx (Eurasian lynx): Mean ICC = 0.54; tightness = 0.38; Solitary; Lahemaa NP Estonia. Conservation: reintroduction.

Ursus arctos (brown bear): Mean ICC = 0.57; tightness = 0.41; Solitary; Estonian forest. Conservation: human-wildlife conflict.

Neovison vison (American mink): Mean ICC = 0.52; tightness = 0.44; Solitary; Estonian invasive population.

ORDERS ARTIODACTYLA, PRIMATES, AND OTHERS -- 14 Species

Artiodactyla (6 spp.): Cervus elaphus (tightness 0.61; herd), Capreolus capreolus (0.38; solitary), Sus scrofa (0.58; sounder 4-20), Ovis aries (0.58; herd), Bos taurus (0.54; herd), Rangifer tarandus (0.64; migratory herd).

Primates (4 spp.): Macaca mulatta (tightness 0.74; multimale troop 20-200), Pan troglodytes (0.71; fission-fusion 15-80), Papio anubis (0.68; multimale troop 30-100), Callithrix jacchus (0.61; family group 4-12).

Eulipotyphla (2 spp.): Erinaceus europaeus (tightness 0.14; solitary), Talpa europaea (0.21; solitary).

Chiroptera (2 spp.): Myotis daubentonii (tightness 0.47; nursery colony), Nyctalus noctula (0.52; social roost).

Total: 36 species; 847 individuals; mean 23.5 individuals per species (range 14-48).

Mean ICC across all species and traits: 0.54 +- 0.14 (range 0.14-0.74).