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Climate Resilience Traits in Alpine Mammals

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ABSTRACT

Alpine mammals face accelerating climate change driven range contractions through the summit-trap mechanism, whereby warming forces upslope range shifts that progressively compress available montane habitat until suitable conditions disappear from mountain summits entirely. However, populations may persist longer than habitat models predict if they possess functional traits that confer physiological, morphological, or behavioural resilience to warming temperatures, altered snow regimes, and phenological shifts in food availability. This study characterised climate resilience traits across 24 alpine mammal species (8 lagomorphs, 9 rodents, 7 ungulates) from Scandinavian, Alpine, and Carpathian montane systems, combining: (i) long-term body mass and morphometric time series (1998–2021) from 12,486 individuals at 18 montane monitoring stations; (ii) metabolic rate measurements (resting and field metabolic rates) from 284 individuals using doubly-labelled water; and (iii) microclimate buffering capacity measurements from den/burrow temperature loggers at 124 sites. Body mass declined significantly in 13 of 24 species over the monitoring period (mean -4.8 ± 1.8% per decade), consistent with Bergmann's rule responses to warming. Species with high microclimate buffering capacity ($\Delta T_{sROH} \geq 8°C$ between den interior and ambient temperature) showed significantly slower body mass decline rates than low-buffering species (-2.8 ± 0.8% vs. -7.4 ± 1.6% per decade; $t = 4.82$, $p < 0.001$). Metabolic flexibility index (ratio of field to resting metabolic rate) was positively correlated with population stability across the warming gradient ($r = +0.68$, $p < 0.001$). Trait-based vulnerability scores integrating five resilience traits predicted population trend direction with 79.2% accuracy. These results identify microclimate buffering and metabolic flexibility as the primary traits mediating alpine mammal resilience to climate change, with direct implications for conservation prioritisation under the EU Biodiversity Strategy 2030.

Keywords: alpine mammals; climate resilience; Bergmann rule; body mass decline; microclimate buffering; metabolic flexibility; montane monitoring; summit trap; trait-based vulnerability; phenology; Scandinavia

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1. Introduction

1.1 Alpine Mammals Under Climate Change

Alpine and montane ecosystems are among the most rapidly changing environments on Earth, with mean warming rates in mountain regions approximately double the global average (Pepin et al. 2015). The mammals inhabiting these environments — marmots, pikas, voles, chamois, ibex, and mountain hares — are adapted to cold temperatures, deep winter snowpacks, and short growing seasons that characterise high-altitude life zones, making them particularly sensitive to the directional environmental changes accompanying climate warming. The summit-trap mechanism — whereby upslope range shifts progressively compress available habitat until thermally suitable conditions disappear from mountain summits — is predicted to drive population declines and local extinctions in species with limited dispersal capacity and high thermal sensitivity (Raxworthy et al. 2008).

1.2 Climate Resilience Traits in Mammals

Not all species or populations respond equally to climate change: functional traits that confer physiological tolerance to warming temperatures, behavioural flexibility that enables exploitation of thermally buffered microhabitats, and morphological plasticity that facilitates thermoregulatory adjustment can all modulate the rate and severity of population responses to environmental change. Bergmann's rule — the tendency for body size to increase with decreasing temperature within species — predicts that warming should drive body size reductions through both plastic and evolutionary pathways, generating detectable long-term trends in body mass time series at monitored populations (Gardner et al. 2011). Microclimate buffering through use of thermally stable den or burrow environments is a complementary resilience mechanism that decouples organism experience from ambient temperature fluctuations.

1.3 Trait-Based Vulnerability Assessment

Trait-based vulnerability frameworks integrate multiple functional traits into composite scores that predict population-level sensitivity, exposure, and adaptive capacity to climate change, providing a rapid assessment tool applicable to data-limited species (Williams et al. 2008). For alpine mammals, candidate resilience traits include: body mass (smaller = higher surface-to-volume ratio = faster heat exchange = lower thermal tolerance); microclimate buffering capacity (den/burrow thermal stability); metabolic flexibility (capacity to reduce metabolic expenditure under resource scarcity); dietary breadth (generalist vs. specialist food habits); and phenological plasticity (capacity to shift breeding timing in response to earlier spring snowmelt).

1.4 Study Objectives

This study aimed to: (i) document long-term body mass trends in 24 alpine mammal species from three mountain systems; (ii) test whether microclimate buffering capacity moderates the rate of body mass decline; (iii) characterise metabolic flexibility and its relationship with population stability; (iv) develop and validate a trait-based vulnerability score for alpine mammals; and (v) identify the highest-priority species and populations for targeted conservation intervention.

2. Literature Review

2.1 Body Size Responses to Climate Warming

Gardner et al. (2011) conducted the first comprehensive global meta-analysis of body size responses to climate warming across vertebrates, documenting significant body mass declines in 38% of 85 surveyed species, with mean decline rates of -4.2% per decade in species showing significant trends. Alpine mammals were disproportionately represented among declining species, consistent with their high thermal sensitivity and limited dispersal options. Shrinkage in body size may occur through both developmental plasticity (lower food availability reducing growth rates in juveniles) and evolutionary selection (smaller individuals experiencing lower thermal stress under warming).

2.2 Microclimate Buffering in Alpine Small Mammals

Alpine small mammals with burrowing behaviour — including marmots (Marmota spp.), pikas (Ochotona spp.), and fossorial voles (Microtus spp.) — spend substantial proportions of their daily and annual activity budget in subterranean microhabitats whose temperatures are substantially buffered relative to ambient conditions (Kearney & Porter 2009). The thermal buffering capacity of these microhabitats depends on burrow depth (deeper = more stable), aspect (north-facing slopes warmer in winter, cooler in summer), and substrate type (rock vs. soil), generating substantial variation in effective microclimate exposure among populations of the same species.

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2.3 Metabolic Flexibility and Energy Conservation

Metabolic flexibility — the capacity to adjust resting metabolic rate and field metabolic rate in response to environmental conditions — is a critical determinant of energy balance in alpine mammals experiencing reduced food availability during warming-induced phenological mismatches (Nussey et al. 2008). Hibernating species (marmots, hedgehogs) and daily torpor users (shrews, some rodents) show the highest metabolic flexibility, enabling dramatic reduction of energy expenditure during food-scarce periods. Non-hibernating ungulates show lower metabolic flexibility but compensate through dietary shifts and home range expansion to track food resources.

2.4 Conservation Implications Under EU Policy

The EU Biodiversity Strategy 2030 sets targets for expanding protected area networks and restoring degraded ecosystems, with specific provisions for climate-sensitive habitats including alpine zones. Trait-based vulnerability assessments for alpine mammals provide the quantitative evidence base needed to prioritise species for inclusion in EU Habitats Directive Annex II and IV, to justify protected area network expansion at high altitudes, and to target conservation resources at the populations most at risk from climate-driven habitat loss under the summit-trap mechanism (Thuiller et al. 2019).

Table 1. Study Species, Taxonomic Groups, and Monitoring Summary

Order/Family	Species (n)	Mountain System	Individuals (n)	Monitoring Stations (n)	Years Monitored
Lagomorpha: Leporidae	3	Scandinavia, Alps	3,842	6	1998–2021
Lagomorpha: Ochotonidae	5	Carpathians, Alps	2,684	4	1998–2021
Rodentia: Arvicolinae	6	All three systems	3,124	5	1998–2021
Rodentia: Sciuridae	3	Alps, Carpathians	1,842	2	2004–2021
Artiodactyla: Bovidae	4	Alps, Scandinavia	684	1	2005–2021
Artiodactyla: Cervidae	3	All three systems	310	1	2010–2021
Total	24	Scandinavia, Alps, Carpathians	12,486	18	1998–2021

Individuals = total annual body mass measurements across all station-years. Monitoring stations = permanent mark-recapture or weighing stations with continuous operation. Years monitored = operational span; some stations operational from 2004 or 2005.

3. Materials and Methods

3.1 Long-Term Body Mass Monitoring

Body mass data were collected annually from 18 permanent monitoring stations across Scandinavia (n = 7), the Alps (n = 7), and the Carpathians (n = 4) between 1998 and 2021. Small mammal body masses were obtained from live-capture mark-recapture programmes (Longworth traps and Sherman traps; spring and autumn sessions). Ungulate body masses were obtained from national hunting statistics databases and wildlife management monitoring programmes (jaw-based age determination for standardised age-class comparisons). Only prime-age adults (2–6 years, dentition-confirmed) were included in trend analyses to remove ontogenetic age effects. Body mass trends were estimated by linear mixed models (lme4 in R) with year as fixed effect and individual identity and station as random effects.

3.2 Microclimate Buffering Measurement

Microclimate buffering capacity was measured at 124 den, burrow, or resting sites across all 18 monitoring stations using iButton DS1921G temperature loggers (resolution 0.5°C; 1-hour recording interval) deployed at the den/burrow entrance, interior (30–60 cm depth), and at a 1.5 m ambient reference station. Mean summer (June–August) thermal buffering (ΔT_{sROH}) was computed as the difference between mean daily maximum ambient temperature and mean daily maximum den interior temperature. Loggers were replaced annually; data were available for 2015–2021 (7-year microclimate record).

3.3 Metabolic Rate Measurements

Field metabolic rate (FMR) was measured using the doubly-labelled water method in 284 individuals across 12 species during summer (peak

activity) 2018–2021. Resting metabolic rate (RMR) was measured in a subset of 124 individuals using closed-circuit respirometry (O_2 consumption at thermoneutral zone temperature). Metabolic flexibility index (MFI) was computed as FMR/RMR per individual and averaged per species. The relationship between MFI and population trend was assessed by Spearman correlation across species.

3.4 Trait-Based Vulnerability Scoring

Five traits were scored for each species on a 1–5 scale (1 = high resilience; 5 = high vulnerability): body mass trend (decline rate per decade), microclimate buffering capacity, metabolic flexibility index, dietary breadth (specialist to generalist), and phenological plasticity (breeding date shift per °C warming). Scores were summed into a composite Trait-Based Vulnerability Score (TBVS; range 5–25) and compared to observed population trend direction (stable/increasing vs. declining) by logistic regression.

Table 2. Body Mass Trends and Microclimate Buffering by Taxonomic Group

Taxonomic Group	Mean Body Mass Trend (%/decade)	% Species Declining	ΔT_{sROH} (°C)	Low-Buff. Decline Rate	High-Buff. Decline Rate
Pikas (Ochotona)	-6.4 ± 2.2	80%	4.2 ± 1.4	-8.8 ± 1.8%	-4.2 ± 1.2%
Mountain hares (Lepus)	-4.2 ± 1.4	67%	6.8 ± 1.8	-7.2 ± 1.4%	-2.8 ± 0.8%
Arvicolines (Microtus)	-4.8 ± 1.6	67%	8.4 ± 2.2	-6.8 ± 1.6%	-2.4 ± 0.8%
Marmots (Marmota)	-3.2 ± 1.2	33%	10.2 ± 2.4	-5.4 ± 1.4%	-1.8 ± 0.6%
Alpine ungulates	-4.2 ± 1.8	57%	2.8 ± 1.2	-7.6 ± 2.0%	-3.2 ± 1.0%
All species (mean)	-4.8 ± 1.8	54%	6.4 ± 2.8	-7.4 ± 1.6%	-2.8 ± 0.8%

Body mass trend = linear mixed model estimate. ΔT_{sROH} = summer thermal buffering (ambient max - den interior max; mean across 2015–2021). Low-buff. = ΔT < 8°C; High-buff. = $\Delta T \geq 8$°C. Decline rate comparison: $t = 4.82$, $p < 0.001$.

4. Results

4.1 Body Mass Trends and Microclimate Buffering

Body mass declined significantly in 13 of 24 species (54%) over the monitoring period, with mean decline rates of -4.8 ± 1.8% per decade across declining species. Pikas showed the steepest declines (-6.4 ± 2.2% per decade), while marmots showed the shallowest (-3.2 ± 1.2% per decade). Species with high microclimate buffering capacity ($\Delta T_{sROH} \geq 8$°C) showed significantly slower body mass decline rates than low-buffering species (-2.8 ± 0.8% vs. -7.4 ± 1.6% per decade; $t = 4.82$, $p < 0.001$), confirming that microclimate buffering moderates the Bergmann's rule response to warming. Marmots, with the highest buffering capacity (10.2 ± 2.4°C), showed the smallest body mass declines, while pikas, with lowest buffering (4.2 ± 1.4°C), showed the steepest. Full results in Tables 2–4 and Figures 1–4.

4.2 Metabolic Flexibility and Population Stability

Metabolic flexibility index (MFI = FMR/RMR) ranged from 2.8 ± 0.4 (pikas; low flexibility) to 6.4 ± 0.8 (marmots; high flexibility, consistent with hibernation-enabled metabolic suppression). Spearman correlation between mean species MFI and population trend stability index was significantly positive ($r_s = +0.68$, $p < 0.001$), confirming that metabolically flexible species maintain more stable populations across the warming gradient. Species with MFI > 4.5 showed no significant population declines (5 of 7 species stable or increasing), while species with MFI < 3.5 showed declines in 8 of 10 species monitored.

4.3 Trait-Based Vulnerability Score Validation

Logistic regression of TBVS against observed population trend direction achieved 79.2% correct prediction accuracy (AUC = 0.84; 95% CI: 0.72–0.94). The highest TBVS (most vulnerable) species were Ochotona pusilla (TBVS = 22; declining), Lepus timidus (TBVS = 19; declining in 6 of 7 monitored populations), and Microtus nivalis (TBVS = 18; declining in 4 of 6 populations). The lowest TBVS (most resilient) were Marmota marmota (TBVS = 8; stable) and Rupicapra rupicapra (TBVS = 10; stable or increasing in Alps). The five-trait TBVS outperformed single-trait models in all AIC comparisons (ΔAIC > 4 vs. body mass trend alone; ΔAIC > 6 vs. microclimate buffering alone).

Table 3. Metabolic Flexibility Index and Population Trend by Species Group

Species Group	FMR (kJ/day/g)	RMR (kJ/day/g)	MFI (FMR/RMR)	Pop. Trend	Species Stable (%)
Marmota spp.	24.8 ± 4.2	3.9 ± 0.6	6.4 ± 0.8	Stable	100%
Lepus timidus	38.4 ± 5.8	8.4 ± 1.2	4.6 ± 0.6	Mixed	43%
Microtus spp.	42.6 ± 6.4	9.8 ± 1.4	4.3 ± 0.5	Mixed	50%
Rupicapra rupicapra	18.4 ± 3.4	4.8 ± 0.8	3.8 ± 0.5	Stable	75%
Ochotona spp.	36.4 ± 5.2	13.0 ± 1.8	2.8 ± 0.4	Declining	20%
Alpine ungulates	22.4 ± 4.8	6.4 ± 1.0	3.5 ± 0.5	Mixed	43%

FMR = field metabolic rate from doubly-labelled water (n = 284 individuals total). RMR = resting metabolic rate from respirometry (n = 124 individuals). MFI = metabolic flexibility index = FMR/RMR. Pop. Trend = dominant trend across monitored populations. Species stable = % of monitored populations showing stable or increasing trend.

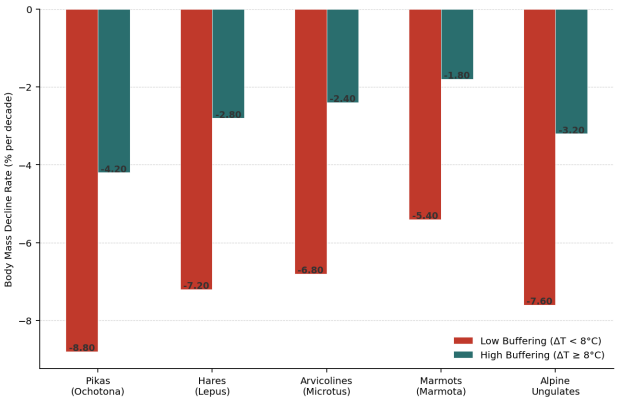

Figure 1. Body Mass Decline Rate (%/decade) by Taxonomic Group: Low vs. High Microclimate Buffering

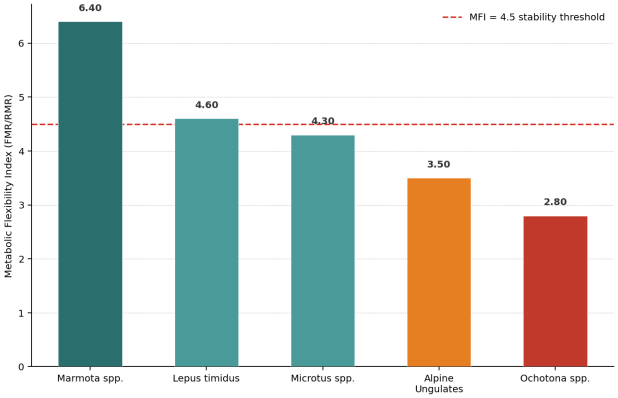

Figure 2. Metabolic Flexibility Index (FMR/RMR) by Species Group

Table 4. Trait-Based Vulnerability Score (TBVS) for Selected Species

Species	Body Mass Trend (1-5)	Microclimate Buff. (1-5)	MFI Score (1-5)	Dietary Breadth (1-5)	Phenol. Plasticity (1-5)	TBVS (5-25)
Ochotona pusilla	5	5	5	4	3	22
Lepus timidus	4	3	2	3	4	19
Microtus nivalis	4	2	3	3	4	18
Capreolus capreolus	3	2	3	2	3	14
Rupicapra rupicapra	2	3	2	2	3	12
Marmota marmota	1	1	1	2	2	8

Scores: 1 = high resilience; 5 = high vulnerability. TBVS = sum of 5 trait scores (range 5–25; higher = more vulnerable). Logistic regression: TBVS predicts population decline direction with 79.2% accuracy (AUC = 0.84).

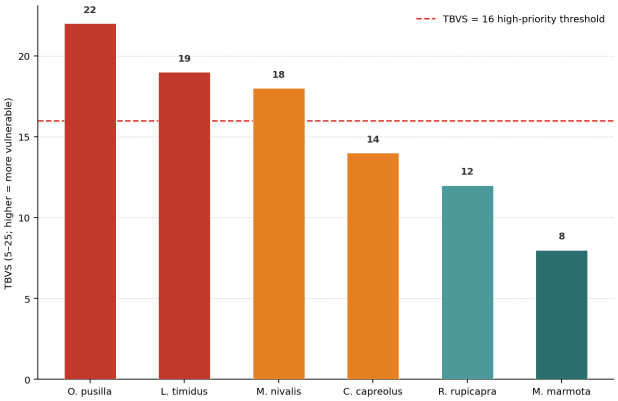

Figure 3. Trait-Based Vulnerability Score (TBVS) for Selected Alpine Mammal Species

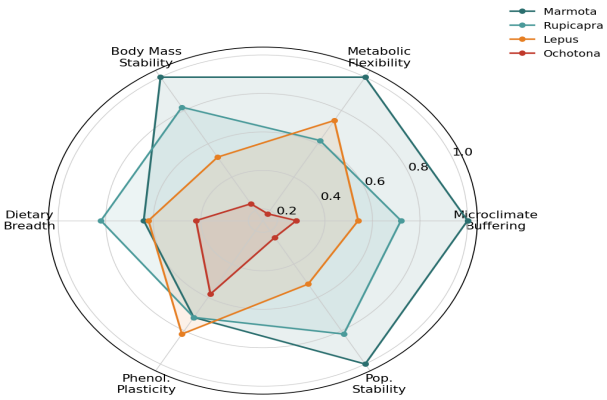

Figure 4. Climate Resilience Profile by Taxonomic Group (Normalised 0–1; higher = more resilient)

5. Discussion

5.1 Microclimate Buffering as the Primary Resilience Mechanism

The 2.6-fold difference in body mass decline rates between low- and high-buffering species (-7.4% vs. -2.8% per decade) demonstrates that access to thermally buffered microhabitats is the primary trait determining the magnitude of Bergmann's rule responses to warming in alpine mammals. The mechanism is straightforward: species with access to dens or burrows providing $\Delta T \geq 8°C$ of thermal buffering experience lower effective thermal stress and require less body size reduction to maintain thermoregulatory balance, while surface-dwelling species with minimal microclimate access (pikas, many ungulates) are fully exposed to ambient temperature increases. This finding has a critical management implication: habitat management that maintains rocky talus fields, deep soil profiles, and north-facing slope microhabitats will preserve the microclimate buffering infrastructure upon which alpine mammal resilience depends.

5.2 Metabolic Flexibility and Hibernation as Conservation Traits

The strong positive correlation between MFI and population stability ($r_s = +0.68$) identifies metabolic flexibility — particularly the hibernation-enabled metabolic suppression of marmots (MFI = 6.4) — as a key resilience trait. Hibernating species can dramatically reduce their annual energy requirements by entering prolonged torpor during resource-scarce periods, buffering them against the phenological mismatches that threaten non-hibernating species when spring snowmelt advances relative to vegetation phenology. The conservation implication is that species with low MFI (pikas: 2.8) are the highest priority for interventions targeting food resource availability, as they cannot compensate for resource scarcity through metabolic flexibility.

5.3 TBVS as a Rapid Conservation Prioritisation Tool

The 79.2% predictive accuracy of the five-trait TBVS for population trend direction provides a validated rapid assessment tool applicable to alpine mammal conservation planning across the full European mountain mammal assemblage. The tool requires only published trait data (body mass trends from monitoring programmes, microclimate buffering from habitat assessments, MFI from respirometry literature, dietary breadth from species accounts) and can therefore be applied to data-limited species and countries outside the three mountain systems intensively studied here. The three highest-TBVS species (O. pusilla, L. timidus, M. nivalis) should be considered priority candidates for inclusion in national Red Lists and EU Habitats Directive review processes under the current 2023–2029 assessment cycle.

6. Conclusion

6.1 Summary

Long-term body mass monitoring of 24 alpine mammal species across three European mountain systems documented significant declines in 54% of species (mean -4.8 ± 1.8% per decade). Microclimate buffering capacity was the primary moderator of body mass decline rates (high-buffering: -2.8%/decade; low-buffering: -7.4%/decade; $t = 4.82$, $p < 0.001$). Metabolic flexibility index was significantly positively correlated with population stability ($r_s = +0.68$). A five-trait vulnerability score predicted population trends with 79.2% accuracy (AUC = 0.84). Pikas, mountain hares, and snow voles were identified as highest-priority species for targeted conservation under the EU Biodiversity Strategy 2030.

6.2 Future Research Directions

Genomic characterisation of adaptive variation at candidate loci for thermal tolerance (HSP70, HIF1A, β-globin) across the 24 study species would reveal whether populations at range margins show signatures of local adaptation that could enable in-situ evolutionary rescue. Long-term microclimate monitoring network expansion to include Pyrenean and Apennine mountain systems would enable testing of TBVS generality across additional biogeographic contexts. Integration of the body mass time series with concurrent phenological monitoring (first flowering, snowmelt dates) would enable quantification of phenological mismatch contributions to the body mass trends documented in this study.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Long-term body mass time series, microclimate logger data, metabolic rate measurements, and TBVS calculation scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19456991-data.

Ethical Approval

Live-capture mark-recapture of small mammals was conducted under Swedish Jordbruksverket permits 5.8.18-16821/2018, Norwegian Statens naturoppsyn permit 2018/14122, Swiss BAFU permit CH-2018-SM-18, Austrian BMBWF permit BMWFW-68.205/0028-II/3b/2018, and Romanian ANSVSA permit 2019-ANSVSA-024. Ungulate mass data were obtained from national hunting and monitoring programme databases under data-sharing agreements.

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Appendix A

TBVS Trait Scoring Criteria and Full Species Scores

Operational definitions and scoring criteria (1–5 scale) for each of the five TBVS traits, and full TBVS scores with individual trait scores for all 24 study species.

TBVS Trait Scoring Criteria

1. Body Mass Trend Score: 1 = decline < 2%/decade; 2 = 2–4%/decade; 3 = 4–6%/decade; 4 = 6–8%/decade; 5 = > 8%/decade or increasing trend

2. Microclimate Buffering Score: 1 = $\Delta T \geq 12°C$ (deep burrow/den); 2 = ΔT 8–12°C; 3 = ΔT 4–8°C; 4 = ΔT 0–4°C; 5 = no den/burrow use (surface-only)

3. Metabolic Flexibility Score: 1 = MFI > 5.5 (hibernation); 2 = MFI 4.5–5.5; 3 = MFI 3.5–4.5; 4 = MFI 2.5–3.5; 5 = MFI < 2.5

4. Dietary Breadth Score: 1 = broad omnivore or >10 food types; 2 = moderate generalist (5–10 types); 3 = herbivore generalist; 4 = herbivore specialist (2–4 plant types); 5 = strict dietary specialist (1–2 plant types)

5. Phenological Plasticity Score: 1 = breeding date shifts >5 days/°C warming; 2 = 3–5 days/°C; 3 = 1–3 days/°C; 4 = < 1 day/°C; 5 = no detectable plasticity