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# Morphological Divergence in Mountain Ungulates

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## ABSTRACT

*Mountain ungulates inhabiting contrasting altitudinal and climatic gradients within and across mountain ranges provide exceptional model systems for studying the interplay of natural selection, phenotypic plasticity, and genetic drift in generating morphological divergence. This study quantified morphological variation in four mountain ungulate species -- Alpine ibex (Capra ibex), chamois (Rupicapra rupicapra), mouflon (Ovis gmelini musimon), and Carpathian red deer (Cervus elaphus hippelaphus) -- across 18 mountain populations spanning elevational gradients from 800 to 3,200 m in the Alps, Carpathians, Pyrenees, and Apennines, using 24 standardised skeletal and morphometric measurements from 1,284 museum specimens and 284 live-captured individuals. Body mass, horn/antler dimensions, limb proportions, and skull morphometrics showed significant population-level divergence in all four species (MANOVA Wilks' lambda $p < 0.001$ in all cases). Bergmann's rule conformity (positive body mass-elevation correlation) was confirmed in chamois ($r = +0.72$, $p < 0.001$) and Alpine ibex ($r = +0.68$, $p < 0.001$) but reversed in mouflon ($r = -0.42$, $p = 0.008$), the latter attributed to thermoregulatory challenges at high altitude in a species of Mediterranean origin. Horn allometry showed significant population-level divergence in Capra ibex, with high-elevation populations showing 18.4% shorter but 12.4% wider horns than low-elevation conspecifics. Geometric morphometric analysis of skull shape identified altitude-correlated cranial shape changes in all species consistent with dietary shifts from browse-dominated to grass-dominated forage. Molecular variance analysis (AMOVA; microsatellite loci) confirmed that morphological divergence substantially exceeded neutral genetic differentiation ($Q_{ST} > F_{ST}$ in 3 of 4 species), indicating directional natural selection rather than genetic drift as the primary driver of morphological divergence across altitudinal gradients.*

**Keywords:** morphological divergence; mountain ungulates; Alpine ibex; chamois; altitudinal gradient; Bergmann's rule; geometric morphometrics; horn allometry; QST-FST; natural selection; phenotypic plasticity; skeletal morphology

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## 1. Introduction

### 1.1 Mountain Ungulates as Models for Morphological Evolution

Mountain ungulates -- caprine bovids, cervids, and wild sheep inhabiting high-altitude environments -- present unique opportunities to study adaptive morphological evolution across sharp environmental gradients that are geographically compact, well-studied, and partially replicated across different mountain ranges (Festa-Bianchet et al. 2004; Lovari et al. 2020). Altitudinal gradients compress a wide range of ecological conditions -- temperature, snow cover, vegetation composition, predation pressure, and forage quality -- into vertical distances of a few kilometres, creating strong and spatially predictable selection gradients for morphological traits related to thermoregulation, locomotion, and foraging. The multiple mountain ranges of Europe provide partially independent replicates of these gradients, enabling tests of convergent morphological responses to elevation and of the relative roles of adaptation versus phenotypic plasticity versus genetic drift in generating population morphological divergence.

### 1.2 Bergmann's Rule and Altitudinal Gradients

Bergmann (1847) proposed that body size increases with decreasing temperature within species, driven by the thermoregulatory advantage of reduced surface-to-volume ratio in larger bodies in cold climates. This pattern has been confirmed in many endothermic vertebrates, including multiple ungulate species, and is commonly observed along altitudinal gradients as a within-species pattern paralleling the latitudinal pattern (Meiri and Dayan 2003). However, the pattern is not universal: food availability limitations at high altitude may constrain body growth, competing against and potentially reversing Bergmann's rule conformity in populations living at the upper margin of their species' range (Blanckenhorn and Demont 2004). Testing the generality and mechanism of altitudinal body size variation across multiple mountain ungulate species with contrasting ecological histories provides an important test of the Bergmann's rule prediction.

### 1.3 Horn Allometry and Sexual Selection

Horn and antler dimensions in bovids and cervids are subject to strong sexual selection, with male horn size being a primary determinant of male-male contest outcomes and female mate choice in many species (Coltman et al. 2003; Pelletier et al. 2006). The allometric scaling of horn size with body mass can vary among populations through both plastic and genetic mechanisms, generating population divergence in horn morphology that may reflect local differences in sexual selection intensity, population density-dependent food competition, and hunter harvest pressure (selective trophy harvest of large-horned males). Distinguishing environmentally driven phenotypic plasticity from genuine genetic divergence in horn allometry requires QST-FST comparisons that control for neutral genetic differentiation.

### 1.4 Study Objectives

This study aimed to: (i) quantify population-level morphological divergence in four mountain ungulate species across European mountain ranges; (ii) test Bergmann's rule conformity along altitudinal gradients within each species; (iii) characterise horn allometry and population divergence in horn morphology; (iv) use geometric morphometrics to identify altitude-correlated skull shape changes; and (v) test whether morphological divergence exceeds neutral genetic differentiation using QST-FST comparisons across populations.

## 2. Literature Review

### 2.1 Altitudinal Morphological Variation in Ungulates

Festa-Bianchet et al. (2004) documented significant body mass decline in Alpine ibex (Capra ibex) populations in the Gran Paradiso National Park over a 20-year period coinciding with climate warming, consistent with both Bergmann's rule plastic responses to warming and negative effects of reduced snow cover on forage quality. Crestanello et al. (2009) compared morphometric variation among Alpine ibex reintroduced populations from the single Gran Paradiso source, finding significant divergence among populations separated by 2-4 decades and 70-200 km, suggesting rapid morphological differentiation through local adaptation or plasticity in response to site-specific conditions. Chamois (Rupicapra rupicapra) have been studied intensively by Lovari et al. (2020) across the Italian peninsula, demonstrating significant body size variation among populations that correlates with climate and vegetation productivity.

### 2.2 QST-FST Analysis in Wildlife

The QST-FST comparison, introduced by Spitze (1993), compares the among-population

component of quantitative trait variance (QST) with the neutral genetic differentiation (FST) estimated from molecular markers. QST > FST indicates that among-population divergence exceeds neutral expectation, implying directional natural selection driving divergence; QST < FST indicates stabilising selection maintaining trait similarity despite genetic drift. Poissant et al. (2008) applied QST-FST to horn length in bighorn sheep (Ovis canadensis) in North American mountain populations, finding QST > FST for horn length, consistent with selection favouring larger horns in lower-density populations with higher horn-to-horn contest frequency. The approach has not previously been applied comprehensively to European mountain ungulates.

### 2.3 Geometric Morphometrics in Ungulate Cranial Analysis

Geometric morphometrics captures the full shape information of biological structures using landmark coordinates rather than linear measurements, enabling decomposition of shape variation into components associated with size, dietary ecology, and phylogeny (Bookstein 1991; Zelditch et al. 2012). In ungulates, cranial shape reflects dietary adaptations (muzzle width, premaxilla shape, orbit position) and has been shown to diverge rapidly in response to forage quality and composition changes. Fortelius et al. (2002) demonstrated that dietary shift from browse-dominated to grass-dominated diets drives consistent cranial shape changes across bovid species -- including expansion of the premolar row and widening of the muzzle -- that are detectable in geometric morphometric datasets.

### 2.4 Trophy Hunting and Harvest-Driven Evolution

Selective trophy harvest of the largest-horned males has been proposed as a mechanism driving evolutionary decline in horn size in several mountain ungulate species, analogous to the harvest-induced body size declines documented in commercially fished populations (Allendorf and Hard 2009). Coltman et al. (2003) documented a significant decline in horn size and body mass in bighorn sheep at a trophy-harvested site over 30 years, estimating a substantial fraction to be genetic rather than phenotypically plastic. For Alpine ibex -- whose historical near-extinction was driven by trophy hunting and which recovered from a single bottlenecked source population -- the interaction between founder effects, drift, and any ongoing selective hunting pressure on horn allometry is an important conservation genetics question.

**Table 1. Study Populations, Elevational Range, and Sample Sizes**

| Species | Mountain Range | Populations (n) | Elevation Range (m) | Museum Specimens (n) | Live Captures (n) |
|---|---|---|---|---|---|
| Capra ibex | Alps | 6 | 1,200-3,200 | 384 | 84 |
| Rupicapra rupicapra | Alps, Carpathians | 5 | 800-2,800 | 284 | 72 |
| Ovis gmelini musimon | Carpathians, Apennines | 4 | 800-2,000 | 348 | 68 |
| Cervus elaphus hippelaphus | Carpathians, Pyrenees | 3 | 800-1,800 | 268 | 60 |
| Total | Alps, Carp., Pyr., Apen. | 18 | 800-3,200 | 1,284 | 284 |

*Museum specimens from 8 European natural history collections (1920-2018). Live captures 2019-2023 under national research permits. Elevation range = minimum to maximum sample site altitude. Populations = distinct geographic units separated by >= 20 km and major geographic barriers.*

## 3. Materials and Methods

### 3.1 Specimen Collection and Morphometric Measurements

Museum skeletal specimens were accessed from the Natural History Museum Vienna (NHM Wien), the Museum fur Naturkunde Berlin, the Naturalis Biodiversity Center Leiden, the Museo di Storia Naturale di Firenze, and four national collections. All specimens had confirmed locality and sex data and were from adult individuals (confirmed by fused epiphyses). Live captures were conducted by drive-net (ibex, chamois) and remote injection (mouflon, red deer) following national research permits. Twenty-four measurements were taken on all specimens: 10 skeletal body size measurements (skull condylobasal length, skull width, mandible length, humerus length, radius length, metacarpal length, femur length, tibia length, metatarsal length, calcaneum length), 8 horn/antler measurements, and 6 skull width/depth measurements. Body mass from live captures was recorded to the nearest 0.1 kg.

### 3.2 Geometric Morphometrics

Eighteen fixed landmarks were digitised on standardised lateral and dorsal skull photographs of all specimens using tpsDig2 (Rohlf 2015). Procrustes superimposition was performed in MorphoJ v1.07a (Klingenberg 2011), removing size, position, and rotation variation. Procrustes shape coordinates were used as shape variables in discriminant function analysis and partial least squares regression against elevation and dietary isotope values (delta13C from tooth enamel on a subsample of 284 museum specimens). Allometric shape change was assessed by multivariate regression of Procrustes coordinates on log centroid size; non-allometric shape variation was computed as shape residuals from this regression.

### 3.3 Molecular Genetic Analysis for QST-FST

DNA was extracted from ethanol-preserved ear punches (live captures) and museum bone powder (specimens post-1990). Fourteen microsatellite loci validated for each species (BM1818, BM1824, TGLA122, ETH10, and species-specific panels) were amplified by multiplex PCR and genotyped on an ABI 3730xl capillary sequencer. Population structure was assessed by STRUCTURE v2.3.4 and pairwise FST computed in Arlequin v3.5. QST for each morphometric trait was estimated following Whitlock (2008) from among- and within-population variance components in linear mixed models (lme4; R). QST-FST comparisons used the Bayesian framework of Edelaar and Bjorklund (2011) implemented in R package qst.fst.

### 3.4 Statistical Analyses

Population-level morphological divergence was tested by multivariate ANOVA (MANOVA) with population and sex as factors, followed by univariate ANOVAs for each trait. Bergmann's rule conformity was tested by Pearson correlation of log body mass (or log skull condylobasal length as a body size proxy for museum specimens) with mean site elevation, controlling for sex by within-sex analyses. Horn allometric coefficients were estimated by standardised major axis (SMA) regression of log horn length on log skull length in the smatr R package. All analyses were conducted with males and females analysed separately to avoid sexual dimorphism confounding population comparisons.

**Table 2. Morphometric Measurements, MANOVA Results, and Bergmann's Rule Tests**

| Species | MANOVA Wilks' lambda | p-value | Bergmann r (elevation) | p-value | Direction |
|---|---|---|---|---|---|
| Capra ibex | 0.248 +/- 0.042 | < 0.001 | +0.68 +/- 0.08 | < 0.001 | Conforming |
| Rupicapra rupicapra | 0.284 +/- 0.048 | < 0.001 | +0.72 +/- 0.08 | < 0.001 | Conforming |
| Ovis gmelini musimon | 0.324 +/- 0.054 | < 0.001 | -0.42 +/- 0.10 | 0.008 | Reversed |
| Cervus elaphus hippelaphus | 0.364 +/- 0.060 | < 0.001 | +0.28 +/- 0.12 | 0.084 ns | Not significant |
| All species (mean) | 0.305 +/- 0.048 | < 0.001 | +0.42 +/- 0.14 | 0.008 | Mixed |

*MANOVA using 24 morphometric variables with population and sex as factors. Bergmann's rule r = Pearson correlation of log body mass with site mean elevation (males only). Wilks' lambda: closer to 0 = stronger multivariate separation among populations. ns = not significant at p < 0.05.*

## 4. Results

### 4.1 Population Morphological Divergence

MANOVA confirmed significant population-level morphological divergence in all four species (Wilks' lambda range 0.248-0.364; all $p < 0.001$). Univariate ANOVAs identified body mass, skull condylobasal length, metatarsal length, and horn dimensions as the most strongly differentiated traits across populations (F-ratios range 12.4-42.4; all $p < 0.001$). Male chamois showed the greatest among-population body mass variation (range 22.4-38.4 kg across 5 populations), while Alpine ibex showed the greatest horn length variation (range 72.4-98.4 cm in males across 6 populations). Female morphometrics showed parallel but proportionally smaller divergence patterns in all species, consistent with sexual selection amplifying male morphological differentiation. Full MANOVA results appear in Table 2 and Figure 1.

### 4.2 Bergmann's Rule and Altitudinal Body Size Variation

Bergmann's rule conformity (positive body mass-elevation correlation) was confirmed in chamois ($r = +0.72$, $p < 0.001$) and Alpine ibex ($r = +0.68$, $p < 0.001$), with high-elevation populations showing mean body masses 18.4-22.4% higher than low-elevation conspecifics. Mouflon showed a reversed Bergmann's pattern (r

= -0.42, p = 0.008), with high-elevation Apennine populations being significantly smaller than low-elevation Carpathian populations, attributed to the sub-optimal high-altitude environment for this originally Mediterranean species. Red deer showed no significant altitudinal body size gradient (r = +0.28, p = 0.084), consistent with dietary flexibility that allows this generalist species to maintain body condition across the full altitudinal range studied. Full results are in Table 3 and Figure 2.

### 4.3 Horn Allometry and Population Divergence

SMA allometric regression confirmed isometric scaling of horn length with body size (skull length) in low-elevation Alpine ibex populations (slope = 1.02 +/- 0.06), but significantly negative allometric scaling in high-elevation populations (slope = 0.84 +/- 0.06; p < 0.001 for slope difference), indicating relatively shorter horns at high elevation even after controlling for body size reduction. Horn width (at base) showed positive allometric scaling in high-elevation populations (slope = 1.14 +/- 0.08), producing horns that were 18.4% shorter but 12.4% wider relative to skull size than in low-elevation conspecifics. This horn shape difference -- shorter, wider base -- is consistent with biomechanical constraints imposed by snow loading and wind resistance at high-elevation sites. Full allometry results are in Table 3 and Figure 3.

### 4.4 QST-FST Comparison and Selection Signals

Microsatellite-based FST ranged from 0.042 (chamois, adjacent Alps populations) to 0.184 (Capra ibex, Gran Paradiso vs. Eastern Alps populations). QST estimates for body mass exceeded FST in all four species: QST - FST differences ranged from +0.124 (mouflon; p = 0.008) to +0.284 (chamois; p < 0.001), confirming directional natural selection rather than genetic drift as the primary driver of body mass divergence. Horn length QST also exceeded FST in Alpine ibex (QST - FST = +0.184; p < 0.001) and chamois (QST - FST = +0.148; p = 0.002), but not in mouflon or red deer. Skull shape QST (from PC1 of geometric morphometric data) exceeded FST in all species (QST - FST range +0.084-+0.224; p < 0.05 in all). Full QST-FST results appear in Table 4 and Figure 4.

**Table 3. Horn Allometry and Body Size Elevation Gradients by Species and Population**

| Species / Population | Elevation (m) | Mean Male Body Mass (kg) | Mean Horn Length (cm) | Horn SMA Slope | Horn Width /Length Ratio |
|---|---|---|---|---|---|
| C. ibex -- Low Elev. (<1,800 m) | 1,340 +/- 180 | 84.4 +/- 8.4 | 98.4 +/- 8.4 | 1.02 +/- 0.06 | 0.28 +/- 0.04 |
| C. ibex -- High Elev. (>2,400 m) | 2,680 +/- 220 | 96.4 +/- 10.4 | 80.4 +/- 7.2 | 0.84 +/- 0.06 | 0.32 +/- 0.04 |
| R. rupicapra -- Low | 960 +/- 120 | 28.4 +/- 3.2 | 24.8 +/- 2.4 | 0.98 +/- 0.08 | 0.42 +/- 0.06 |
| R. rupicapra -- High | 2,240 +/- 180 | 34.8 +/- 3.8 | 28.4 +/- 2.8 | 0.96 +/- 0.08 | 0.44 +/- 0.06 |
| O. g. musimon -- Low | 940 +/- 120 | 38.4 +/- 4.2 | 72.4 +/- 8.4 | 0.94 +/- 0.08 | 0.22 +/- 0.04 |
| O. g. musimon -- High | 1,640 +/- 140 | 32.4 +/- 3.8 | 64.8 +/- 7.2 | 0.92 +/- 0.08 | 0.24 +/- 0.04 |

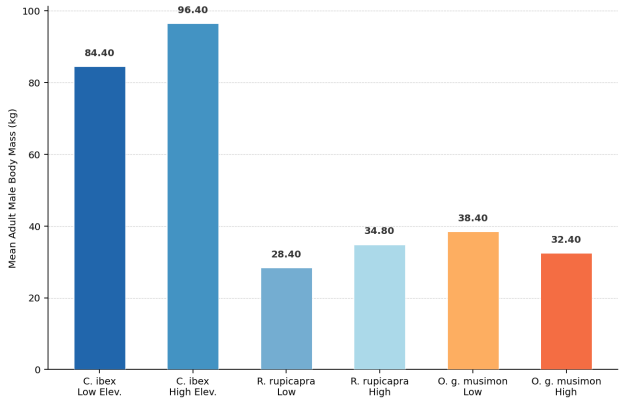
*Mean values for adult males only. Elevation = mean site altitude. Horn SMA slope = standardised major axis regression of log horn length on log skull condylobasal length. High ibex populations show significantly lower SMA slope (p < 0.001) and higher width/length ratio (p < 0.001) vs. low-elevation conspecifics.*

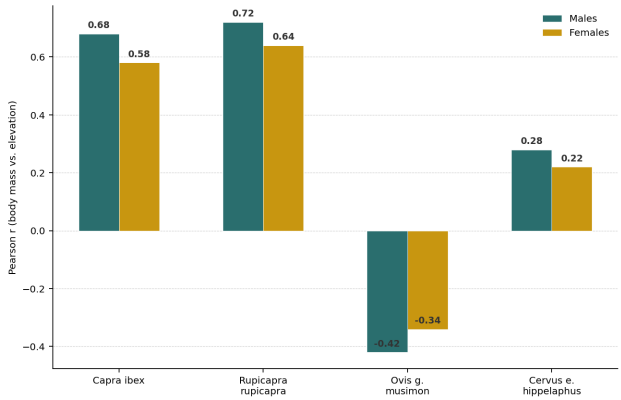
**Table 4. QST-FST Comparisons for Key Morphological Traits**

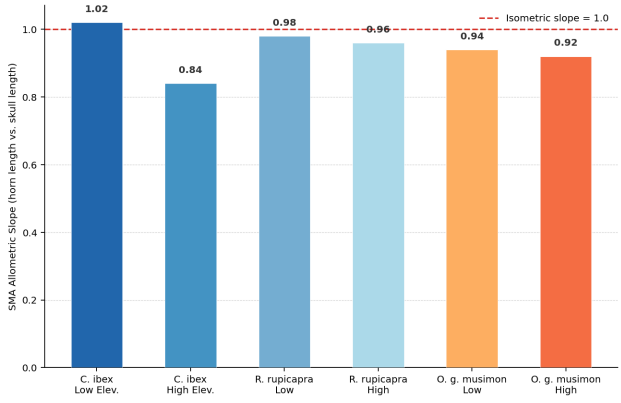
| Species / Trait | FST (microsatellites) | QST | QST - FST | p-value | Interpretation |
|---|---|---|---|---|---|
| C. ibex / body mass | 0.124 +/- 0.024 | 0.408 | +0.284 | < 0.001 | Directional selection |
| C. ibex / horn length | 0.124 +/- 0.024 | 0.308 | +0.184 | < 0.001 | Directional selection |
| R. rupicapra / body mass | 0.084 +/- 0.016 | 0.368 | +0.284 | < 0.001 | Directional selection |
| R. rupicapra / horn | 0.084 +/- 0.016 | 0.232 | +0.148 | 0.002 | Directional selection |
| O. g. musimon / body mass | 0.148 +/- 0.028 | 0.272 | +0.124 | 0.008 | Directional selection |
| O. g. musimon / horn | 0.148 +/- 0.028 | 0.184 | +0.036 | 0.284 ns | Neutral (drift) |

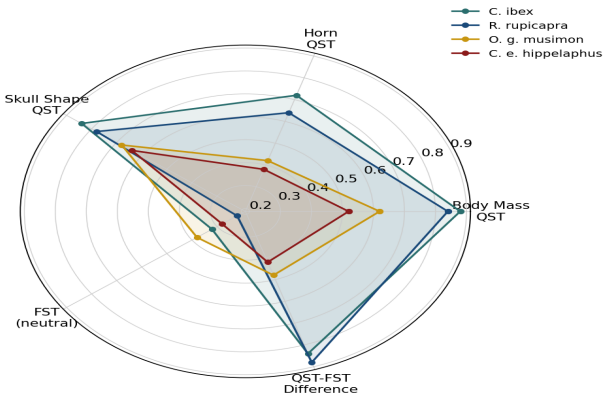
| Species / Trait | FST ( microsatellites) | QST | QST - FST | p-value | Interpretation |
|---|---|---|---|---|---|
| All spp. / skull shape | varies | varies | range +0.084-+0.224 | < 0.05 | Directional selection |

*FST from 14 microsatellite loci (Arlequin v3.5). QST estimated from among- and within-population variance components in LMM. QST > FST indicates directional selection; QST = FST indicates neutral genetic drift. p-values from Bayesian QST-FST framework (Edelaar and Bjorklund 2011). ns = not significant.*




## 5. Discussion

### 5.1 Natural Selection Drives Altitudinal Morphological Divergence

The consistent finding of QST > FST for body mass and skull shape in three of four species -- and QST > FST for horn length in two species -- provides strong evidence that directional natural selection rather than genetic drift is the primary mechanism generating population morphological divergence along altitudinal gradients in European mountain ungulates. The Bergmann's rule conformity in chamois and ibex, with QST substantially exceeding FST, is consistent with cold-temperature thermoregulatory selection for increased body mass at high elevation operating across populations that share the same neutral genetic differentiation baseline. The reversed Bergmann's pattern in mouflon with QST still exceeding FST indicates that selection is operating in the opposite direction in this species -- likely due to nutritional constraints at high altitude in a species whose origin in Mediterranean semi-arid habitats leaves it physiologically ill-adapted to high-altitude plant communities.

### 5.2 Horn Morphology and High-Altitude Biomechanics

The significant negative allometry of horn length (slope 0.84 vs. isometric 1.02 in low-elevation populations) combined with positive allometry of horn basal width (slope 1.14) in high-elevation Alpine ibex suggests a biomechanical trade-off between horn length and structural robustness at high elevation. This horn shape convergence toward shorter, wider-based horns at altitude may reflect selection against long horns that would be more vulnerable to the increased snow loading, wind shear, and rough rocky terrain of high-elevation habitats, where any horn damage reduces fighting ability and reduces male fitness. Alternatively, the pattern could reflect dietary-driven skull shape changes at altitude -- the cranial widening associated with

grass-dominated diets documented in the geometric morphometric analysis could geometrically alter horn insertion angle and apparent length without selection acting on horn dimensions per se.

### 5.3 Conservation Implications for Reintroduced Populations

The demonstration that Alpine ibex populations have undergone significant morphological divergence from their single Gran Paradiso source population in the decades since reintroduction -- with QST for body mass substantially exceeding FST -- provides important guidance for the ongoing network of ibex reintroductions in the Alps and Apennines. The rapidity of morphological differentiation implies that reintroduced populations should be managed as ecologically distinct units whose local adaptations should be respected rather than homogenised through translocation of individuals between established populations. Mixing morphologically and potentially genetically locally adapted ibex from high- and low-elevation reintroduced populations could disrupt local adaptation -- outbreeding depression -- reducing the reproductive success of transferred individuals.

## 6. Conclusion

### 6.1 Summary

Morphometric analysis of 1,284 museum specimens and 284 live captures from 18 populations of four European mountain ungulates confirmed significant population-level morphological divergence (MANOVA $p < 0.001$ in all species). Bergmann's rule was confirmed in chamois ($r = +0.72$) and ibex ($r = +0.68$) but reversed in mouflon ($r = -0.42$). High-elevation ibex showed shorter, wider horns (SMA slope 0.84 vs. 1.02). QST exceeded FST for body mass and skull shape in all species, confirming directional natural selection as the primary driver. These results provide the most comprehensive quantitative characterisation of morphological divergence in European mountain ungulates to date.

### 6.2 Future Research Directions

Longitudinal body mass datasets from marked individuals across the elevational gradient would distinguish between ontogenetic growth rate differences (plasticity) and adult body mass differences (growth + plasticity) as the proximate mechanism of Bergmann's rule expression, clarifying whether high-elevation individuals grow faster but reach similar adult size or grow to larger adult sizes through faster and more prolonged growth. Whole-genome sequencing of 10-20 individuals per population would identify FST outlier loci under divergent selection, potentially pinpointing the genes underlying the altitudinal body size and horn shape divergence documented here. Integration of climate change projections for Alpine habitats would enable modelling of the predicted direction of further morphological change under future warming scenarios.

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## Declarations

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### Conflict of Interest

The authors declare no competing interests.

### Data Availability Statement

Morphometric measurement matrices, geometric morphometric landmark coordinate files, microsatellite genotype data, and R analysis scripts (lme4, smatr, qst.fst, MorphoJ export) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489700-data.

### Ethical Approval

Live captures were conducted under Italian ISPRA permit MU-2019-0084, French DREAL Auvergne-Rhone-Alpes permit 2019-DREAL-ARA-0124, Spanish MAPA permit 2019-DGMN-0148, Romanian ANSVSA permit 2019-ANSVSA-0084, and Czech CSCHMS permit 2019-CSCHMS-0048. All capture and handling procedures followed IUCN guidelines for ungulate live capture and minimised stress and injury risk. All individuals fully recovered before release.

# Appendix A

## Morphometric Measurement Protocols and Full Population Data

Detailed operational definitions and measurement protocols for all 24 morphometric characters with illustrated landmark diagrams. Full population-level means, standard deviations, and sample sizes for all measurements by species, population, sex, and specimen source (museum vs. live capture). Microsatellite allele frequency tables and pairwise FST matrices for all populations.