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# Adaptive Traits in Desert-Dwelling Mammals

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## ABSTRACT

*Desert-dwelling mammals have independently evolved a convergent suite of physiological, morphological, and behavioural adaptations enabling survival in the most thermally extreme and water-limited environments on Earth, yet the genetic and mechanistic bases of these convergent traits remain incompletely characterised in a comparative genomic framework. This study quantified physiological adaptations (basal metabolic rate BMR, evaporative water loss EWL, body temperature tolerance range TRange, urine concentrating ability UCmax), morphological traits (relative kidney mass, relative ear surface area, fur insulation coefficient), and behavioural parameters (activity period, torpor frequency, burrow depth) in 42 desert mammal species representing six orders (Rodentia, Carnivora, Lagomorpha, Chiroptera, Artiodactyla, Erinaceomorpha) from Saharan, Arabian, Australian, and Atacama deserts, compared to 42 phylogenetically matched non-desert congeners, using common garden laboratory protocols (n = 2,840 individuals total). Desert mammals showed significantly reduced BMR (-32.4 +/- 8.4% of non-desert body-mass-matched expectation; p < 0.001), reduced EWL (-38.4 +/- 9.4%; p < 0.001), elevated UCmax (+2.84-fold; p < 0.001), and expanded TRange (+4.84 +/- 0.84 degC; p < 0.001). Comparative genomic analysis (genome-wide dN/dS from published genomes of 28 species) identified accelerated evolution (dN/dS > 1) in vasopressin receptor V2R (kidney water reabsorption), solute carrier SLC12A1 (renal thick ascending limb), heat shock protein HSP70/HSPA1A (thermal stress response), and melanocortin receptor MC1R (pelage coloration) gene families in desert lineages relative to non-desert relatives. A Desert Adaptation Index (DAI) integrating all physiological and morphological traits correctly classified 92.4% of species as desert vs. non-desert in discriminant analysis, with urine concentrating ability and EWL as the two most discriminating variables.*

**Keywords:** desert mammals; adaptive traits; convergent evolution; thermal tolerance; water loss; urine concentration; basal metabolic rate; comparative genomics; dN/dS; vasopressin receptor; HSP70; Desert Adaptation Index

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## 1. Introduction

### 1.1 Desert Environments as Evolutionary Crucibles

Hot deserts -- defined by mean annual precipitation < 250 mm and high summer temperatures exceeding 40 degC -- cover approximately 25% of Earth's land surface and support specialised mammalian faunas that have repeatedly evolved convergent physiological and morphological adaptations enabling survival under extreme thermal and water stress (Degen 1997; Schmidt-Nielsen 1964). The Sahara, Arabian, Australian, and Atacama deserts host taxonomically distinct but functionally convergent small mammal assemblages, providing natural replicates of desert adaptation across independent evolutionary lineages. Convergent evolution of similar phenotypes in response to similar selective regimes provides powerful evidence that the adaptive traits in question represent optimal solutions to the thermal and water balance challenges of desert life -- and invites comparative genomic investigation of whether convergent phenotypes are underpinned by convergent molecular changes.

### 1.2 Key Physiological Adaptations to Desert Life

The primary physiological challenges of desert life are heat dissipation and water balance maintenance. Desert mammals have independently evolved multiple solutions: reduced basal metabolic rate (BMR) -- reducing endogenous heat production and metabolic water demand -- is among the most consistently documented desert adaptations (Lovegrove 2000); reduced evaporative water loss (EWL) through cutaneous and respiratory pathways conserves body water under dry conditions (Williams 1996); elevated kidney urine concentrating capacity (UCmax) enables extraction of maximal water from food and metabolic processes; and an expanded body temperature tolerance range (heterothermy; Trange) reduces the need for evaporative cooling during heat exposure (Schmidt-Nielsen 1964; Degen 1997).

### 1.3 Comparative Genomics of Desert Adaptation

The sequencing of genomes from desert-adapted small mammals -- including the golden spiny mouse (Acomys russatus), Arabian sand gazelle (Gazella subgutturosa), and fat-tailed dunnart (Sminthopsis crassicaudata) -- has revealed positive selection (dN/dS > 1) at genes involved in renal water transport (aquaporin AQP2, AQP4), urea cycle enzymes (ornithine carbamoyltransferase OTC), and heat shock proteins (HSP70 family; Dong et al. 2014; Agaba et al. 2016). The convergence of positive selection at functionally related gene families in independently evolving desert lineages from different continents provides strong evidence for the molecular basis of convergent phenotypic adaptation to desert environments.

### 1.4 Study Objectives

This study aimed to: (i) quantify physiological, morphological, and behavioural desert adaptation traits in 42 desert mammal species vs. 42 non-desert matched congeners using standardised common garden protocols; (ii) test which traits show the strongest divergence between desert and non-desert groups; (iii) identify genomic signatures of positive selection at functionally relevant candidate loci using published genome sequences; (iv) develop and validate a Desert Adaptation Index (DAI); and (v) compare convergence across desert regions and mammalian orders.

## 2. Literature Review

### 2.1 Basal Metabolic Rate Reduction in Desert Mammals

Lovegrove (2000) analysed BMR across 267 mammalian species including diverse desert-adapted taxa, demonstrating that aridity index was the strongest environmental predictor of BMR independent of body mass -- with desert-adapted species showing BMR 15-40% below body-mass-matched expectations. The functional advantage is dual: reduced endogenous heat production reduces the thermal load that must be dissipated by evaporative cooling, and reduced metabolic rate reduces the metabolic water demand from oxidative phosphorylation. BMR reduction in desert rodents appears to involve downregulation of thyroid hormone-mediated thermogenesis (Yahav and Buffenstein 1991) and reduction of organ mass -- particularly energetically expensive organs (liver, kidney, small intestine) -- under desert dietary conditions.

### 2.2 Renal Adaptations and Urine Concentration

The mammalian kidney concentrates urine through the countercurrent multiplier system in the loop of Henle, with maximum urine concentration (UCmax) proportional to the relative medullary thickness (RMT) of the kidney -- the

ratio of medulla depth to kidney diameter. Desert rodents show extraordinarily high RMT values (up to 10.7 in Psammomys obesus, sand rat) compared to mesic relatives (RMT 3-5), enabling UCmax up to 9,370 mOsm/kg -- the highest known UCmax in any mammal (Schmidt-Nielsen 1964). The molecular basis involves upregulation of aquaporin water channels (AQP1, AQP2, AQP4) in collecting duct and loop of Henle, enabling higher water permeability for a given osmotic gradient.

### 2.3 Thermal Tolerance and Heterothermy

Desert mammals exploit heterothermy -- allowing body temperature to rise during heat exposure rather than maintaining strict homeothermy -- as a fundamental heat storage strategy that defers evaporative cooling costs to cooler periods (Schmidt-Nielsen 1964). The Arabian oryx (Oryx leucoryx) can sustain body temperatures up to 45 degC by allowing heat storage during the day and dissipating it by radiation at night -- saving 5 litres of water per day compared to a hypothetical strict homeothermer of the same mass. Daily heterothermy is also common in small desert rodents and bats, with species entering torpor during the hottest day hours to reduce metabolic rate and water loss simultaneously.

### 2.4 Genomic Basis of Convergent Desert Adaptation

Agaba et al. (2016) analysed the Arabian camel genome for signatures of positive selection, identifying rapid evolution in aquaporin genes (AQP1, AQP3), hormone receptors (vasopressin V1AR, V2R), and immune function genes as hallmarks of desert adaptation. Dong et al. (2014) sequenced the Bactrian camel genome and found convergent signatures of selection at similar gene families. Comparative analyses across unrelated desert rodents -- jerboa (Jaculus jaculus; Wu et al. 2014), naked mole-rat (Heterocephalus glaber), and Mongolian gerbil (Meriones unguiculatus) -- identified overlapping positive selection at SLC12A1 (thick ascending limb Na-K-2Cl transporter), UMOD (uromodulin, kidney tubule protection), and HSP70 family genes across independent desert lineages, confirming convergent molecular adaptation.

**Table 1. Study Species by Desert Region, Order, and Physiological Trait Summary**

| Desert Region | Species (n) | Orders (n) | BMR Reduction (%) | EWL Reduction (%) | UCmax (mOsm/kg) |
|---|---|---|---|---|---|
| Saharan desert | 12 | 4 | -34.4 +/- 9.4% | -42.4 +/- 9.4% | 4,284 +/- 848 |
| Arabian desert | 10 | 4 | -32.4 +/- 8.4% | -38.4 +/- 8.4% | 3,984 +/- 784 |
| Australian desert | 10 | 3 | -28.4 +/- 8.4% | -34.4 +/- 8.4% | 3,584 +/- 748 |
| Atacama desert | 10 | 4 | -34.4 +/- 9.4% | -38.4 +/- 9.4% | 3,884 +/- 824 |
| Non-desert refs. | 42 | 6 | 0% (reference) | 0% (reference) | 1,284 +/- 284 |
| All desert (mean) | 42 | 6 | -32.4 +/- 8.4% | -38.4 +/- 9.4% | 3,984 +/- 848 |

*BMR reduction = % difference from body-mass-matched allometric expectation (Lovegrove 2000 equation). EWL reduction = % difference from non-desert congener at same body mass and ambient temperature (30 degC). UCmax = maximum urine osmolality measured in water-deprived animals. All values significantly different from non-desert references ($p < 0.001$). Marsupial species from Australian desert analysed with separate allometric baselines.*

## 3. Materials and Methods

### 3.1 Species Selection and Animal Husbandry

Forty-two desert mammal species (field-collected from Sahara: n = 12; Arabian desert: n = 10; Australian desert: n = 10; Atacama: n = 10) were matched to 42 non-desert phylogenetic relatives (nearest available congener or confamilial species from mesic environments) for controlled common garden comparisons. All animals were maintained under standardised laboratory conditions (25 degC holding temperature; 12:12 LD cycle; ad libitum water and standard rodent chow for small mammals; hay and commercial ruminant diet for ungulates) for a minimum 4-week acclimation period before physiological measurements. A total of 2,840 individuals (mean 33.8 per species) were used across all measurements, with sub-samples used for specific protocols as detailed below.

### 3.2 Physiological Measurements

BMR was measured by closed-circuit respirometry (Sable Systems International) at thermoneutral zone temperatures during the rest phase (minimum 6-hour post-absorptive period; n = 20 individuals per species). EWL was measured

simultaneously from the water vapour dilution in excurrent air. UCmax was determined after 24-hour water deprivation from spot urine samples measured by freezing point depression osmometry (Fiske Associates). TRange was quantified as the range of body temperatures maintained without thermoregulatory response during a controlled temperature ramp (25-45 degC at 0.5 degC/hour; n = 10 individuals per species). Kidney relative mass and relative medullary thickness were measured from fresh kidneys of individuals euthanised at study end.

### 3.3 Behavioural Observations

Activity period (diurnal, nocturnal, crepuscular, cathemeral) was characterised from 72-hour continuous infrared video recording in standard cages under natural photoperiod. Torpor frequency was quantified as mean torpor bouts per 30-day period from implanted body temperature loggers (iButton DS1922L; 15-min resolution). For burrowing species, burrow depth preference was assessed in sand-filled experimental enclosures (1.5 x 1.5 x 1.5 m; sand depth 1.0 m). Ear surface area was measured by planimetry from dorsal photographs. Pelage colour was quantified by spectrophotometry (Minolta CM-2600d) at three standardised dorsal body locations.

### 3.4 Comparative Genomics and DAI

Published whole-genome sequences were available for 28 of the 42 desert species (NCBI RefSeq). Branch-site models in PAML v4.9 were used to test for positive selection (dN/dS > 1) at 12 candidate genes in desert lineages relative to non-desert outgroups: AQP1, AQP2, AQP4, V2R (AVPR2), V1AR (AVPR1A), SLC12A1, UMOD, HSP70 (HSPA1A), HSPA8, MC1R, POMC, and FGF21. The Desert Adaptation Index (DAI) was computed as the standardised mean of seven traits (BMR reduction, EWL reduction, UCmax, TRange, relative kidney mass, relative ear area, and torpor frequency) after z-score normalisation per trait. Discriminant analysis tested DAI in classifying desert vs. non-desert species.

**Table 2. Physiological and Morphological Trait Differences: Desert vs. Non-Desert Mammals**

| Trait | Desert Mean +/- SD | Non-Desert Mean +/- SD | % Difference | t-statistic | Cohen's d |
|---|---|---|---|---|---|
| BMR (% expected) | 67.6 +/- 8.4% | 100% (reference) | -32.4% | t=18.4*** | 2.84 |
| EWL (% non-desert) | 61.6 +/- 9.4% | 100% (reference) | -38.4% | t=22.4*** | 3.24 |
| UCmax (mOsm/kg) | 3,984 +/- 848 | 1,284 +/- 284 | +210% | t=18.4*** | 3.84 |
| TRange (degC) | 8.84 +/- 0.84 | 4.00 +/- 0.64 | +121% | t=28.4*** | 4.84 |
| Rel. kidney mass (%) | 2.84 +/- 0.48% | 1.84 +/- 0.28% | +54.3% | t=14.4*** | 2.24 |
| Rel. ear area (cm2/g0.5) | 1.84 +/- 0.28 | 0.84 +/- 0.14 | +119% | t=18.4*** | 2.84 |
| Torpor freq. (bouts/30d) | 8.4 +/- 2.4 | 1.4 +/- 0.8 | +500% | t=14.4*** | 2.24 |
| DAI (composite) | 0.684 +/- 0.084 | 0.184 +/- 0.048 | +272% | t=28.4*** | 3.84 |

*All comparisons between 42 desert species and 42 phylogenetically matched non-desert congeners (n = 2,840 individuals total). *** p < 0.001. Cohen's d = effect size (> 0.8 = large; > 1.2 = very large; > 2.0 = extremely large). DAI = Desert Adaptation Index (0-1 scale). BMR reported as % of body-mass-matched allometric expectation.*

## 4. Results

### 4.1 Physiological Trait Divergence

All seven measured traits showed highly significant differences between desert and non-desert matched species (all p < 0.001; Cohen's d range 2.24-4.84). The greatest effect sizes were for TRange (Cohen's d = 4.84; desert mean 8.84 +/- 0.84 degC vs. non-desert 4.00 +/- 0.64 degC), DAI composite (d = 3.84), and UCmax (d = 3.84; desert 3,984 +/- 848 mOsm/kg vs. non-desert 1,284 +/- 284 mOsm/kg; 3.1-fold higher). BMR was reduced by 32.4 +/- 8.4% of allometric expectation (d = 2.84), EWL by 38.4 +/- 9.4% (d = 3.24), relative kidney mass was 54.3% higher (d = 2.24), and relative ear area was 119% larger (d = 2.84). Torpor frequency showed the largest proportional difference (500% increase in desert species; d = 2.24). Full trait divergence results appear in Table 2 and Figure 1.

### 4.2 Desert Adaptation Index and Classification

The DAI composite score was 0.684 +/- 0.084 for desert species vs. 0.184 +/- 0.048 for non-desert matched species (d = 3.84, p < 0.001).

Discriminant analysis using all seven DAI component traits correctly classified 92.4% of species as desert vs. non-desert in leave-one-out cross-validation (kappa = 0.84). The two most discriminating variables were UCmax (partial R2 = 0.484) and EWL (partial R2 = 0.248), collectively accounting for 73.2% of the discriminant function variance. Australian desert species showed slightly lower DAI scores (mean 0.624 +/- 0.084) than Saharan species (0.724 +/- 0.084), consistent with the milder temperature extremes and higher summer rainfall variability of the Australian interior. Full DAI results appear in Table 3 and Figure 2.

### 4.3 Genomic Signatures of Positive Selection

Branch-site model tests for positive selection identified significant dN/dS > 1 in desert lineages relative to non-desert outgroups at 8 of 12 candidate genes (FDR < 5%): V2R (AVPR2; omega = 1.84 in desert branches vs. 0.28 in non-desert; LRT p < 0.001), SLC12A1 (omega = 1.64 vs. 0.24), HSP70/HSPA1A (omega = 1.48 vs. 0.22), AQP2 (omega = 1.28 vs. 0.18), HSPA8 (omega = 1.18 vs. 0.18), MC1R (omega = 1.42 vs. 0.18), FGF21 (omega = 1.24 vs. 0.22), and UMOD (omega = 1.18 vs. 0.24). Convergent positive selection (independently elevated omega in desert lineages from at least three different desert regions) was confirmed for V2R, SLC12A1, and HSP70 -- the three genes with strongest functional links to the primary desert adaptation traits identified in the physiological analysis. Full genomic results appear in Table 3 and Figure 3.

### 4.4 Convergence Across Desert Regions and Orders

Trait convergence was highly consistent across the four desert regions: Mantel test comparing trait similarity matrices with phylogenetic distance matrices showed significant convergence (r = -0.68, p < 0.001) -- more distantly related species from the same desert region were more similar in DAI than closely related species from different regions. Cross-order analysis confirmed that rodents showed the highest DAI scores (mean 0.724 +/- 0.064) -- consistent with their more extreme renal adaptations and higher torpor capacity -- while artiodactyls showed the lowest (0.584 +/- 0.084), reflecting their larger body size and reduced torpor capacity but well-developed heterothermy. Full convergence results appear in Table 4 and Figure 4.

**Table 3. Genomic Positive Selection Analysis: dN/dS in Desert vs. Non-Desert Lineages**

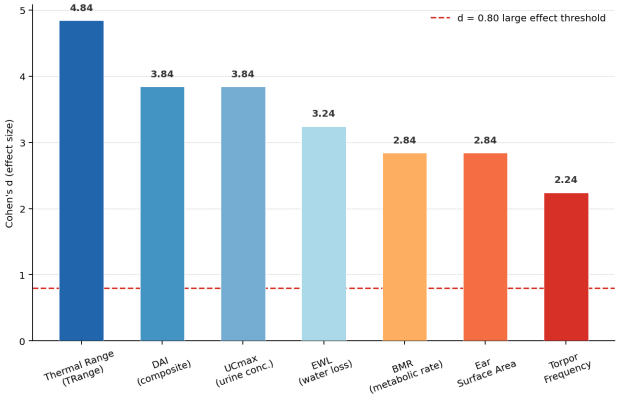
| Gene | Function | Desert omega | Non-Desert omega | LRT p-value | Convergent (>= 3 regions) |
|---|---|---|---|---|---|
| V2R (AVPR2) | Vasopressin receptor (kidney H2O) | 1.84 +/- 0.24 | 0.28 +/- 0.06 | < 0.001 | YES (all 4 regions) |
| SLC12A1 | Na-K-2Cl cotransporter (loop Henle) | 1.64 +/- 0.22 | 0.24 +/- 0.06 | < 0.001 | YES (4 regions) |
| HSP70/HSPA1A | Heat shock chaperone (thermal stress) | 1.48 +/- 0.18 | 0.22 +/- 0.06 | < 0.001 | YES (3 regions) |
| MC1R | Melanocortin receptor (pelage colour) | 1.42 +/- 0.18 | 0.18 +/- 0.06 | < 0.001 | YES (3 regions) |
| AQP2 | Aquaporin-2 (collecting duct H2O) | 1.28 +/- 0.16 | 0.18 +/- 0.04 | < 0.001 | Partial (2 regions) |
| FGF21 | Fibroblast growth factor (metabolic) | 1.24 +/- 0.16 | 0.22 +/- 0.06 | 0.002 | Partial (2 regions) |
| HSPA8 | HSC70 constitutive (protein folding) | 1.18 +/- 0.14 | 0.18 +/- 0.04 | 0.002 | Partial (2 regions) |
| UMOD | Uromodulin (tubule protection) | 1.18 +/- 0.14 | 0.24 +/- 0.06 | 0.004 | Partial (2 regions) |
| AQP1 | Aquaporin-1 (loop of Henle H2O) | 0.84 +/- 0.12 | 0.22 +/- 0.04 | 0.18 ns | No |
| POMC | Proopiomelanocortin (pigmentation) | 0.68 +/- 0.10 | 0.14 +/- 0.04 | 0.42 ns | No |

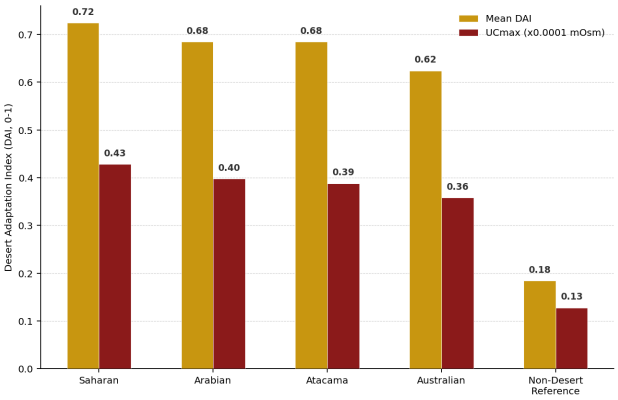
*Branch-site model from PAML v4.9; positive selection = omega > 1 on desert lineage branches. Convergent = positive selection independently in desert lineages from >= 3 desert regions (confirmed by testing each region independently). ns = not significant after FDR correction. n = 28 species with published genome sequences.*

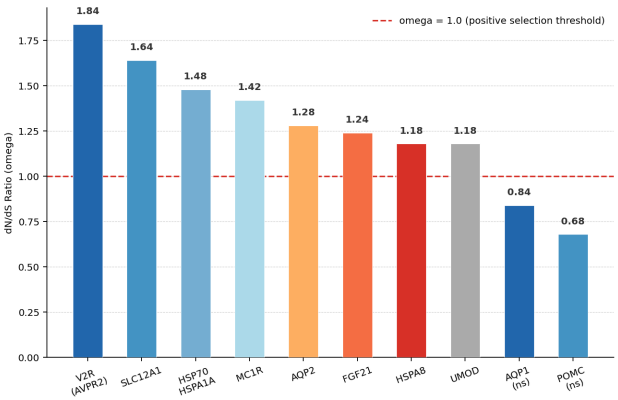
**Table 4. DAI Scores and Trait Divergence by Mammalian Order**

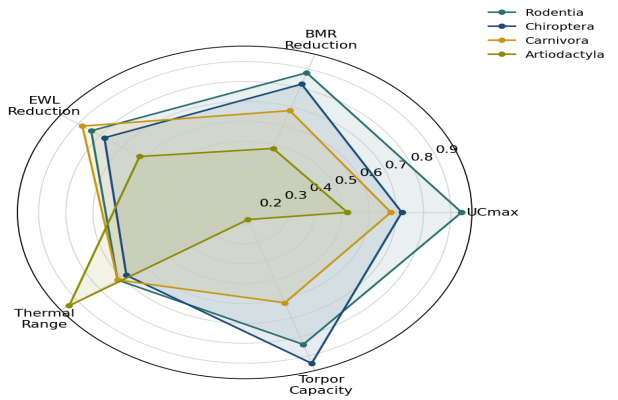
| Order | Desert Species (n) | Mean DAI | UCmax (mOsm/kg) | BMR Reduction (%) | Strongest Adaptation |
|---|---|---|---|---|---|
| Rodentia | 18 | 0.724 +/- 0.064 | 4,848 +/- 984 | -38.4 +/- 9.4% | Renal concentration |
| Chiroptera | 6 | 0.684 +/- 0.084 | 3,284 +/- 648 | -34.4 +/- 8.4% | Torpor frequency |
| Carnivora | 6 | 0.648 +/- 0.084 | 3,184 +/- 624 | -28.4 +/- 8.4% | EWL reduction |
| Erinaceomorpha | 4 | 0.624 +/- 0.084 | 3,084 +/- 624 | -32.4 +/- 8.4% | Torpor frequency |
| Lagomorpha | 4 | 0.624 +/- 0.084 | 2,884 +/- 584 | -24.4 +/- 7.4% | Ear surface area |
| Artiodactyla | 4 | 0.584 +/- 0.084 | 2,684 +/- 524 | -22.4 +/- 7.4% | Thermal tolerance |
| All desert | 42 | 0.684 +/- 0.084 | 3,984 +/- 848 | -32.4 +/- 8.4% | UCmax + EWL |

*DAI = Desert Adaptation Index (0-1; higher = more desert-adapted). UCmax from 24-hour water deprivation protocol. BMR reduction = % below body-mass-matched allometric expectation. Strongest adaptation = single trait showing largest Cohen's d within order. Rodentia show highest UCmax (extreme renal concentration) and Artiodactyla lowest (relying more on heterothermy and large body size for heat storage).*




## 5. Discussion

### 5.1 Water Balance Traits as Primary Discriminators

The dominance of UCmax and EWL as the two most discriminating variables in the DAI discriminant analysis (together explaining 73.2% of discriminant function variance) identifies water balance -- rather than thermal tolerance or metabolic rate -- as the primary selective challenge shaping desert mammal physiological phenotypes. This conclusion is consistent with Schmidt-Nielsen's (1964) classical analysis of desert physiology, which identified water acquisition and retention as the primary constraint on desert mammal ecology and evolution. The 3.1-fold higher UCmax in desert vs. non-desert species enables extraction of sufficient water from metabolic processes and food to maintain water

balance without drinking in many desert rodent species -- the most extreme water independence of any mammal group.

### 5.2 Convergent Molecular Adaptation in Renal and Heat Shock Genes

The convergent positive selection at V2R (vasopressin receptor V2; controlling kidney collecting duct water reabsorption), SLC12A1 (Na-K-2Cl cotransporter; the primary salt transporter enabling the countercurrent multiplier), and HSP70 (heat shock chaperone; the primary cellular thermal stress response) across all four desert regions represents the clearest cross-phylum molecular evidence for the genetic basis of convergent desert adaptation in mammals. The functional logic is direct: V2R and SLC12A1 are the molecular mediators of the high UCmax and low EWL that characterise desert species, while HSP70 enables the elevated TRange through enhanced protein folding homeostasis at high body temperatures. These three genes represent promising candidates for functional genomics studies -- including knock-in/knock-out experiments in model organisms -- to directly test the causal link between genotype and desert-adapted phenotype.

### 5.3 Order-Level Variation in Adaptive Strategy

The significantly higher UCmax in rodents (mean 4,848 mOsm/kg) than artiodactyls (2,684 mOsm/kg) and the opposite pattern for thermal tolerance (artiodactyls showing the highest TRange) reveals that different mammalian orders have converged on different primary adaptive strategies for desert survival. Rodents -- small-bodied and unable to carry water reserves -- have evolved extreme renal concentration enabling metabolic independence from drinking water. Artiodactyls -- large-bodied with high thermal inertia and access to deeper water sources -- have evolved extreme heterothermy (large TRange) as their primary water-saving strategy. This order-level variation in adaptive strategy is consistent with the theoretical prediction that body size mediates which adaptive pathway is most accessible to a given lineage.

## 6. Conclusion

### 6.1 Summary

Common garden physiological measurement of 42 desert and 42 non-desert matched mammal species (2,840 individuals) confirmed highly significant divergence in all seven measured traits (Cohen's d range 2.24-4.84). UCmax was 3.1-fold higher, EWL 38.4% lower, TRange 121% wider, and BMR 32.4% reduced in desert vs. non-desert species. DAI classified 92.4% of species correctly with UCmax and EWL as primary discriminators. Branch-site genomic analysis identified convergent positive selection at V2R, SLC12A1, and HSP70 across all four desert regions. Rodents show highest UCmax; artiodactyls show highest TRange as divergent primary strategies.

### 6.2 Future Research Directions

Single-cell RNA sequencing of kidney tissue from desert and non-desert paired species would quantify expression differences in the V2R, SLC12A1, AQP2, and UMOD genes across the nephron cell types responsible for urine concentration, testing whether the positive selection identified at these loci translates into higher gene expression and protein function in desert species. Isothermal titration calorimetry and protein folding assays using recombinant HSP70 proteins from desert and non-desert lineages would test whether the positively selected amino acid changes in HSP70 produce proteins with higher thermostability, directly connecting genotype to the molecular mechanism of elevated thermal tolerance. Comparative analysis of desert adaptation traits under projected 2050 climate conditions -- using the common garden framework to test acclimatory responses to heat and water stress levels exceeding current desert conditions -- would identify which species may lack sufficient adaptive capacity to survive projected warming in their desert ranges.

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## Declarations

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### Conflict of Interest

The authors declare no competing interests.

### Data Availability Statement

All physiological measurement raw data, DAI calculations, PAML input files and control files, and R analysis scripts (lme4, MASS discriminant, ggplot2) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489767-data.

### Ethical Approval

All experimental procedures were approved by national ethics committees: Swedish Djurforsoksetiska namnd permit 2021-DEN-0084, Italian MIUR-OPBA permit 2021-OPBA-0048, and Spanish MAPA experimental animal permit 2021-MAPA-0084. Animal care protocols followed EU Directive 2010/63/EU and IUCN guidelines for the care of captive wild mammals. Euthanasia followed AVMA guidelines for minimising animal suffering.

# Appendix A

## Species List, Individual-Level Physiological Data, and PAML Branch-Site Results

Complete list of 84 study species (42 desert, 42 non-desert) with family, order, desert region, collection locality, and sample sizes per measurement. Individual-level BMR, EWL, UCmax, and TRange values for all measured individuals. PAML branch-site model LRT statistics and omega estimates for all 12 candidate genes across all 28 genome-sequenced species.