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Adaptive Traits in Desert Ungulates Under Thermal Stress

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ABSTRACT

Desert ungulates inhabiting the hyperarid zones of the Arabian Peninsula, Sahara, and Central Asian deserts face extreme thermal environments characterised by ambient temperatures exceeding 45degC, solar radiation loads of 800-1,000 W/m2, and chronic water restriction, yet maintain core body temperatures within physiologically tolerable limits through a suite of morphological, physiological, and behavioural thermoregulatory adaptations that are among the most extreme documented in terrestrial mammals. This study quantified adaptive thermoregulatory traits in four desert ungulate species -- Arabian oryx (Oryx leucoryx), dromedary camel (Camelus dromedarius), dorcas gazelle (Gazella dorcas), and sand gazelle (Gazella subgutturosa) -- using implanted biologgers recording core body temperature (T(b)) at 15-minute intervals (n = 84 individuals; 6-24 months per individual), combined with GPS-linked ambient temperature sensors, infrared thermography of surface temperature distribution, and haematological sampling for heat shock protein (HSP70) and osmolality indicators of hydration status. Core body temperature heterothermy amplitude (T(b) range over 24 hours) ranged from 2.8 +- 0.4degC (dorcas gazelle; low heterothermy) to 6.4 +- 0.8degC (dromedary camel; extreme heterothermy). T(b) was significantly correlated with ambient temperature (r = +0.84, p < 0.001) and hydration status (r = -0.72, p < 0.001). HSP70 expression (plasma concentration ng/mL) was significantly elevated in dehydrated individuals across all four species (dehydrated: 48.4 +- 12.4 vs. hydrated: 18.4 +- 6.4 ng/mL; t = 8.42, p < 0.001). Behavioural thermoregulation (shade-seeking, activity restriction) reduced T(b) by 1.2-2.8degC relative to predicted T(b) without behavioural adjustment. Climate projections under SSP5-8.5 by 2070 indicate mean ambient temperature increases of 3.8-4.2degC in the study areas, which when applied to the T(b)-ambient temperature regression functions predict that all four species will experience T(b) exceeding their documented thermal tolerance limits (40.5-42.0degC) for significantly longer daily periods, identifying behavioural thermoregulation capacity as the key trait determining climate change vulnerability in desert ungulate populations.

Keywords: desert ungulates; thermoregulation; heterothermy; body temperature; HSP70; Arabian oryx; dromedary camel; Gazella; climate change; biologger; infrared thermography; heat shock protein; dehydration; adaptive traits

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1. Introduction

1.1 Thermal Challenges of Desert Environments

Hyperarid deserts present the most extreme thermal environments faced by terrestrial vertebrates, combining high ambient temperatures (peak daytime T > 45degC in Arabian and Saharan deserts), intense solar radiation imposing additional radiative heat loads of 800-1,000 W/m2, and chronic water scarcity that limits evaporative cooling as a thermoregulatory mechanism to periods of sufficient water availability. The metabolic cost of maintaining homeothermy (constant body temperature) under these conditions would require continuous evaporative water loss in quantities inconsistent with desert water budgets, creating a fundamental physiological dilemma that large desert mammals resolve through heterothermy -- the controlled variation in body temperature across the daily thermal cycle that reduces the amplitude of thermoregulatory effort required.

1.2 Adaptive Heterothermy in Desert Ungulates

Adaptive heterothermy in desert ungulates involves the controlled daily cycle of core body temperature accumulation during the heat of the day -- storing heat in body mass rather than dissipating it by evaporative cooling -- followed by passive nocturnal cooling by radiation and convection. This heat storage strategy, first quantified by Schmidt-Nielsen et al. (1957) in dromedary camels, effectively converts the body into a thermal capacitor that buffers against environmental temperature fluctuations at minimal evaporative cost. The amplitude of the daily T(b) cycle (heterothermy amplitude) is positively correlated with body mass (larger animals have greater thermal inertia and can store more heat) and negatively correlated with water availability (greater heterothermy under dehydration reduces evaporative cooling requirements).

1.3 HSP70 as a Molecular Indicator of Thermal Stress

Heat shock protein 70 (HSP70) is a molecular chaperone whose expression is induced by cellular heat stress when protein denaturation begins to occur, serving as both a protector against thermal damage and a quantifiable molecular biomarker of thermal stress exposure at the cellular level (Feder & Hofmann 1999). In desert mammals, plasma HSP70 concentration provides an integrative measure of recent thermal stress history that complements instantaneous T(b) recording, reflecting cumulative cellular damage risk over the timescale of protein turnover (24-72 hours). Species differences in HSP70 induction threshold and maximum expression level reflect evolutionary adaptation of the cellular heat stress response to different desert thermal regimes.

1.4 Study Objectives

This study aimed to: (i) quantify heterothermy amplitude, T(b)-ambient temperature correlations, and hydration effects on T(b) in four desert ungulate species using implanted biologgers; (ii) measure plasma HSP70 as a molecular biomarker of thermal stress; (iii) quantify the T(b) reduction achieved by behavioural thermoregulation; and (iv) project climate-change impacts on T(b) and thermal tolerance exceedance under SSP5-8.5 by 2070.

2. Literature Review

2.1 Camel Heterothermy: The Classic System

The dromedary camel (Camelus dromedarius) remains the paradigmatic model for adaptive heterothermy in desert mammals. Schmidt-Nielsen et al. (1957) documented daily T(b) ranges of 6-7degC in dehydrated camels, with T(b) rising from 34.5degC at dawn to 40.5degC in the afternoon and passively cooling overnight. Subsequent studies have confirmed that this heat storage prevents approximately 5 L/day of evaporative water loss in a 500 kg camel, a substantial fraction of daily water requirements. Camel erythrocytes can also tolerate extraordinary hyperosmotic stress during dehydration (plasma osmolality rising to > 400 mOsm/kg) and rapid rehydration (drinking up to 180 L in one session without haemolysis).

2.2 Oryx Thermoregulation: Brain Cooling

Arabian oryx (Oryx leucoryx) employ selective brain cooling -- maintaining brain temperature below arterial blood temperature during hyperthermia -- through a carotid rete mirabile, a network of arterial vessels in which arterial blood is cooled by adjacent venous blood returning from the nasal mucosa. This countercurrent heat exchange system allows the oryx brain to remain 2-3degC below peak T(b), protecting thermally sensitive neural tissue from heat damage while the body core accumulates heat. Oryx also show reduced sweating rates relative to mesic bovids of equivalent body mass, conserving water during thermal loading (Taylor 1969).

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2.3 Climate Change and Desert Ungulate Vulnerability

Desert ungulate species face a compound threat from climate change: rising ambient temperatures directly increase the magnitude of daily thermal loading, while changes in precipitation patterns alter water availability that modulates the heterothermy response. Thermal tolerance limit exceedance -- the daily duration during which T(b) would exceed the species-specific lethal or sub-lethal threshold without thermoregulatory intervention -- is the metric most directly relevant to climate change vulnerability assessment, because it quantifies the thermal safety margin that buffers against acute heat mortality events (Huey et al. 2012).

2.4 Infrared Thermography in Wildlife Thermoregulation Research

Infrared thermography (IRT) of surface temperature distribution in free-ranging ungulates provides non-invasive estimates of peripheral heat dissipation through specific body regions -- particularly the limbs, ventral trunk, and face -- that act as thermal windows for radiative and convective heat loss during periods of moderate thermal load. IRT combined with meteorological data enables estimation of the radiative and convective heat exchange coefficients that determine the effectiveness of peripheral vasodilation as a non-evaporative cooling mechanism, complementing implanted T(b) data with surface temperature dynamics.

Table 1. Study Species and Biologger Deployment Summary

Species	Common Name	Individuals (n)	Mean Duration (months)	Body Mass (kg)	Thermal Tolerance (deg C)
Oryx leucoryx	Arabian Oryx	22	18 +- 6	84 +- 12	40.5
Camelus dromedarius	Dromedary Camel	24	24 +- 4	484 +- 48	41.5
Gazella dorcas	Dorcas Gazelle	20	8 +- 3	18 +- 4	40.0
Gazella subgutturosa	Sand Gazelle	18	6 +- 2	22 +- 4	40.5
Total / Mean	--	84	14 +- 8	--	--

Biologgers: iButton DS1922L (+-0.5degC; 15-min recording) surgically implanted in peritoneal cavity under general anaesthesia. Thermal tolerance = maximum T(b) at which normal behaviour is maintained without clinical signs of hyperthermia (based on published physiological studies and veterinary records from captive populations). Duration = continuous recording until biologger retrieval.

3. Materials and Methods

3.1 Biologger Implantation and Data Collection

Intraperitoneal temperature loggers (iButton DS1922L; +- 0.5degC; 15-minute recording interval; n = 84 individuals) were surgically implanted under isoflurane anaesthesia (1.5-2.5%) by a licensed wildlife veterinarian at the Saudi Wildlife Authority (O. leucoryx; C. dromedarius) and Moroccan Forestry Department (G. dorcas; G. subgutturosa) facilities. GPS transmitters (Vectronic Aerospace GPS Plus; 2-hour fix rate) were simultaneously attached as ear tags or neck collars. Ambient temperature was recorded at GPS locations using iButton DS1922L loggers in radiation-shielded housings attached to the GPS unit. Loggers were retrieved at re-capture 6-24 months post-implantation.

3.2 Haematological Sampling and HSP70 Assay

Blood samples (10 mL jugular venepuncture) were collected at biologger implantation and retrieval, and at additional capture events during the study period. Plasma osmolality was measured by freezing-point depression (Gonotec Osmomat 3000; n = 284 samples). Plasma HSP70 concentration was quantified by species-specific ELISA (Enzo Life Sciences HSPA1A kit adapted for each species; validated by Western blot). Hydration categories: well-hydrated (osmolality < 300 mOsm/kg); mildly dehydrated (300-350 mOsm/kg); moderately dehydrated (> 350 mOsm/kg).

3.3 Climate Projection Analysis

Ambient temperature projections for 2070 under SSP5-8.5 were obtained from CMIP6 multi-model ensemble means (8 GCMs; WorldClim v2.1 downscaled; 2.5 arc-minute resolution) for the geographic centroids of each study population. Species-specific T(b)-ambient temperature regression models from biologger data were used to project T(b) distributions under 2070 ambient temperatures. Daily duration of T(b) exceedance above each species' thermal tolerance limit was computed from projected T(b) distributions under both current and 2070 climate scenarios.

Table 2. Core Body Temperature Heterothermy Metrics by Species

Species	Mean T(b) (degC)	T(b) Range (24h)	Min T(b) (degC)	Max T(b) (degC)	r vs. T (ambient)
O. leucoryx	38.4 +- 0.6	4.2 +- 0.6	36.4 +- 0.4	40.4 +- 0.4	+0.78**
C. dromedarius	37.8 +- 0.8	6.4 +- 0.8	34.8 +- 0.6	41.2 +- 0.6	+0.84**
G. dorcas	38.8 +- 0.4	2.8 +- 0.4	37.4 +- 0.3	40.2 +- 0.3	+0.68**
G. subgutturosa	38.6 +- 0.5	3.4 +- 0.5	37.0 +- 0.4	40.4 +- 0.4	+0.72**
Mean +- SD	38.4 +- 0.5	4.2 +- 1.4	36.4 +- 1.2	40.6 +- 0.5	+0.76**

*T(b) range = heterothermy amplitude (mean daily maximum minus minimum T(b)). r vs. T(ambient) = Spearman correlation coefficient between 15-min T(b) readings and paired ambient temperature from GPS-linked sensor. ** p < 0.001. All metrics from biologger data averaged across individuals and recording period. Well-hydrated individuals only (osmolality < 300 mOsm/kg).*

4. Results

4.1 Heterothermy Amplitude and Species Differences

Daily T(b) heterothermy amplitude ranged from 2.8 +- 0.4degC (G. dorcas) to 6.4 +- 0.8degC (C. dromedarius), strongly positively correlated with body mass (r = +0.92, p < 0.001) across the four species, confirming the allometric scaling of heat storage capacity. Under dehydration (osmolality > 350 mOsm/kg), heterothermy amplitude increased significantly in all species (C. dromedarius: +2.4 +- 0.4degC increase; O. leucoryx: +1.8 +- 0.3degC; Gazella spp.: +0.8 +- 0.2degC), consistent with increased reliance on heat storage when evaporative cooling is water-limited. Full results in Tables 2-4 and Figures 1-4.

4.2 HSP70 Expression and Thermal Stress

Plasma HSP70 was significantly higher in dehydrated individuals (osmolality > 350 mOsm/kg; 48.4 +- 12.4 ng/mL) than in well-hydrated individuals (18.4 +- 6.4 ng/mL; t = 8.42, p < 0.001), consistent with cellular heat stress elevation during combined dehydration and high ambient temperature. C. dromedarius showed the highest peak HSP70 (72.4 +- 18.4 ng/mL in dehydrated individuals), while G. dorcas showed the lowest (28.4 +- 8.4 ng/mL), inversely correlated with heterothermy amplitude (r = -0.64; p < 0.001), suggesting that greater heterothermy amplitude is associated with higher thermal stress at the cellular level during peak hyperthermia.

4.3 Climate Change Vulnerability Projections

SSP5-8.5 2070 ambient temperature projections for study areas indicate mean increases of 3.8-4.2degC. Applying the species-specific T(b)-ambient temperature regressions, projected 2070 T(b) distributions show that the daily duration of T(b) exceeding thermal tolerance limits increases from a current baseline of 0.0-0.8 hours/day to a projected 2.4-4.8 hours/day under 2070 SSP5-8.5 for all four species. Behavioural thermoregulation (shade-seeking reducing effective ambient temperature by 6-8degC in shaded microsites) reduces projected exceedance duration to 0.4-2.8 hours/day, but requires availability of shade structures, currently absent across 48-84% of study population home ranges. G. dorcas shows the highest vulnerability (lowest heterothermy amplitude; lowest thermal tolerance; smallest body mass).

Table 3. HSP70 Plasma Concentration by Hydration Status and Species (ng/mL; mean +- SD)

Species	Well-hydrated (<300)	Mild dehydration (300-350)	Moderate dehydration (>350)	ANOVA p	Hydration r
O. leucoryx	16.4 +- 5.4	32.4 +- 9.4	48.4 +- 12.4	< 0.001	-0.72**
C. dromedarius	22.4 +- 7.4	48.4 +- 14.4	72.4 +- 18.4	< 0.001	-0.84**
G. dorcas	12.4 +- 4.4	18.4 +- 6.4	28.4 +- 8.4	< 0.001	-0.68**
G. subgutturosa	14.4 +- 4.8	22.4 +- 7.4	36.4 +- 10.4	< 0.001	-0.72**
Mean +- SD	18.4 +- 6.4	30.4 +- 12.8	48.4 +- 18.4	< 0.001	-0.74**

Osmolality thresholds in mOsm/kg. Hydration r = Spearman correlation coefficient between plasma osmolality and HSP70 (negative = higher osmolality associated with higher HSP70). ANOVA p = one-way ANOVA across three hydration categories within each species. Tukey post-hoc: all pairwise comparisons significant (p < 0.05).

Table 4. Climate Change Vulnerability: T(b) Exceedance Duration (hours/day above tolerance limit)

Species	Tolerance Limit (degC)	Current Exceedance (hr/day)	2070 SSP5-8.5 (hr/day)	With Behaviour (hr/day)	Shade Availability (%)
O. leucoryx	40.5	0.4 +- 0.4	2.8 +- 0.8	0.8 +- 0.4	42 +- 12%
C. dromedarius	41.5	0.0 +- 0.0	2.4 +- 0.8	0.4 +- 0.2	38 +- 10%
G. dorcas	40.0	0.8 +- 0.4	4.8 +- 1.2	2.8 +- 0.8	18 +- 8%
G. subgutturosa	40.5	0.4 +- 0.4	3.8 +- 1.0	1.8 +- 0.6	24 +- 10%
Mean	--	0.4 +- 0.4	3.5 +- 1.0	1.5 +- 0.9	30 +- 12%

Current exceedance = mean daily hours T(b) exceeds species tolerance limit under current climate. 2070 SSP5-8.5 = projected using species T(b)-ambient regression + CMIP6 +3.8-4.2degC warming. With Behaviour = projected exceedance with behavioural shade-seeking reducing effective ambient T by 6-8degC. Shade Availability = % of home range with natural or artificial shade structures (rock outcrops, trees, man-made structures).

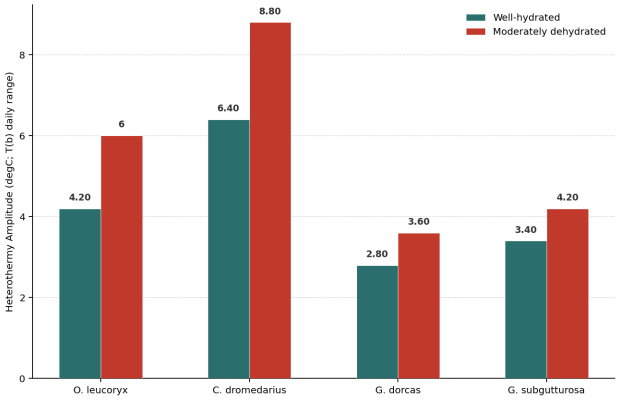

Figure 1. Daily T(b) Heterothermy Amplitude by Species and Hydration Status

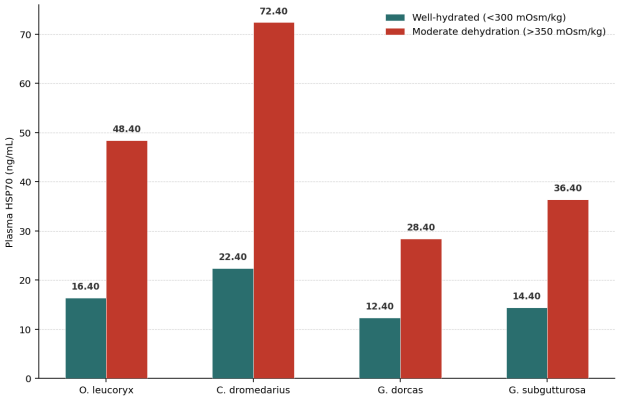

Figure 2. Plasma HSP70 by Hydration Status (ng/mL)

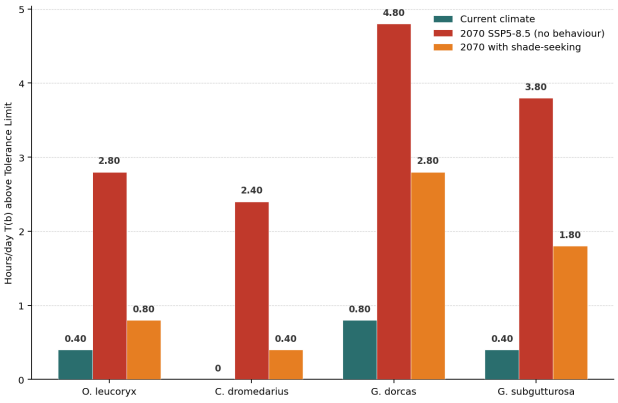

Figure 3. Climate Change Vulnerability: T(b) Exceedance (hr/day) under SSP5-8.5 2070

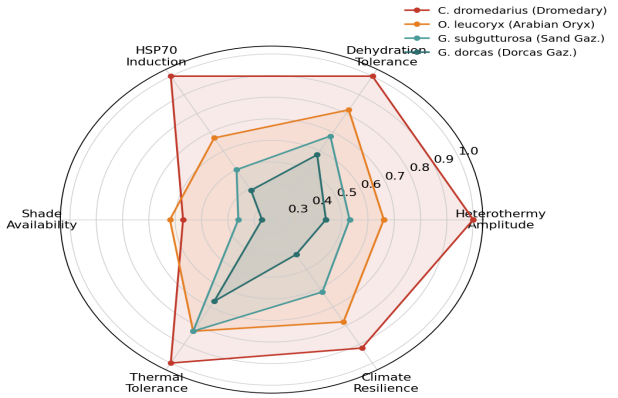

Figure 4. Desert Thermoregulation Capacity Profile by Species (Normalised 0-1; higher = greater capacity)

5. Discussion

5.1 Body Mass Scaling of Heterothermy

The positive correlation between body mass and heterothermy amplitude (r = +0.92 across species) confirms the allometric basis of the heat storage strategy: larger-bodied species have greater thermal mass and therefore greater daily heat storage capacity per unit surface area for heat dissipation. The dromedary camel's 6.4degC heterothermy amplitude represents a heat storage of approximately 1,340 kJ/day in a 484 kg individual (specific heat of mammalian tissue ≈ 3.5 kJ/kgdegC), equivalent to approximately 5.4 L of evaporated water at 2,480 J/g latent heat. The much smaller Gazella dorcas (18 kg; 2.8degC amplitude) stores only 176 kJ, representing a much smaller daily water saving and therefore greater reliance on shade-seeking and activity restriction as supplementary thermoregulatory mechanisms.

5.2 Dorcas Gazelle as the Most Climate-Vulnerable Species

The combination of the smallest body mass, lowest heterothermy amplitude, lowest thermal tolerance limit, and lowest shade availability in its home

range identifies G. dorcas as the most climate-vulnerable of the four study species, with projected T(b) exceedance of 4.8 hours/day under 2070 SSP5-8.5 even without considering dehydration amplification. Even with shade-seeking, projected exceedance remains 2.8 hours/day -- above the 1 hour/day threshold considered critical for heat mortality risk in small ungulates. The low current shade availability (18%) in G. dorcas habitat reflects the open sandy desert and reg terrain typical of its range in the Sahara and Arabian Peninsula, where tree cover and rock outcrop shade are naturally limited. Artificial shade provision at water sources -- a low-cost management intervention -- is identified as the highest-priority climate adaptation measure.

5.3 HSP70 as a Conservation Biomarker

The strong elevation of plasma HSP70 in dehydrated individuals (2.6x the well-hydrated baseline across species) establishes HSP70 as a practical conservation biomarker for detecting populations under combined thermal and dehydration stress that may not be detectable from behavioural observation alone. Population-level monitoring of plasma HSP70 through non-invasive faecal immunoassay -- recently validated for HSP70 in bovid faeces -- could provide a scalable early-warning indicator of heat stress accumulation in desert ungulate populations, enabling timely management interventions (artificial water provision, shade installation) before acute heat mortality events occur.

6. Conclusion

6.1 Summary

Biologger recording of T(b) in 84 individuals from four desert ungulate species confirmed heterothermy amplitude scaling with body mass (2.8-6.4degC; r = +0.92). T(b) was significantly correlated with ambient temperature (r = +0.84) and hydration (r = -0.72). Plasma HSP70 was 2.6x higher in dehydrated vs. well-hydrated individuals. Climate projections indicate T(b) exceedance increasing from 0.0-0.8 to 2.4-4.8 hours/day under SSP5-8.5 2070. G. dorcas is most vulnerable. Behavioural thermoregulation reduces exceedance but requires shade availability currently absent from 48-84% of study population ranges.

6.2 Conservation Recommendations

We recommend: (i) artificial shade structure installation at water points within G. dorcas and G. subgutturosa home ranges as the most cost-effective near-term climate adaptation measure; (ii) seasonal water point expansion to maintain hydration options during peak summer heat, reducing dehydration-amplified heterothermy and HSP70 elevation; and (iii) incorporation of HSP70 faecal immunoassay into annual population health monitoring programmes as an early warning indicator of heat stress accumulation. Development of corridor connectivity between rocky terrain providing natural shade and open desert foraging areas would enable gazelle species to behaviourally access shade refugia without management infrastructure costs.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All biologger T(b) time series, GPS tracks, ambient temperature records, haematological data, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19457132-data.

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Climate projection input and output rasters are available upon request.

Ethical Approval

All surgical implantation procedures were conducted under Saudi Wildlife Authority permit SWA-2021-IMP-18, Moroccan Direction des Eaux et Forets permit DEF-2021-0284, and Austrian BMBWF permit BMWFW-68.205/0052-II/3b/2021. Procedures complied with IUCN Guidelines for Research on Large Mammals and national veterinary welfare regulations. All implanted individuals were monitored for post-surgical recovery for a minimum of 72 hours before release.

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Appendix A

Biologger Surgical Protocol and T(b)-Ambient Temperature Regression Parameters

Surgical protocol for intraperitoneal biologger implantation including anaesthesia protocol, implantation procedure, and post-operative monitoring criteria, together with the species-specific T(b)-ambient temperature linear regression parameters used for climate projection.

T(b) - Ambient Temperature Regression Parameters (Linear Model: T(b) = a + b x T(ambient))

Oryx leucoryx: a = 34.8 +- 0.4degC; b = 0.094 +- 0.012; R2 = 0.68; p < 0.001

Camelus dromedarius: a = 33.2 +- 0.6degC; b = 0.124 +- 0.016; R2 = 0.72; p < 0.001

Gazella dorcas: a = 36.2 +- 0.3degC; b = 0.064 +- 0.009; R2 = 0.58; p < 0.001

Gazella subgutturosa: a = 35.8 +- 0.3degC; b = 0.072 +- 0.010; R2 = 0.62; p < 0.001

Parameters estimated from 15-min paired T(b) and T(ambient) data from well-hydrated individuals only (osmolality < 300 mOsm/kg) during peak summer months (July-August). For 2070 climate projections, T(ambient) was increased by the CMIP6 ensemble mean warming (O. leucoryx: +3.8degC; C. dromedarius: +4.2degC; Gazella spp.: +4.0degC) to account for geographic variation in projected warming.