

Fine-scale body condition dynamics in elk revealed by implanted bioimpedance biologgers

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Body condition shapes ungulate survival and reproduction, but temporally sparse capture-based measurements limit inference about when individuals gain or lose fat reserves in response to environmental change. We evaluated implanted biologgers that measure bioimpedance, based on the electrical conductivity of tissue, as a continuous signal of body condition dynamics in captive elk. Adult female elk ($n = 4$) were implanted with subcutaneous biologgers that recorded bioimpedance every 4 h during a ~6-month feeding experiment inducing gradual condition loss and recovery. We quantified correspondence between bioimpedance and maximum rump fat thickness measured approximately monthly, lagged relationships between daily caloric intake and bioimpedance and whether 4-h bioimpedance variability was associated with camera-derived feeding and drinking time budgets. Weekly bioimpedance showed strong within-individual correlation with maximum rump fat thickness, with Spearman correlations of 0.75–0.96 during dietary restriction (mean = 0.90) and 0.96–0.98 during the normal feeding schedule for three elk (mean = 0.97). Bioimpedance also covaried with caloric intake, but the timing of the association varied among elk: correlations between first differences of smoothed daily calories and smoothed daily impedance peaked at lags spanning 0–60 days, with the fattest individual showing the minimum lag (0 day). Coupling was more consistent during restriction than during the gain phase, suggesting reserve loss may act faster than rebuilding. At the finest scale, feeding and drinking behaviour explained only a portion of 4-h impedance variation and was most consistent with multi-day (72 h) summaries. Together, these results indicate that bilogger-derived bioimpedance provides a continuous, within-individual indicator of condition dynamics across hours to weeks. Although additional calibration will be needed to translate raw impedance into absolute fat estimates across animals, this approach enables inference about the timing, rate and extrema of fat-reserve change, with applications for monitoring nutritional status and evaluating habitat and management outcomes in free-ranging wildlife.

Lay Summary

Body fat drives elk survival and reproduction, but capture-based measures are snapshots. We implanted sensors in captive female elk that measured bioimpedance every 4 h for 6 months during controlled diet restriction and

refeeding. Bioimpedance tracked rump fat and estimated caloric intake, revealing individual-specific lags and slower recovery than loss. This opens a new window into when animals become nutritionally stressed and when recovery truly begins.

Key words: Bioimpedance, body condition, *Cervus canadensis*, controlled feeding experiment, dietary manipulation, nutritional ecology, physiological biollogger

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Introduction

Body condition is a key determinant of demographic performance in ungulates because it integrates energy acquisition and expenditure over time, making it a direct readout of habitat quality and management outcomes. Across many ungulate field studies, adult female body condition is linked to survival and productivity (Bender *et al.*, 2007; Johnson *et al.*, 2019), and habitat or management context can translate into measurable differences in condition with downstream demographic consequences (Bergman *et al.*, 2014). Body condition scales to population-relevant outcomes, most notably survival and recruitment (Monteith *et al.*, 2014; Shallow *et al.*, 2015) but can also help define population nutritional limitations and carrying capacity (Piasecke and Bender, 2009). At a population scale, ungulates that access better forage gain substantially more fat and exhibit higher survival and projected population growth than individuals occupying poorer ranges (Stephenson *et al.*, 2020; Ortega *et al.*, 2026). As such, ultrasound-measured rump fat thickness has become the standard non-invasive metric for body condition in cervids and provides the fitness-relevant benchmark against which emerging tools are evaluated (Stephenson *et al.*, 2002; Monteith *et al.*, 2014).

Seasonal environments impose predictable constraints on energy balance, with many ungulates commonly switching between net positive energy balance during the growing season and net negative energy balance when productivity ceases, such as winter in temperate environments, with analogous dry-season constraints in arid and tropical systems (Parker *et al.*, 2009; Cook *et al.*, 2013; Monteith *et al.*, 2013). In temperate environments, overwinter performance depends in part on the phenology, availability and quality of forage that shape fat accumulation during the growing season (Cook *et al.*, 2004, 2013; Monteith *et al.*, 2013; Middleton *et al.*, 2018). Increasing evidence indicates that nutrient availability and nutritional quality of summer range play a critical role in replenishing depleted body reserves, and that body condition entering winter is largely dependent on access to high-quality forage during summer and autumn (Cook *et al.*, 2004, 2013; Monteith *et al.*, 2013; Denryter *et al.*, 2022). These seasonal linkages can generate carryover effects, where differences in condition persist across seasons and influence subsequent performance (Norris, 2005; Norris and Marra, 2007; Harrison *et al.*, 2011). Furthermore, energy loss during winter is exacerbated by snow which restricts

forage access and elevates locomotion costs (Fancy and White, 1987; Dailey and Hobbs, 1989; Hudson *et al.*, 2002). Individuals that deplete fat reserves before spring green-up may face elevated late-winter mortality risk (Kautz *et al.*, 2020; LaSharr *et al.*, 2023). Tools that resolve intraseasonal changes in body condition are therefore needed to identify when energetic bottlenecks occur and which environmental factors shape seasonal energy balance.

Despite the importance of seasonal condition trajectories, obtaining fat measurements in free-ranging ungulates remains temporally sparse because conventional condition assessments require capture and handling. This sampling limitation constrains inference about rates of fat reserve gain and loss and reduces our ability to attribute shorter-duration factors or disturbances (e.g. acute drought, deep snowpack, forage pulses and behavioural shifts) to subsequent physiological change (Parker *et al.*, 2009). Ortega *et al.* (2023) demonstrate why improved temporal resolution matters by showing that winter fat expenditure can be strongly non-linear and state-dependent. Importantly, they noted that short-timescale changes in fat reserves remain difficult to resolve when datasets capture only a small number of within-season measurements (Ortega *et al.*, 2023). Even where condition is used to evaluate habitat or management effects, coarse sampling can obscure the timing of physiological responses (Bergman *et al.*, 2014).

Physiological biollogging has been framed as a key tool for quantifying both physiological and ecological responses to climatic variation (Chmura *et al.*, 2018). Biolloggers provide a pathway for reducing gaps in fat measurement data by enabling sustained, high-frequency measurements that can be aligned with movement rate and other ecological contexts Chimienti *et al.* (2021). Work in mule deer (*Odocoileus hemionus*) using biolloggers shows that continuous biollogger-derived heart rate data can reveal landscape-linked energetic costs (Laforge *et al.*, 2026; Parlin *et al.*, 2026). These biolloggers also provide continuous, fine-scale measures of bioimpedance (i.e. ability of biological tissues to impede electric current), deemed to relate to fat content in the body (Khalil *et al.*, 2014). However, whether a continuous, condition-focused bioimpedance signal can be used to monitor within-individual fat-reserve dynamics and link those dynamics to environmental conditions, movement and management outcomes in wildlife remains unresolved.

Recent deployments of subcutaneous biologgers in free-ranging mule deer show that this platform can provide high-resolution physiological data capable of revealing energy landscapes and acute responses to anthropogenic stressors when paired with Global Positioning System (GPS) movement data (Laforge *et al.*, 2026; Parlin *et al.*, 2026). These applications have focused on heart rate, demonstrating the ecological value of continuous physiological monitoring in ungulates. However, the same biologgers also record bioimpedance, a localized electrical signal influenced by tissue composition and fluid balance near the implant. Here we aim to assess whether the bioimpedance stream can be interpreted as a condition-relevant signal in large mammals. We use a controlled captive elk (*Cervus canadensis*) system to quantify (i) correspondence between bioimpedance and maximum rump fat thickness, (ii) the lag structure linking experimentally manipulated caloric intake to daily impedance dynamics and (iii) behavioural correlates of 4-h impedance variability using camera-derived feeding and drinking time budgets. Rump fat thickness provides a field-standard, management-relevant benchmark for subcutaneous fat reserves, but bioimpedance does not measure rump fat or whole-animal fat directly. Instead, the bilogger records a localized electrical signal influenced by tissue composition and fluid balance near the implant, allowing us to test whether a safe and practical implant location tracks within-individual changes in condition through time. Together, these analyses provide empirical expectations for how bioimpedance integrates nutritional and hydration processes across hours to weeks, and establish a foundation for interpreting fine-scale fat-reserve dynamics in future free-ranging animal studies.

Materials and Methods

Captive elk and facilities

Four adult female elk were housed at the Colorado Parks and Wildlife (CPW) Foothills Wildlife Research Facility (FWRf), Fort Collins, CO, USA, in individual outdoor pens (~200 m²) with *ad libitum* access to fresh water and mineral supplements. Each elk had its own feeding station and automatic waterer. This housing arrangement allowed feed provided and feed remaining to be assigned to a known individual and allowed camera-derived feeding and drinking observations to be summarized at the individual level. The use of four elk reflected the intensive nature of the study, which required surgical implantation, repeated handling and controlled diet manipulation under veterinary oversight. All animals were captive born and ranged in age from 2 years (Elk 1–3) to 9 years (Elk 4) at study onset. The elk were visually monitored at least daily and could be held temporarily in smaller interconnected paddocks to facilitate handling. Of the four elk included in this study, one was highly habituated to humans, while the remaining three were not habituated to close human contact and displayed avoidance behaviour during routine handling and husbandry. Prior to the start of the experiment and dietary restriction, maximum rump fat thickness differed markedly among individuals. Pre-restriction maximum rump fat thickness measurements, collected on 5 December 2023, were 12, 6 and 11 mm for Elk 1–3. In contrast, Elk 4, the habituated individual, was 49 mm. We focused on rump fat thickness because it is a widely used, management-relevant condition metric and provides a direct, single-site measurement of subcutaneous

fat thickness. Composite indices such as ingesta-free body fat integrate multiple measurements and model assumptions; while valuable for some applications, they were not required for our objective of validating whether implanted bioimpedance tracks changes in a standard fat-thickness metric.

Implantable biologgers and bioimpedance sampling

We used Reveal LINQ Generation 3 implantable biologgers (Medtronic), a device platform previously adapted for wildlife studies in large mammals, including bears (Laske *et al.*, 2018) and recent free-ranging mule deer deployments that used subcutaneous biologgers to quantify heart-rate responses to movement, landscape conditions and road crossings (Laforge *et al.*, 2026; Parlin *et al.*, 2026). These ungulate applications demonstrate the ecological value of continuous physiological monitoring with this bilogger platform, but they focused on heart rate rather than bioimpedance. The device is miniaturized for human medical use (1.2 cc; 4.0 mm × 7.2 mm × 44.8 mm; 2.4 g), and the wildlife software configuration records subcutaneous temperature and bioimpedance every 4 h in addition to heart rate and activity/posture metrics. Bioimpedance is a localized measurement from the implanted device and is interpreted as reflecting electrical properties of tissue near the implant rather than whole-animal impedance. Before implantation, devices were cold-sterilized and assigned to individual elk; no animal-specific calibration of bioimpedance was applied before deployment. The present study was designed to test whether this localized 4-h bioimpedance stream could resolve within-individual body condition dynamics at temporal scales rarely available from conventional capture-based assessments.

Elk handling, bilogger implantation and data retrieval

We collected handling-based measurements, including body mass and rump fat thickness, approximately monthly because repeated capture and sedation had to be balanced against animal welfare, veterinary availability and the need to monitor condition during gradual diet manipulation. Handling intervals averaged 33.3 days, with most intervals falling between 27 and 39 days and one longer interval of 47 days. During each handling event, handlers moved elk through alleyways to a restraint chute equipped with a scale for weighing. A veterinarian tailored sedation to the individual, delivered either by hand injection in the chute or by remote dart (Pneudart, Williamsport, PA, USA; 2 cc powder-charged dart from a CO₂-powered projector) in the pen.

Sedation protocols used 1.5–2.0 cc BAM (27.3 mg/ml butorphanol, 0.1 mg/ml azaperone and 10.9 mg/ml medetomidine) or NaMedA (40 mg/ml nalbuphine, 10 mg/ml medetomidine and 10 mg/ml azaperone), with or without 40–100 mg ketamine, all from Wedgewood Pharmacy, Swedesboro, NJ, USA. We antagonized sedation with 75–100 mg atipamezole IM, with or without 25 mg naltrexone IM. Throughout sedation, animals received supplemental intranasal oxygen at 2–3 l/min, and we monitored body temperature, heart rate and respiratory rate.

The left axillary region of the thorax was selected because it is an appropriate subcutaneous location for detecting cardiac activity

signals with this biollogger platform, which is one of the primary uses of the device, while also providing a safe, practical, low-profile implant site that minimized interference with movement and allowed stable placement. We did not expect bioimpedance measured at this location to directly measure rump fat thickness. Instead, we used the controlled feeding experiment to test whether this localized physiological signal, collected from a placement optimized for the broader biollogger platform, tracked within-individual changes in a management-standard fat-thickness metric through time.

Before implantation, we cold-sterilized biolloggers in EtOH. We clipped and cleaned a ~10-cm area over the left axillary region of the thorax (lateral chest just behind the elbow) with chlorhexidine scrub and 70% isopropyl alcohol (MWI, Boise, ID, USA), administered 1 ml lidocaine intradermally for local analgesia and made a 1–2 cm incision to allow subcutaneous insertion of the biollogger using a sterile applicator. We closed incisions with 1–2 simple interrupted sutures using 2–0 absorbable monofilament. Flunixin meglumine (Merck Animal Health, Madison, NJ, USA) was administered intravenously at 1.1 mg/kg following implant and removal of biolloggers, and as needed during study-related handling events under veterinary direction.

All implantation and removal procedures occurred under direct veterinary supervision, and all animal handling was approved by IACUC (US Forest Service #2023–015; CPW #07–2023). During handling events, we downloaded biollogger data non-invasively using transcutaneous telemetry to a CareLink Model 2090 programmer (Medtronic), and exported data were analysed in R (R Core Team, 2024). Implants were removed during the final handling event of the study. In free-ranging applications using this device configuration, biollogger data would be retrieved during recapture, device recovery or mortality recovery, allowing retrospective reconstruction of continuous physiological and condition trajectories between handling events.

Nutritional manipulation and estimating caloric intake

Elk underwent a series of diet manipulations designed to induce gradual body condition loss and subsequent gain (while maintaining *ad libitum* water and mineral supplements) to mimic reduced winter forage and subsequent spring green-up. Long-term dietary reductions began on 11 December 2023 and consisted of eliminating pelleted ration (Deer and Elk Ration, Hubbard Feeds, Fort Collins, CO) while providing *ad libitum* high-quality grass hay, with an additional contingency to reduce hay availability up to ~33% if needed to achieve weight loss. Dietary restrictions were scheduled to occur over a 4-to-5-month phase; however, if weight loss exceeded 18% of the initial body weight or if maximum rump fat measurements fell below 1 mm, both predefined welfare thresholds established under veterinary oversight, we ceased dietary restrictions and began dietary increases. Dietary increases for weight gain involved reintroducing and increasing the pelleted ration up to ~2× normal pre-restriction levels while maintaining *ad libitum* grass hay. Periodic complete blood counts and serum chemistries were performed to monitor the health of the elk during the study. Maximum rump fat thickness fell below 1 mm for three elk and increased feeding began on 25 March 2024 for Elk 1 and 3 and 18 April 2024 for Elk 2. The remaining elk, Elk 4, did

not reach an intervention point and restrictions continued for the planned restriction phase with increases occurring on 22 April 2024. Short-term perturbations in forage access were also incorporated (e.g. varying daily feed amounts while holding total 1–2-week intake stable; brief multi-day restrictions and occasional ≤ 48-h fasting events; see [Supplemental Table S1](#) for weekly estimated caloric intake). Caloric intake (used in analyses in the Calories section, see below) was estimated from the measured daily pelleted feed and hay consumed. The measured weight of pelleted feed provided was logged each day and the elk consistently consumed all provided pelleted feed. Facility staff logged the number of hay flakes provided and the estimated number of flakes consumed each day. The weight of a flake of hay was estimated by weighing three different flakes of hay pulled from different bales by three different staff members and calculating the average. Estimated amounts consumed were converted to total net energy on a dry matter basis in megacalories calculated based on laboratory analysis of pellets and hay (Midwest Laboratories, Omaha, NE) and then summarized to a daily time series aligned with daily mean bioimpedance ([Supplemental Table S1](#)). Analyses used one estimated caloric-intake value per elk per day, aligned with that elk's daily mean bioimpedance calculated from the six 4-h measurements; [Supplemental Table S1](#) reports weekly averages only as a readable summary of the daily feeding record. Natural vegetation became available within enclosures during spring green-up, likely causing total caloric intake to be underestimated during that period.

Camera-trap monitoring of feeding and drinking time budgets

To support the finest temporal scale analysis of intradaily bioimpedance variation (Drinking and eating section), we deployed passive infrared Reconyx PC 800 digital cameras (Reconyx, Holmen, WI) at each elk's feeding station and at their automatic waterer during a period of the study from 22 March 2024 to 19 May 2024. We extracted the timestamp information from camera trap photos using the *exifr* v0.3.2 R package ([Dunnington and Harvey, 2021](#)) for all images where elk were drinking or feeding. Images were used to quantify time budgets for feeding and drinking by calculating the proportion of time spent eating or drinking within fixed windows corresponding to the 4-h bioimpedance sampling interval, and over rolling windows used in the fine-scale models (e.g. 12, 24 and 72 h).

Body condition

To assess whether implanted bioimpedance tracked changes in body condition measured using standard rump fat thickness assessments, we compared maximum rump fat thickness collected according to [Stephenson et al. \(1998\)](#) at handling events using an Ibex Pro portable ultrasound unit with a 5–9 MHz linear transducer (E.I. Medical Imaging, Loveland, CO) with contemporaneous bioimpedance values for each elk. The maximum thickness of the subcutaneous fat layer was recorded in millimetres. Because impedance can show short-term variability, we summarized impedance at each handling event as the mean value across a 7-day window spanning 3 days before through 3 days after the handling date (inclusive). This 7-day summary was used only for comparison with ultrasound-measured rump fat, whereas 4-h observations were analysed separately to evaluate

short-term impedance variability associated with feeding and drinking behaviour. To focus on within-individual trajectories rather than absolute differences among animals, maximum rump fat thickness and impedance were each scaled within individual and within variable (e.g. rump fat and impedance scaled separately for each elk). We then quantified the association using Spearman rank correlations computed separately for (i) the dietary restriction phase and (ii) the post-restriction weight-gain phase, where the latter was defined using elk-specific diet transition dates (when individuals were moved to increased caloric intake after reaching the predefined lower condition threshold). Scaled values were used for Spearman rank correlations, which were chosen to evaluate monotonic within-individual tracking with few handling events rather than to estimate a linear calibration. For descriptive comparison, we also calculated (iii) correlations across the full experimental phase. Phase-specific correlations were not estimated when the number of handling events within a phase was insufficient (i.e. <3). All analyses for the Body condition, Calories and Drinking and eating sections were conducted in program R (R Core Team, 2024).

As a complementary analysis, we evaluated whether unscaled bioimpedance was associated with absolute maximum rump fat thickness while accounting for repeated measurements and among-individual baseline differences. We fit a linear mixed model with raw maximum rump fat thickness (mm) as the response, contemporaneous 7-day mean raw bioimpedance as the fixed effect, and an elk-specific random intercept. We also fit an individual-centred linear model in which raw bioimpedance and rump fat thickness were each centred within elk before model fitting. This centred model evaluated whether within-individual deviations in bioimpedance corresponded to within-individual deviations in rump fat thickness without relying on scaled variables.

Calories

To quantify how daily energetic intake related to day-to-day bioimpedance dynamics, we analysed each elk's daily time series of estimated caloric intake and daily mean bioimpedance, with both variables scaled within individual. We first fit generalized additive models (GAMs), with a $k = 20$ used as the maximum basis dimension, separately to impedance and calories as smooth functions of time (cubic regression spline; common basis dimension across individuals) using the package 'mgcv' (Wood, 2011). The resulting fitted values were used to represent the broad temporal trends. We then computed first differences of the fitted series ($\Delta\text{impedance}$ and $\Delta\text{calories}$) to focus on directional change ('up vs down') rather than shared seasonal smoothness (Shumway and Stoffer, 2017). Lagged coupling was evaluated by correlating $\Delta\text{impedance}(t)$ with $\Delta\text{calories}(t - \text{lag})$ across candidate lags (0–60 days, 5-day increments), following established approaches for assessing time-lagged associations in ecological time series (Probst *et al.*, 2012). We summarized each elk by the lag with the maximum positive correlation within the tested window. To examine whether coupling differed between feeding regimes, we repeated the lagged-correlation analysis separately within the restriction and weight-gain phases. We limited the maximum lag tested in each phase to approximately half the phase duration to ensure adequate overlap between series at all lags considered. We also

quantified phase consistency as the proportion of tested lags yielding positive correlations and summarized this metric across elk. Finally, we qualitatively compared peak lag times to baseline maximum rump fat thickness to assess whether response timescales were state dependent.

Drinking and eating

To examine potential drivers of intradaily variability in bioimpedance beyond the longer-timescale trends described above, we paired 4-h bioimpedance measurements with behavioural observations from camera traps deployed at each elk's feeding station and water source. For each 4-h interval between successive bioimpedance observations, we quantified the proportion of time each elk spent feeding and drinking. We then fit elk-specific linear models (one model per individual) predicting bioimpedance at time t as a function of (i) lag-1 bioimpedance to account for short-term dependence, (ii) time of day to account for potential temporal structure and (iii) feeding and drinking activity summarized over candidate temporal windows. Feeding and drinking proportions were transformed to the logit scale (after adding a small constant to avoid 0 values; $+0.0001$), and hour was modelled using a natural spline. The 4-h interval was determined by the biollogger sampling schedule. We did not expect measurable fat-reserve changes over a single 4-h period; instead, the 4-h data allowed us to quantify short-term impedance variability and evaluate whether recent feeding or drinking behaviour contributed to that variation around longer-term condition trajectories. To evaluate the timescale over which behaviour best explained impedance dynamics, we calculated rolling summaries of feeding and drinking over four windows: the 'matching' 4-h interval, and prior averages over 12 h (three 4-h intervals), 24 h (six intervals), and 72 h (18 intervals). For each window, we considered models with feeding and drinking entered as linear terms on the logit scale and as non-linear terms using natural splines ($df = 2$) where the data allowed, while keeping hour as a natural spline ($df = 4$) and including lagged impedance in all candidate models. We compared candidate models within each elk using Akaike's Information Criterion, including reduced models containing only feeding or only drinking and a base model excluding the eating and drinking covariates. Inference focused on the best-supported model(s) per elk and on consistent patterns across individuals in the temporal window and predictors retained.

Results

Bioimpedance relationship with body condition

Weekly average bioimpedance (± 3 days of handling date) showed strong within-individual correlation with monthly maximum rump fat thickness during both the dietary restriction phase and the subsequent return to a normal diet (Fig. 1). Spearman correlations between maximum rump fat thickness and bioimpedance during restriction were consistently high across elk ($\rho = 0.75$ – 0.96 ; mean = 0.90) and were similarly high during the post-diet phase for the three elk with sufficient observations ($\rho = 0.96$ – 0.98 ; mean = 0.97 ; Table 1). In contrast, correlations calculated across the entire experiment were lower and more variable among individuals ($\rho = 0.52$ – 0.88 ; mean = 0.71), consistent with a phase-dependent

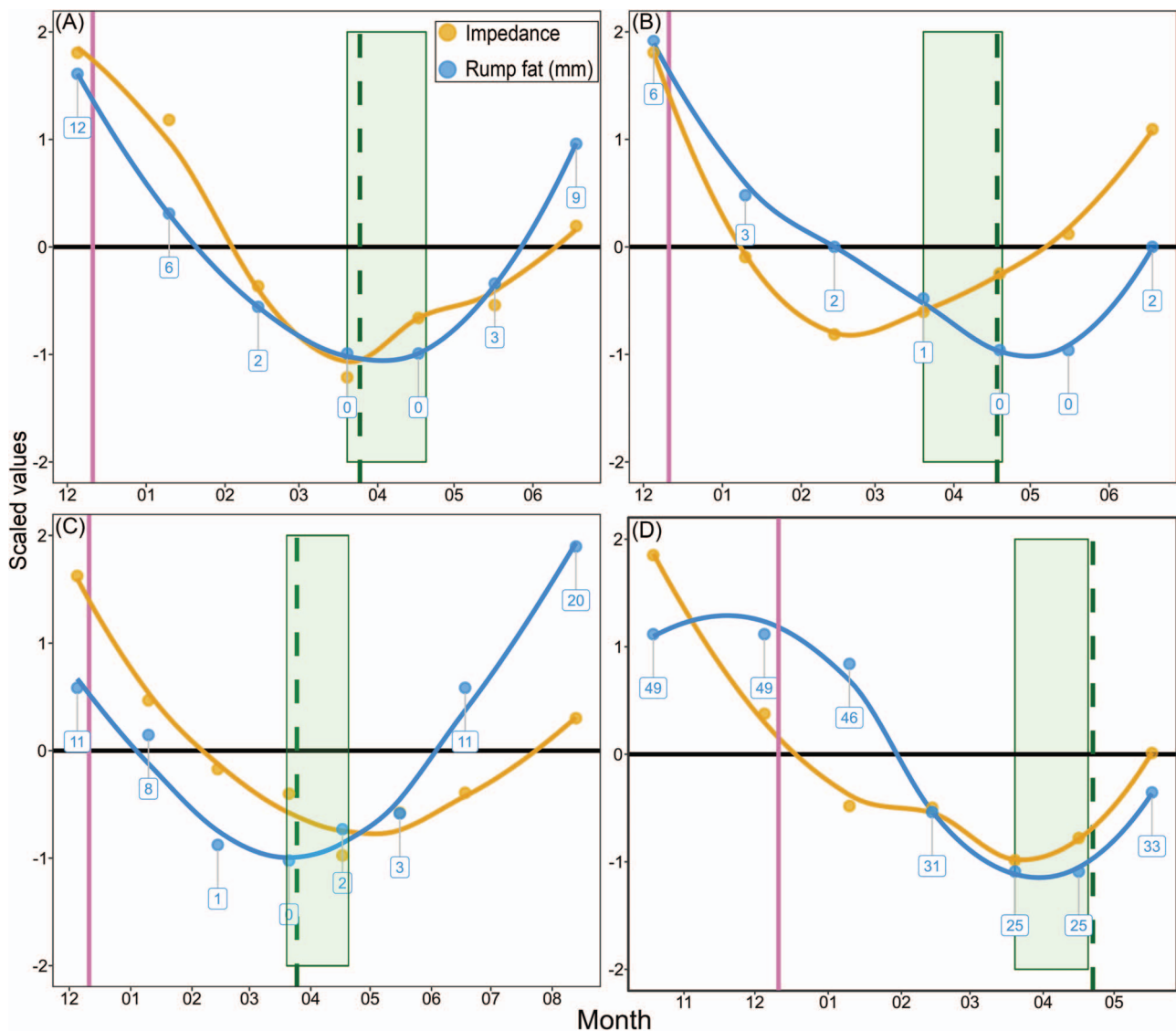


Figure 1: Weekly average bioimpedance (± 3 days of handling date) and measured maximum rump fat thickness (taken approximately monthly) for four captive elk (*C. canadensis*) housed at the CPW FWRF (2023–24). Panels A–D represent individual Elk 1–4 respectively. Bioimpedance and maximum rump fat thickness values were scaled for visualization purposes and were lines created using a loess fit. Actual maximum rump fat thickness measurements (mm) are listed in blue by each point. The vertical solid pink line demarcates the start of the dietary restriction phase while the vertical dashed green line is associated with the refeeding phase of the diet. The resumption of a normal diet was based on an individual's predefined condition threshold. Light green polygons represent the approximate time period when natural green vegetation became available within each enclosure, reducing the accuracy of caloric intake estimates.

relationship and limited handling-time sample sizes when pooling across both restriction and recovery. Post-diet correlations were not calculated for Elk 4 due to insufficient post-diet handling events (intervention point was never reached; increased caloric availability started far later than the other elk; $n = 1$).

Complementary analyses clarified how bioimpedance should be interpreted. When elk-specific baselines were accounted for with a random intercept, raw bioimpedance was positively associated with

rump fat thickness ($\beta = 0.0263 \pm 0.0079$ SE, $P = 0.0029$; marginal $R^2 = 0.062$, conditional $R^2 = 0.930$). An individual-centred model further showed that within-elk deviations in bioimpedance corresponded to within-elk deviations in rump fat thickness ($\beta = 0.0277 \pm 0.0075$ SE, $P = 0.0010$, $R^2 = 0.335$). Together, these results indicate that bioimpedance is most informative as a within-individual indicator of condition dynamics through time, enabling inference about the timing, rate and extrema of condition change rather than providing a universal conversion to absolute fat thickness across animals.

Table 1: Spearman correlations of weekly average bioimpedance (± 3 days of handling date) and measured maximum rump fat thickness (taken approximately monthly) for four captive elk (*C. canadensis*) housed at the CPW FWRF (December 2023–August 2024) during the dietary restriction phase of the experiment, during the increased feeding/weight gain phase, and for the entire duration of the experiment

	Elk 1	Elk 2	Elk 3	Elk 4	Average
Dietary restriction	0.95	0.96	0.95	0.75	0.90
Normal (added/refeeding) diet	0.98	0.96	0.96	—	0.97
Entire experiment	0.88	0.68	0.52	0.74	0.71

Bioimpedance relationship with caloric intake

Across individuals, daily bioimpedance trajectories showed clear correlations with estimated daily caloric intake, but the timing of coupling varied among elk (Fig. 2). Lagged correlations between changes in calories and changes in impedance (r_{diff}) were positive for all four elk within the tested 0–60-day window (Supplemental Table S2). Peak coupling occurred at ~ 25 days for Elk 2 (peak $r_{\text{diff}} = 0.781$), ~ 50 days for Elk 3 (0.598) and 0 days for Elk 4 (0.467), while Elk 1 increased through the maximum tested lag with its largest r_{diff} at 60 days (0.395), indicating no uniquely identified peak within the tested window for Elk 1 (Supplemental Table S3). With $n = 4$, we did not test predictors of peak lag statistically. However, Elk 4, the fattest individual at the onset of restriction, exhibited the minimum lag (0 days). Because the feeding protocol imposed comparable phases of restriction and increased intake across animals, differences in the estimated response lags are unlikely to be driven solely by differences in the diet schedule. Instead, they suggest individual variation in the timescale at which internal condition tracked caloric consumption. When the time series was partitioned into restriction and weight-gain phases, restriction phases showed more uniformly positive lagged associations than gain phases. Across elk, a median of 92.3% of tested lags yielded positive r_{diff} values during restriction (range across individuals: 54–100%), compared with 69.2% during the gain phase (range: 15–100%). This indicates stronger and more consistent coupling during caloric restriction, with more individual- and lag-dependent relationships during the gain phase. Together, these results demonstrate that bioimpedance captures energetically driven condition dynamics at daily resolution, but with individual-specific lags that can span weeks.

Bioimpedance relationship with eating and drinking

Intradaily bioimpedance variability at the 4-h sampling interval was most consistently explained by multi-day (72 h) behavioural summaries for eating and drinking (18×4 -h intervals) relative to shorter windows considered (Supplemental Table S4). Support for behavioural covariates varied among individuals. Elk 1 showed no improvement from including feeding or drinking at any window; the best-supported model retained only hour-of-day and lag-1 impedance and had low explanatory power (adj. $R^2 = 0.004$). Elk 2 maintained non-linear associations with both drinking and feeding over the prior 72 h (spline terms $P \leq 0.015$ and $P = 0.002$,

respectively) and showed evidence of diurnal structure (hour term components $P \leq 0.021$), whereas lag-1 impedance was only marginal ($P = 0.062$; adj. $R^2 = 0.085$). Elk 3 retained positive linear effects of both feeding ($\beta = 80.0 \pm 33.6$ SE, $P = 0.018$) and drinking ($\beta = 35.9 \pm 18.1$, $P = 0.048$) over the prior 72 h along with supported lag-1 impedance ($\beta = 0.249 \pm 0.054$, $P < 0.001$); a competing feeding-only model performed nearly as well ($\Delta\text{AIC} < 1$), indicating limited additional support for drinking beyond feeding (adj. $R^2 = 0.133$). Elk 4 showed strong lag-1 dependence ($\beta = 0.483 \pm 0.049$, $P < 0.001$) and retained drinking time over the prior 72 h as a positive predictor of impedance ($\beta = 37.8 \pm 11.1$, $P = 0.0008$), whereas feeding time was not supported (adj. $R^2 = 0.317$). Full coefficient summaries and model-fit diagnostics for the best-supported model per elk are reported in Supplemental Tables S5 (fixed effects including hour-of-day) and S6 (residual SE, R^2 and adjusted R^2). Overall, these fine-scale analyses indicate that a portion of intradaily impedance variability is associated with recent feeding/drinking behaviour in some individuals, and is most consistent when behaviour is integrated over multi-day windows. However, substantial 4-h variance remains unexplained relative to the stronger longer-timescale coupling with body condition and caloric intake.

Discussion

Resolving physiological condition at fine temporal scales reveals processes shaping animal fitness that remain hidden in conventional sparse measurements. In this controlled feeding experiment, implanted bioimpedance tracked within-individual changes in rump fat across an ~ 6 -month phase of dietary restriction and subsequent refeeding designed to mimic seasonal nutritional paucity and abundance. Weekly bioimpedance showed strong within-individual correlation with maximum rump fat thickness, daily bioimpedance covaried with caloric intake and a portion of intradaily variation was associated with recent feeding and drinking behaviour when those behaviours were integrated across multiple days. Together, these results indicate that implanted biologgers capture a biologically meaningful signal of changing energetic state across hours to weeks in electrical bioimpedance. The primary advance is therefore not simply continuous measurement, but the ability to identify when condition is declining, stabilizing or recovering at temporal scales that are largely inaccessible using conventional capture-based assessments.

A second key insight is that fat reserve loss may proceed more directly than reserve rebuilding. In our experiment, coupling between caloric intake and bioimpedance was more consistent

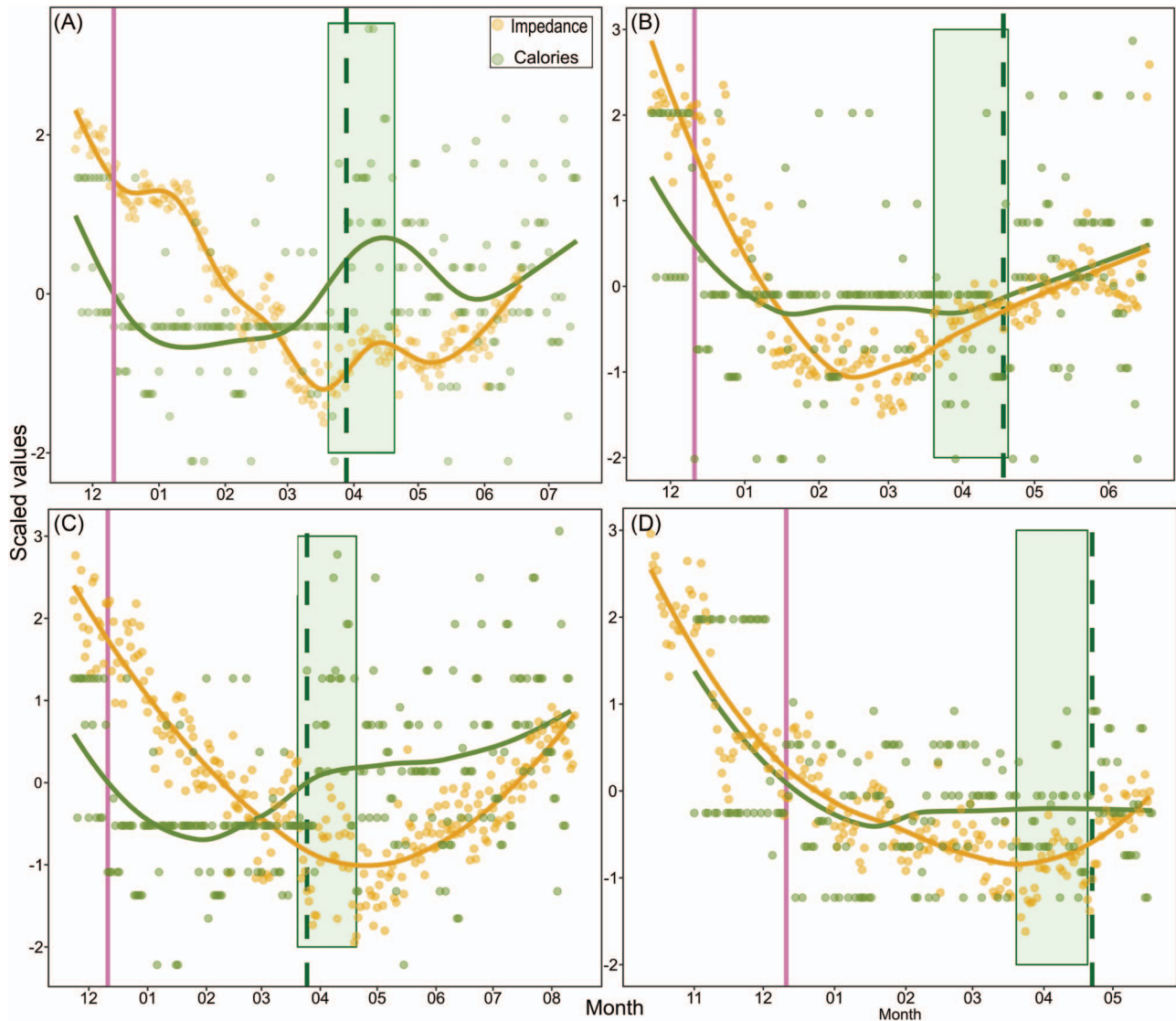


Figure 2: Daily average bioimpedance (six measures per day) and caloric intake for four captive elk housed at the CPW FWRP. Panels A–D represent individual Elk 1–4 respectively. Bioimpedance and caloric intake values were scaled for visualization purposes and lines were created using a GAM fit. The vertical solid pink line demarcates the start of the dietary restriction phase while the vertical dashed green line is associated with the refeeding phase of the diet. The resumption of a normal diet was based on an individual's predefined condition threshold. Light green polygons represent the approximate time period when natural green vegetation became available within each enclosure, reducing the accuracy of caloric intake estimates.

during restriction than during the gain phase, and fat-impedance correspondence was strongest within phases but weaker when pooled across the full experiment. Together, these patterns suggest that recovery from winter nutritional decline may lag behind improving forage conditions. Delayed recovery after restriction may reflect physiological prioritization at low-reserve states, where essential tissue repair and functional capacity are restored before fat accretion accelerates (Torbit *et al.*, 1985; Chilliard *et al.*, 1998). This distinction has important ecological implications because fat expenditure in ungulates can be non-linear over winter (Ortega *et al.*, 2023), while spring phenology can strongly influence fat gain in elk (Middleton

et al., 2018) and the timing and rate of vegetation green-up can affect growth and survival in mountain ungulates more broadly (Pettorelli *et al.*, 2007). Together, these patterns suggest that late winter and early spring are likely to be a critical bottleneck: individuals that reach their seasonal energetic minimum shortly before green-up may remain physiologically vulnerable if recovery is delayed, especially when spring phenology is late or disrupted. Continuous bioimpedance may therefore be especially valuable for identifying not only when fat reserves decline, but also whether recovery occurs quickly enough to avoid prolonged nutritional stress and downstream carryover effects.

We also observed substantial individual variation in the timing of coupling between caloric intake and bioimpedance, ranging from near-synchronous alignment in one elk to peak correlations that occurred weeks later in others. We view this heterogeneity as potentially informative rather than simply as noise. One plausible explanation is state dependence in fat-reserve dynamics. Consistent with this idea, the individual that entered restriction with substantially greater fat reserves (Elk 4; mean pre-restriction maximum rump fat thickness 49 mm vs 6–12 mm in Elk 1–3) also exhibited the minimum lag in the calorie–bioimpedance coupling (peak lag = 0 days), whereas the leaner individuals showed multi-week lags. The early divergence in Elk 4, where rump fat thickness increased slightly while bioimpedance declined, may reflect this same state dependence. Because bioimpedance is influenced by local tissue and fluid properties, this pattern could arise if changes in fat composition, hydration or reserve mobilization occurred before they were reflected in a single thickness measurement. Although our sample size precludes formal inference, this pattern motivates the hypothesis that response timescales may vary predictably with initial condition. In ruminants, adipose tissue responses to undernutrition can be amplified in fatter animals, suggesting that individuals beginning restriction with greater reserves may exhibit stronger or more readily detectable mobilization signals (Chilliard *et al.*, 2000). More generally, dynamic energy-balance models indicate that initial adiposity can influence both the magnitude and timescale of tissue change under a given energy deficit (Hall *et al.*, 2011). This broader framework is consistent with the possibility that comparable nutrition need not produce identical impedance trajectories across ungulates. Differences in recent intake, gut fill, hydration or the relative contribution of slower tissue remodelling vs shorter-term physiological shifts could also contribute to the heterogeneity we observed (Dixon *et al.*, 2006; Khalil *et al.*, 2014; Androutsos *et al.*, 2015; Charles *et al.*, 2015; Schierbauer *et al.*, 2023). Importantly, this individual variation suggests that continuous impedance measures may help reveal meaningful differences among individuals in how fat reserve dynamics unfold through time.

The mechanistic basis of the implanted biollogger signal also merits careful interpretation. Our data do not support treating bioimpedance as a direct measurement of rump fat per se. Instead, the device captures a localized physiological signal whose electrical properties covary with body composition and hydration in ways that remain tightly linked to broader fat reserve dynamics. Similarly, maximum rump fat thickness should be interpreted here as a management-standard index of subcutaneous fat reserves rather than a direct estimate of total body fat, particularly when animals approach very low reserve states. This distinction reinforces our focus on within-individual condition trajectories and timing of change rather than absolute estimates of whole-body fat. In our fine-scale analysis, drinking behaviour provided only an indirect index of hydration and explained a limited portion of 4-h impedance variation, while periodic clinical measures collected during handling were too sparse to evaluate hydration effects directly. Thus, hydration likely contributes to short-term variability in the signal, but it does not appear to explain away the stronger association between bioimpedance and longer-term fat reserve dynamics. That interpretation is consistent with general bioimpedance theory and with work on implanted thoracic impedance showing that measured impedance can primarily reflect

tissue and water in proximity to the electrodes rather than a single deep anatomical compartment (Khalil *et al.*, 2014; Charles *et al.*, 2015). In our system, the strongest ecological relevance may therefore arise not because the device isolates one tissue compartment, but because the localized signal responds in a repeatable way to the suite of physiological changes that accompany body condition decline and recovery. The present study establishes the biological interpretation that the signal tracks meaningful condition dynamics. However, a mechanistic determination of the exact tissue and fluid components contributing to that signal remains an important next step for future calibration work.

The primary value of this captive validation is that it anchors interpretation of implanted bioimpedance in a system where energetic inputs and body condition trajectories were known. That foundation is critical because the broader promise of this approach lies in free-ranging systems, where body condition is otherwise difficult to resolve at fine temporal resolution. In wild elk and other ungulates, continuous bioimpedance could reveal when individuals first enter negative energy balance, how rapidly reserves erode during severe winter conditions or drought, whether recovery begins immediately after forage green-up or only after a lag and how those trajectories differ among migratory tactics, reproductive states, predation pressure, disease status or habitat conditions. This opportunity is important because recent work in migratory mule deer showed that access to superior forage translated into greater fat gain, higher survival and more robust population growth, whereas deer remaining in resource-limited desert habitat showed poorer average body condition and demographic performance (Ortega *et al.*, 2026). Continuous bioimpedance could help resolve the physiological timing underlying such patterns by identifying when the benefits of migration, green-wave surfing or favourable habitat conditions are expressed as fat reserve recovery, and when late-winter bottlenecks or spring delays prolong nutritional vulnerability. When paired with GPS locations, activity, heart rate and environmental covariates, bioimpedance could therefore help identify the places and times where animals incur or offset physiological costs that remain hidden if movement is the only response variable (e.g. Laforge *et al.*, 2026; Parlin *et al.*, 2026). Our results suggest that this application is strongest when bioimpedance is used to quantify within-individual trajectories rather than as an uncalibrated conversion to absolute fat reserves Harlow *et al.* (1996), Hundertmark and Schwartz (2002). This trajectory-based interpretation is central to the value of high-frequency biollogging because it allows investigators to identify the timing, rate and extrema of condition change and align those changes with environmental conditions, movement decisions and exposure to risk. More broadly, inference may differ among taxa in both feeding regime and reserve-use strategy. Where intake is continuous, as in grazers and browsers, the finest-scale coupling between food acquisition and bioimpedance may be muted relative to longer integration windows, whereas species consuming large, infrequent meals (e.g. carnivores) may show sharper event-scale responses. Similarly, species towards the capital end of the capital-income continuum (Jönsson, 1997; Stephens *et al.*, 2009), which rely on stored reserves accumulated in advance of high-demand periods, should show bioimpedance dynamics tracking seasonal reserve trajectories, while species toward the income end, which track contemporaneous intake more closely, may show dynamics dominated by short-term variation rather than reserve state.

Overall, our results support implanted bioimpedance as a new window into the temporal dynamics of nutritional ecology in large mammals. Rather than replacing established condition metrics, bioimpedance complements them by filling the long-standing gap between sparse handling-based measurements and the continuous physiological changes that unfold within and across seasons. The broader significance is that body condition can now be studied as a process rather than only as a before-and-after state. That shift should improve our ability to link body condition dynamics with movement, habitat use, weather and disturbance, and ultimately better understand how free-ranging animals physiologically experience changing environments.

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Author Contributions

M.A.D., G.W. and M.E.W. conceived of the research design. Animal husbandry, handling and elk measurement data collection were led by M.E.W., P.N. and M.L.L. M.A.D., M.P.L., A.F.P. and G.W. collected and processed the biollogger data. M.A.D. analysed the data with input from G.W., M.P.L. and A.F.P. T.G.L. provided expertise in device deployment and data interpretation. M.A.D. developed the first draft of the manuscript and all co-authors contributed to the editing of additional drafts.

Conflicts of Interest

The authors have no conflicts to disclose.

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Data Availability

Data associated with the analyses can be found at <https://doi.org/10.5281/zenodo.21828302>.

Supplementary Materials

Supplementary material is available at *Conservation Physiology* online.

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