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Biologging in a free-ranging mammal reveals apparent energetic trade-offs among physiological and behavioural components of the acute-phase response

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The acute-phase response (APR) is an adaptive emergency life-history stage, wherein vertebrates exhibit fever and anorexia to survive an infection. However, induced immune responses are energetically costly, and sick animals may reduce physical activity to compensate. Tests of this predicted energetic trade-off in free-ranging animals are rare due to difficulties in measuring individual physiology and behaviour under immune challenge in natural settings. However, recent advances in biologging technology now make such studies possible. We surgically implanted heart rate/temperature loggers in free-ranging adult male Arctic ground squirrels, fitted the squirrels with collar-mounted accelerometers and light/temperature loggers, and injected animals with lipopolysaccharide (LPS) to simulate an immune challenge. LPS-injected squirrels exhibited approximately 1°C overnight fevers accompanied by slightly elevated (10 bpm) heart rates; LPS-injected squirrels also spent 19% less of their time aboveground the following day and reduced overall movement by 40% compared with saline-injected controls. Thus, we found support for an energetic trade-off between functional immune responses (fever and anorexia) and lethargic sickness behaviour within the APR of a free-ranging mammal. Moreover, our results suggest animal-borne devices can play an important role in future studies of vertebrate immunity and disease dynamics.

1. Introduction

Disease and parasitism are strong agents of selection that shape the evolution of physiological and behavioural immune responses in animals. The acute-phase response (APR), for instance, constitutes an adaptive emergency life-history stage that is evolutionarily conserved across vertebrate lineages [1–4]. This non-specific response to infection often includes elevated body temperature (fever) and increased production of certain proteins to inhibit pathogenic propagation [5]. However, these physiological alterations are energetically costly [6–8]. Moreover, the APR frequently involves reduced food intake (anorexia) to deprive pathogens of nutrients required for reproduction [1,9,10]. To compensate for reduced energetic intake and/or increased energetic expenditure, animals undergoing an APR may exhibit lethargy [1,10]. Hence, the APR apparently sacrifices short-term growth and reproductive opportunities to maximize the odds of surviving an infection and so conserve future reproductive opportunities [11–14].

The APR is well documented in domesticated animals and laboratory settings—especially in birds and mammals [15–18]—but relatively few studies have considered fever and sickness behaviour in free-ranging animals [19–

27]. This represents a substantial gap in our understanding of eco-evolutionary immunology given that captive animals often behave differently than free-ranging animals due to differences in their environmental contexts [19,28]. Captive animals may readily exhibit anorexia and fever under immune challenge given ample energetic reserves, ad libitum food, and no predation risk. Whether free-ranging animals likewise accept the costs of mounting an immune response is less clear. This knowledge gap reflects logistical challenges inherent in measuring individual physiology and behaviour in natural settings, especially under immune challenge. Yet, the apparent role of the APR in mediating life-history trade-offs suggests that additional inquiry into the subject may improve our understanding of the evolutionary mechanisms underpinning vertebrate immunity and life histories. Advances in biologging technology now make such field studies possible [29,30]. Temperature and heart rate loggers measure traits associated with fever and accelerometers and geolocators provide detailed information on animal activity (and hence, potentially sickness behaviour; [31]). A primary objective of our study was to assess the performance of animal-borne temperature, heart rate, light, and acceleration loggers in holistically documenting the APR in a free-ranging mammal.

Arctic ground squirrels (*Urocitellus parryii*) are sufficiently large to carry a variety of animal-borne devices, making the species suitable for evaluating the utility of biologgers for studying the APR in natural settings and for testing hypotheses explaining the functionality of the APR in vertebrates [32]. These squirrels have relatively high short-term recapture rates that facilitate device and data recovery. Moreover, the squirrels' semi-fossorial lifestyle, wherein squirrels emerge from burrows daily to forage, lends itself to tests of behavioural theory via light loggers and accelerometers [33]. If an energetic trade-off underpins the adaptive vertebrate APR, squirrels under immune challenge should simultaneously exhibit (i) elevated heart rates and body temperatures as part of a functional fever response, (ii) reduced timed spent foraging aboveground as a result of functional anorexia, and (iii) reduced overall physical activity to subsidize the energetically costly functional components of the APR. This energetic trade-off hypothesis further predicts a negative correlation between fever and lethargy at the individual level if sickness behaviour compensates for energetic reallocation toward physiological immune responses. We used data from a suite of biologgers to test these predictions in free-ranging Arctic ground squirrels.

2. Methods

(a) Experimental design

We captured 17 adult (≥1 year old) male Arctic ground squirrels in baited live traps (Tomahawk Live Trap, Hazelhurst, WI, USA; 14 × 14 × 40 cm) at a tundra site in north-central Alaska, USA (68°27′ N, 149°21′ W; 812 m.a.s.l.) in May 2019 (electronic supplementary material, table S1) and transported them to Toolik Field Station for processing. We anaesthetized squirrels via a 5-min exposure to vapourized isoflurane (2–5% with oxygen). We marked each squirrel with metal ear tags (National Band & Tag Co., Newport, KY, USA; 1005-1) and a passive integrated transponder (PIT) tag (Avid Identification Systems Inc., Norco, CA, USA; Avid FriendChip) for individual identification. We surgically implanted combination heart rate/temperature loggers (Star-Oddi, Gardabaer, Iceland; DST micro-HRT; mass = 3.3 g) in squirrels to document physiological components of the APR. We sutured loggers to the abdominal wall at the incision site to prevent them from migrating within the abdominal cavity and to facilitate device recovery. Temperature loggers recorded core body temperature every 10 min. Heart rate loggers, comprised of a leadless single-channel electrocardiogram (ECG) with electrodes built into the housing, recorded a burst measurement at 600 Hz ECG for 1 s every 10 min and automatically calculated the mean heart rate for each burst. Loggers graded each burst with a quality index (QI; 0–3, where 0 denotes the highest quality readings). We saved individual ECG bursts every 11 h for validation and compared manually calculated heart rate (derived via PatternFinder v.5.20 software; Star-Oddi, Gardabaer, Iceland) to automated heart rate measurements. We were unable to validate most records with QI > 0 because the ECG burst readings were too noisy to identify heart beats. Manual heart rate estimates for records where QI = 0 matched well with automated measurements (figure 1*a*).

We fitted squirrels with collars (total mass <10 g) equipped with light loggers (Migrate Technology, Cambridge, UK; Intigeo C65), which recorded light intensity at 1-min intervals, and tri-axial accelerometers (Technosmart Europe srl, Rome, Italy; Axy-4), programmed at 10 Hz, to document sickness behaviour. Light loggers also measured and recorded temperature every 5 min, allowing us to assess whether collar-mounted and surgically implanted loggers detect fever similarly. We equipped collars with VHF radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA; A2405) to aid in device recovery. We released squirrels at their site of capture after an overnight recovery period.

We conducted a field-based immune challenge experiment following a within individual paired design in eight of the 17 squirrels initially outfitted with biologgers approximately one month after logger deployment (electronic supplementary material, table S1). We recaptured squirrels twice when possible, approximately one week apart (mean = 6.4 days, range = 4–7 days), and injected squirrels with lipopolysaccharide (LPS; 500 μg kg^{-1} in 0.4 ml sterile saline; Sigma Aldrich, Saint Louis, MO, USA; L2630) or saline in a randomly determined order. LPS is an immunogenic agent derived from the cell wall of Gram-negative bacteria (*E. coli* O111:B4) that is often used to induce immune responses in vertebrates without causing infection [3]; saline injections acted as controls. We injected squirrels shortly after their time of capture (LPS: mean = 13.33, range = 10.30–16.30; saline: mean = 14.52, range = 13.30–18.30). We recaptured squirrels approximately one week (mean = 5.4 days, range = 4–11 days) after the final injection to recover biologgers (explantation followed the same procedure as implantation). We recovered collar-mounted light/temperature loggers and accelerometers from seven adult male Arctic ground squirrels; we recovered heart rate/temperature loggers from five of those seven squirrels (sutures holding loggers failed in two animals and we could not recover the devices).

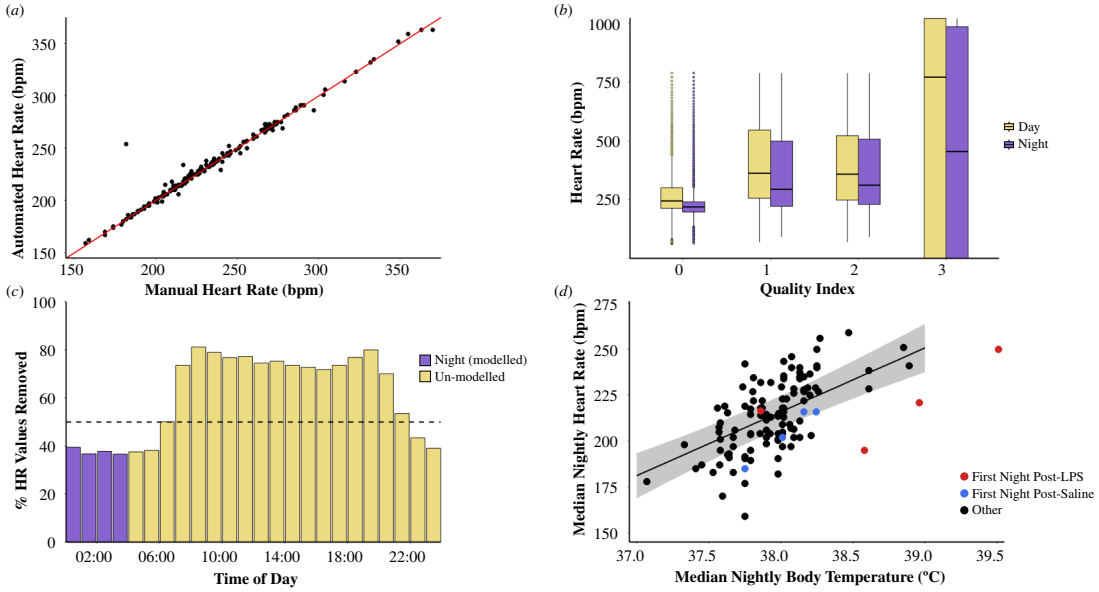

Figure 1. We validated heart rate records derived from free-ranging adult male Arctic ground squirrels via surgically implanted loggers by comparing manual calculations to automatically recorded ECG reads (*a*); we excluded heart rate records with QI > 0 (*b*); we excluded heart rate values outside the range of validated values (89–365 bpm) and modelled only overnight heart rate (*c*); overnight heart rate was positively correlated with overnight body temperature (*d*). The red line in panel (*a*) represents a 1 : 1 relationship; only records for which QI = 0 are shown. The dashed line in panel (*c*) marks 50% of heart rate records excluded. Data from the first night following injections are shown for comparison in panel (*d*) but were excluded from the linear mixed-effects model correlating heart rate and body temperature.

(b) Statistical analyses

We compared pre- and post-injection biologger-derived metrics of behaviour and physiology between LPS-injected and saline-injected adult male Arctic ground squirrels to test for predicted components of the APR. To do so, we built generalized additive mixed-effects models (GAMMs) via the mgcv package [34] in R (v.4.3.2; [35]). We filtered each dataset before conducting statistical analyses. We filtered heart rate records to include only the 14 087 records (35.8% of all records) for which QI = 0 that fell within the range of manually validated values (89–365 bpm; figure 1*b*). We modelled overnight (00.00–04.00) heart rate to ensure we modelled resting heart rates of squirrels, which are diurnal—even during the continuous daylight of Arctic summer (figure 1*c*; [36]). Likewise, we modelled overnight body temperature because activity influences body temperature in Arctic ground squirrels [36]. Using overnight data also allowed for a better comparison between internal and collar-mounted temperature loggers, as sunlight affects the collar-mounted loggers. We excluded 1390 temperature values <36°C (44.8% of all values) recorded by collar-mounted loggers under the assumption that these records captured ambient conditions rather than squirrel body temperature (e.g. the temperature sensor was exposed to cold air or soil; [37]). We excluded heart rate and body temperature data for the first night following the LPS injection for one squirrel because the squirrel left its burrow and was active overnight (determined via the collar-mounted light logger and accelerometer).

We used biologger data from implanted and collar-mounted devices to model squirrel heart rate and body temperature—from two nights before each injection to three nights afterward—as Gaussian distributions. Models of heart rate and body temperature included a p-spline for time of night, a linear term for mean overnight ambient temperature, a two-way interaction between injection type (LPS or saline) and binned time relative to the injection (the two nights prior to the injections binned into a single pre-injection period or one, two, or three nights post-injection), and a random effect for individual ID (electronic supplementary material, tables S2–S4). Models included a continuous autocorrelation structure to account for temporal autocorrelation in the data across single time steps (i.e. the period between consecutive data records). A weather station at the study site provided 15-min resolution temperature and precipitation data for our analyses.

We used light logger and accelerometer data to model squirrel aboveground activity and movement from 07.00 to 21.00 (the daily period when squirrels are most active; [36]) from two days before each injection to three days afterward. We scored light logger records as aboveground or belowground (any light intensity >0 lx indicated that a squirrel was aboveground) and modelled hourly aboveground activity as a binomial distribution via a logit link function. We calculated the hourly mean vector of dynamic body acceleration (VeDBA) from raw tri-axial acceleration data [38], which we modelled as a Gaussian distribution. Activity models included a p-spline for time of day, linear terms for mean hourly ambient temperature and precipitation, a two-way interaction between injection type and binned time relative to the injection (same bins as above), and a random effect for individual ID (electronic supplementary material, tables S5 and S6). Models included a continuous autocorrelation structure to account for temporal autocorrelation in the data across single time steps.

We used temperature and acceleration data from collar-mounted loggers attached to LPS-injected squirrels to test for the predicted negative correlation between fever and lethargy at the individual level. Specifically, we examined the correlation between mean overnight collar temperature the first night post-injection and mean hourly acceleration the following day. The relatively small number of LPS-injected squirrels from which we recovered these data (n = 5) meant that we could only assess the raw correlation between these variables.

3. Results

Adult male Arctic ground squirrels injected with LPS exhibited mildly elevated heart rates the first night post-injection (204.9 ± 5.6 bpm; GAMM estimate ± s.e.) compared with the pre-injection period (200.6 ± 4.1 bpm) and saline-injected squirrels the first night post-injection (195.3 ± 5.4 bpm; $\beta = 14.278 \pm 8.522$, $t = 1.675$, $p = 0.09$; GAMM estimate and statistics for the interaction term; figure 2*a*). LPS-injected squirrels experienced elevated body temperatures for two nights (night 1: 38.63 ± 0.14°C; night 2: 38.10 ± 0.12°C) compared with the pre-injection period (37.64 ± 0.09°C) and saline-injected squirrels the first two nights post-injection (night 1: 37.83 ± 0.14°C; night 2: 37.86 ± 0.14°C; night 1: $\beta = 0.967 \pm 0.216$, $t = 4.483$, $p < 0.001$; night 2: $\beta = 0.407 \pm 0.207$, $t = 1.963$, $p = 0.05$; figure 2*b*). The magnitude of the fever response was particularly large the first night post-injection. Using the collar-mounted temperature loggers, we detected a similar increase in body temperature in LPS-injected squirrels the first night post-injection (37.94 ± 0.10°C) compared with the pre-injection period (36.90 ± 0.08°C) and saline-injected squirrels the first night post-injection (37.10 ± 0.12°C; $\beta = 0.987 \pm 0.163$, $t = 6.060$, $p < 0.001$; figure 2*c*). However, we failed to detect elevated body temperatures beyond the first post-injection night in the collar-derived data. Interestingly, median overnight heart rate was positively correlated with median overnight body temperature (figure 1*d*).

LPS-injected squirrels spent less time aboveground the first day post-injection (49.7 ± 5.5%) compared with the pre-injection period (64.0 ± 5.0%) and saline-injected squirrels the first day post-injection (68.8 ± 6.1%; $\beta = -0.817 \pm 0.072$, $t = -11.391$, $p < 0.001$; figure 3*a*). Moreover, LPS-injected squirrels moved less the first day post-injection (0.116 ± 0.014 mean hourly VeDBA) compared with the pre-injection period (0.178 ± 0.011 mean hourly VeDBA) and saline-injected squirrels the first day post-injection (0.194 ± 0.014 mean hourly VeDBA; $\beta = -0.081 \pm 0.019$, $t = -4.216$, $p < 0.001$; figure 3*b*). We found no evidence that squirrels compensated for this short-term reduction in activity by increasing time spent aboveground or movement during the subsequent two days; instead, activity returned to the pre-injection baseline the second day post-injection and was comparable with saline-injected squirrels. Mean overnight body temperature the first night post-LPS injection, measured by collar-mounted loggers, was negatively correlated with mean hourly VeDBA the following day ($r = -0.88$; figure 3*c*).

4. Discussion

Biologging in free-ranging adult male Arctic ground squirrels provided evidence that the APR comprises an adaptive emergency life-history stage, wherein squirrels temporarily become lethargic and sacrifice foraging opportunities in favour of a robust immune response that promotes survival. Squirrels spent 19% less time aboveground and reduced overall movement by 40% under the simulated immune challenge, indicating a reduction in energetic expenditure through physical activity. This likely also represents a reduction in foraging time as Arctic ground squirrels must emerge from burrows to forage [33] and foraging is the squirrels' primary aboveground activity outside the breeding season [39]. Hence, the sickness behaviour we documented apparently reduced energetic intake. Reduced appetite is likely an adaptive response to infection, as forced feeding further debilitates sick animals and increases mortality [10]. A reduction in foraging potentially increases survival of infected squirrels by depriving pathogens of important nutrients. Curtailed physical activity also likely benefits sick squirrels by compensating for reduced energetic intake and/or by allowing for reallocation of energetic reserves toward physiological immune defences [1,10]. This apparent energetic trade-off matches the predictions we tested and demonstrates that free-ranging animals accept energetic and opportunity costs of mounting an immune response, at least in some contexts. This makes sense in male Arctic ground squirrels during summer (outside the breeding season), as surviving an infection (and hence, increasing the odds of living to the next breeding opportunity) likely outweighs the costs of a temporary reduction in foraging [40].

Energy saved by ground squirrels through reduced activity may have been redirected—at least partially—to a simultaneous fever response characterized by an approximately 1°C increase in body temperature. Elevated body temperature is thought to mitigate infection by hampering pathogenic propagation [2]. We also documented an increase in heart rate under the simulated immune challenge, which makes sense because toll-like receptor 4 (TLR4), a pivotal receptor for recognizing LPS and initiating inflammatory responses, is known to modulate autonomic control of heart rate [41]. However, the observed increase in heart rate compared with saline-injected squirrels was relatively small (10 bpm), which might suggest a somewhat lower metabolic cost of fever in these squirrels than would have been expected *a priori* [41,42]. Nevertheless, squirrels experiencing greater fever following a LPS injection also exhibited greater lethargy. This result suggests an energetic trade-off between physiological immune function and activity that may help explain the evolution of sickness behaviour in vertebrates [1,10]. However, this result should be interpreted cautiously given the small number of individuals in our study.

A reduction in movement and an increase in time spent sheltered (e.g. in a burrow) likely also reduces predation risk during an infection. Sheltering while undergoing an APR may be particularly important if reduced energetic intake or energetic reallocation inhibits physical performance. In support of this possibility, male Algerian psammodromus lizards (*Psammodromus algirus*) exhibit reduced sprint speed following LPS injections [43]. The use of refugia during sickness may alternatively reduce energy expended evading predators. Concealment may additionally reduce the likelihood of conspecific conflict in group-living animals, like ground squirrels. Vervet monkeys (*Chlorocebus pygerythrus*) undergoing an APR do not curtail social interaction and suffer increased rates of attack and injury by conspecifics [24]. In contrast, sick Egyptian fruit bats (*Rousettus aegyptiacus*) self-isolate by leaving social clusters, perhaps to reduce energetic costs of social conflict [25]. Future research might focus on elucidating the relative importance of ecological selection pressures shaping sickness behaviour in vertebrates.

Our results from free-ranging ground squirrels suggest biologgers can aid in studying the effects of disease on wildlife and in monitoring the spread of disease in natural systems. Small, lightweight biologgers collect and store relatively large

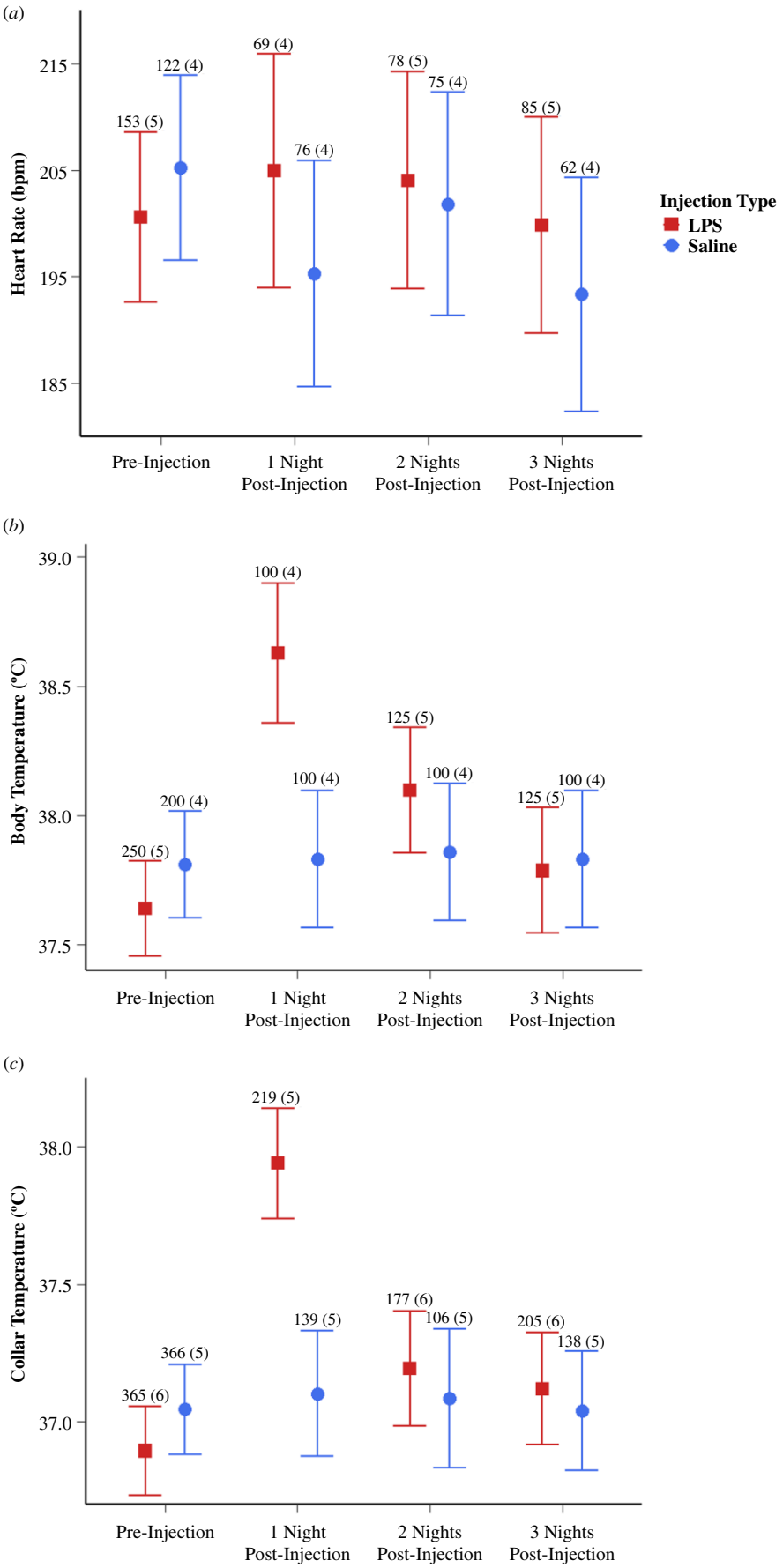

Figure 2. LPS injections induced fever (measured by implanted loggers) that included elevated heart rate (*a*) and body temperature (*b*) for one or two nights in free-ranging adult male Arctic ground squirrels. Collar-mounted temperature loggers also captured the fever response (*c*). Point estimates (± 95% CI) were derived from GAMMs; sample sizes—datapoints (individuals)—are above error bars.

amounts of data from individual animals across relatively short time periods, allowing researchers to document transient effects of infection [24,44,45] or experimentally induced immune responses [21,22,25,27]—as we also demonstrated. The consistency with which biologging studies elucidate fever and/or sickness behaviour further solidifies the degree to which the APR is

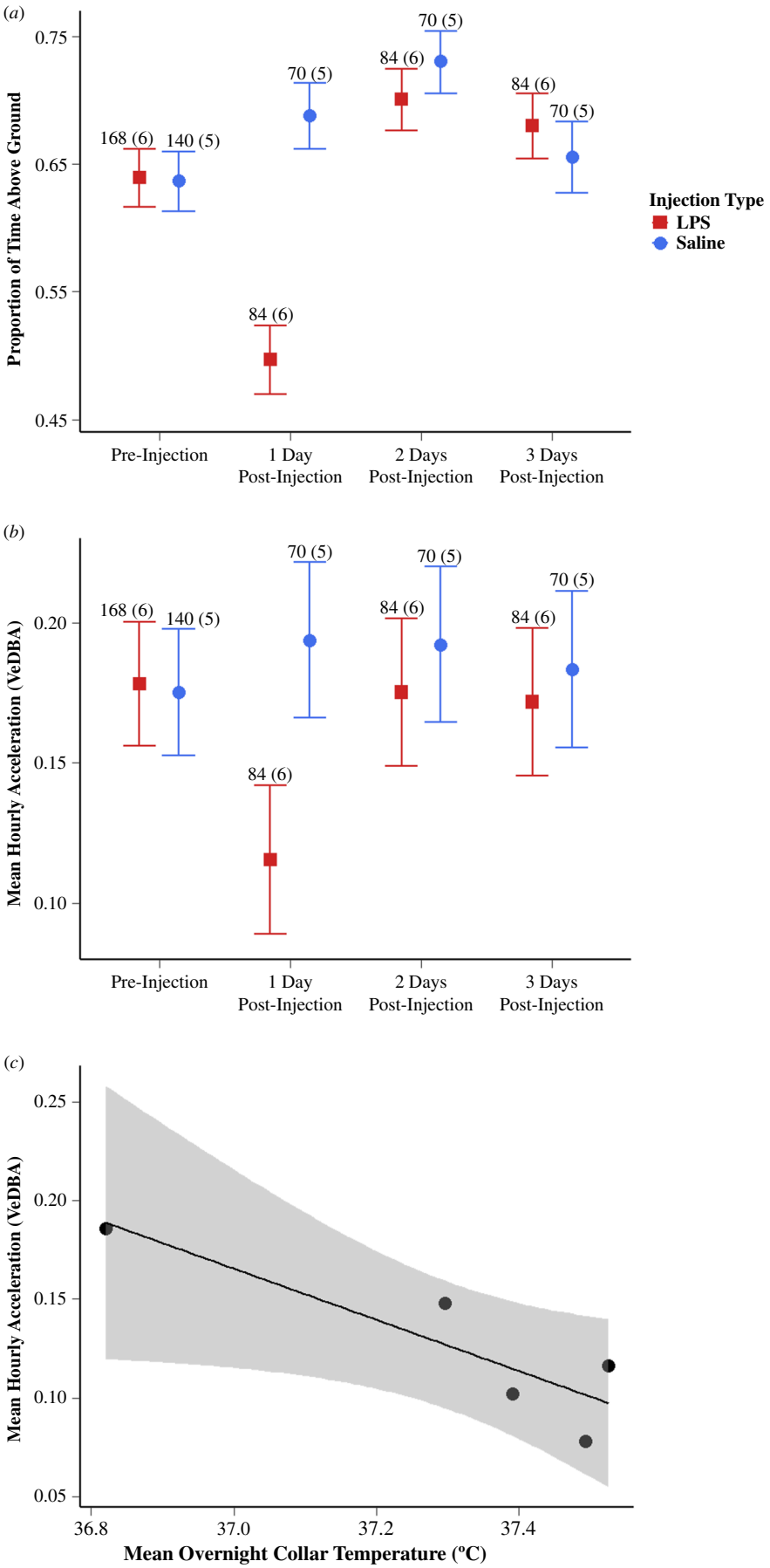

Figure 3. LPS injections induced sickness behaviour (measured by collar-mounted loggers) that included reduced aboveground activity (*a*) and movement (*b*) for one day in free-ranging adult male Arctic ground squirrels. Point estimates (± 95% CI) were derived from GAMMs; sample sizes—datapoints (individuals)—are above error bars. Fever during the first night following a LPS injection was negatively correlated with movement the following day (*c*). Raw datapoints and the best fit line (± 95% CI) are shown.

evolutionarily conserved across vertebrate lineages, although significant variation in the magnitude, duration, and components of the APR among species, populations, and individuals remains to be explained.

Single metrics (e.g. acceleration or body temperature) can detect animal immune responses, but many processes alter these traits in free-ranging animals, complicating data interpretation. Hence, a holistic biologging approach that incorporates (multiple) physiological and behavioural responses is better suited to studying the APR in free-ranging animals. Our results suggest simultaneous hyperthermia and reduced activity indicate activation of the APR. Notably, we detected only a mild increase in heart rate associated with an otherwise robust APR in male Arctic ground squirrels despite our rigorous validation and filtration of data derived from implanted heart rate loggers. We also found that collar-mounted temperature loggers detected fever equally well as surgically implanted temperature loggers during the first night following a LPS injection (importantly, a period of inactivity), although the collar-mounted loggers were perhaps not sensitive enough to detect the mild lingering fever on the second post-injection night suggested by the internal loggers. These results demonstrate that integrated APR research can proceed in a minimally invasive fashion—at least in systems where external temperature loggers are not overly influenced by ambient conditions.

Additional research is needed to characterize patterns of induced immune defenses across space, time, taxa, and demographic groups and to test hypotheses potentially explaining variation in immunity at all biological levels. For example, one study documented a latitudinal gradient in fever and sickness behaviour in song sparrows (*Melospiza melodia*; [21]) and another found differences in APR components among congeneric rodents [17]. The ultimate causes of such variation remain unclear, although both studies are consistent with the idea that intra- and interspecific variation in life histories correlates with measures of immunity, possibly because evolved life-history traits dictate allocation of resources to survival tactics during emergency life-history stages [4,46]. In our study system, it would be interesting to know whether male Arctic ground squirrels modulate the magnitude and/or duration of the APR seasonally as has been documented in song sparrows [20]. Given the brevity of their spring breeding season [40] and relatively low annual survival rates [47], it may be advantageous for male squirrels to suppress the APR during the breeding season. More broadly, the effects of endogenous state and environmental conditions on the APR (i.e. reaction norms) remain largely untested in free-ranging animals, although a small body of theory and laboratory work exists [48,49]. The advent of biologging technology now allows field studies to address these fundamental questions and thereby fill a gap in our understanding of the ultimate causes and consequences of the APR in vertebrates.

Ethics. The research described in this manuscript was approved by the University of Alaska Fairbanks animal care and use committee (IACUC Protocol: 1395041). The field work was additionally permitted by the Alaska Department of Fish and Game (Scientific Permit: 20-142).

Data accessibility. All data and code used in the analyses presented in this paper are permanently stored in the Dryad Digital Repository [50].

Supplementary material is available online [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.Z.T.A.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; H.E.C.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, writing—review and editing; C.T.W.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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