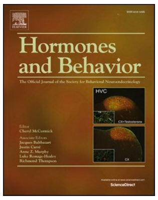
Hormones and Behavior 155 (2023) 105426

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh



Weathering the storm: Decreased activity and glucocorticoid levels in response to inclement weather in breeding Columbian ground squirrels

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ARTICLE INFO

Keywords:
Behavioral shifts
Energy mobilization
Extreme climate events
Hibernating sciurid
HPA activity
Precipitation-modified behavior
Weather-induced stress responses

ABSTRACT

Inclement weather can rapidly modify the thermal conditions experienced by animals, inducing changes in their behavior, body condition, and stress physiology, and affecting their survival and breeding success. For animals living in variable environments, the extent to which they have adapted to cope with inclement weather is not established, especially for hibernating species with a short active season that are constrained temporally to breed and store energy for subsequent hibernation. We examined behavioral (foraging activity) and physiological (body mass and fecal cortisol metabolites) responses of Columbian ground squirrels (*Urocitellus columbianus*), small hibernating rodents inhabiting open meadows in Rocky Mountains, to 3 events of inclement weather (two snow storms in May 2021 and May 2022, one heavy rainfall in June 2022). We found that individuals adapted to inclement weather conditions by (1) reducing above-ground activity, including foraging, (2) decreasing the mobilization of stored resources as indicated by a decrease in the activity of the hypothalamo-pituitary-adrenal (HPA) axis and lower fecal cortisol metabolites in the hours/days following periods of inclement weather; and (3) compensating through increased foraging and more local activity when favorable conditions resumed. As a result, body mass and growth did not decrease following short periods of inclement weather. Columbian ground squirrels were well-adapted to short periods of inclement weather, coping *via* modifications of their behavior and the activity of the HPA axis.

1. Introduction

With global change, the frequency of extreme weather events is increasing along with their effects on organisms, and are predicted to continue increasing in the future (Quante et al., 2021; Seneviratne et al., 2021; van de Pol et al., 2017). Such events can induce marked changes in animal phenology, physiology, and behavior, consequently affecting survival and breeding success (Krause et al., 2016; Kucheravy et al., 2021; van de Pol et al., 2017). Even for animals adapted to harsh climate conditions, the occurrence of extreme heat, long freezing events, or heavy precipitation can threaten individual survival and reproductive success, and as a result population dynamics (see Frederiksen et al., 2008; Ropert-Coudert et al., 2015; Wingfield et al., 2017 in birds). Energy regulation is a key factor in animal life histories (Brown et al., 2004). Energy acquisition and expenditure can be strongly influenced by weather conditions either *via* effects on foraging resources (modifications of resource availability and acquisition; Allison and Conway, 2022) or *via* effects on animal behavior (*e.g.* foraging behavior) and metabolism (*e.g.* thermoregulation) (Levy et al., 2019; Schweiger and Frey, 2021).

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https://doi.org/10.1016/j.yhbeh.2023.105426
Received 30 June 2023; Received in revised form 22 August 2023; Accepted 31 August 2023

From a climatology perspective, extreme weather events may be characterized as unusual weather events, contributing to climate variability, but that lie at the extremes of historical records in a given place (*e.g.* heat and cold waves, heavy rainfalls, and snow storms, Matthews et al., 2021). Another perspective defines extreme weather events from a biological point of view, an event being considered as extreme when it significantly impacts individuals, populations, or ecosystem functions (Ummenhofer and Meehl, 2017; van de Pol et al., 2017). Thus, from an animal's perspective, the extent to which events of inclement weather constitute extremes depends on their effects on the organism, especially on body condition and stress physiology, and on whether and how animals cope with these environmental changes (Bize et al., 2010; Krause et al., 2016; Wingfield et al., 2017). Assessing the extent to which various species are able to cope (behaviorally and physiologically) with inclement weather conditions is necessary for discerning the scope of plasticity that they might exhibit in the current context of rapid global change (Harris et al., 2018; Ummenhofer and Meehl, 2017).

Assessing behavioral and physiological modifications to inclement weather should be particularly relevant for animals inhabiting mountainous temperate ecosystems where variations in thermal conditions are high, favorable living conditions temporally constrained (*viz.* to spring and summer months), and the occurrence and intensity of snowstorms and rainfalls is projected to increase with ongoing climate change (Quante et al., 2021; Seneviratne et al., 2021). Many species rely strongly on foraging conditions during the spring/summer period to sustain their reproduction. This short temporal window is especially challenging for hibernating species, that not only rely on energy income for reproduction, but also for replenishing fat stores in anticipation of the following hibernation (Humphries et al., 2003). Thus, resource acquisition and storage during the active period may have strong influences on survival and reproductive success (Carrier et al., 2022; Murie and Boag, 1984; Zervanos et al., 2014). Inclement weather that occurs during the short spring/summer period can have direct consequences on the mortality of individuals (*e.g.* flooding; Golet et al., 2013, Viblanc et al., *personal observations*), or indirect consequences through food consumption, reflected in reduced body mass (Lenihan and Vuren, 1996; Neuhaus et al., 1999). As an example, Belding's ground squirrels survival, reproduction, and behavior was strongly impacted by a long spring snowstorm inducing sharp mass loss, decreased reproduction, and increased mortality in the population (Morton and Sherman, 1978). What remains unclear however, is how animals that live in fluctuating environments react to inclement weather: their hormonal, physiological, and behavioral responses (Wingfield et al., 2011).

When conditions are beyond those normally experienced, *e.g.* stressful weather events, vertebrate behavior and physiology is modified through the hypothalamic-pituitary-adrenal axis (HPA; Boonstra, 2004; Wingfield et al., 2011). Several studies showed that the activity of HPA axis increases when conditions become more stressful, which can be measured in glucocorticoids concentrations (hormonal mediators of allostasis that trigger a “stress response”, Baker et al., 2013; Boonstra et al., 2020; King et al., 2023; McEwen and Wingfield, 2003; Romero and Wingfield, 2015; Walker et al., 2015). Even though the stress response allows individuals to quickly respond to unpredictable stressful events and is considered adaptive (Angelier and Wingfield, 2013; Boonstra et al., 2001; McEwen, 2019), long exposure to stressful stimuli can also have deleterious effects on individuals and affect their long-term survival (Boonstra et al., 1998; Romero, 2004; Sapolsky et al., 2000; Wingfield and Kitaysky, 2002).

Glucocorticoids are responsible for energy mobilization and fat and protein catabolism, which can ultimately lead to changes in body condition (Angelier et al., 2007; Sapolsky et al., 2000). In case of inclement weather and limited access to food, nutritional stress usually triggers the HPA axis (Jenni-Eiermann et al., 2008; Pravosudov and Kitaysky, 2006) and the response is reflected in increased circulating cortisol concentrations, an important glucocorticoid in mammals (Haase et al., 2016; Vijayan et al., 2010; Zhang and Buck, 2022). In contrast, one hypothesis would be that species adapted to unpredictable environments, such as mountainous ones, could save energy by shutting down the HPA axis and decreasing energy mobilization. This can be the case for hibernating species, which already rely on shelters (*e.g.* burrows, dens) as part of their natural history, and seasonally limit their metabolism. One non-invasive way to assess HPA activity is to examine fecal cortisol metabolites (FCMs, Gormally and Romero, 2020; Palme, 2019; Sheriff et al., 2011; Zhang and Buck, 2022).

We tested the hypothesis that animals inhabiting mountainous ecosystems may have adapted to cope with short periods of inclement weather. For this test, we studied Columbian ground squirrel (*Urocitellus columbianus*), a model species that is regularly subjected to highly variable and unpredictable weather conditions in its montane habitat (Zammuto and Millar, 1985). To do so, we examined the effect of inclement weather on activity patterns, foraging behavior, glucocorticoid levels, and body mass of ground squirrels during two late snowfall events in 2021 and 2022 and one rainfall event in 2022. Specifically, we (1) tested whether these weather events were considered as ‘extreme’ from a climatology perspective, (2) described behavioral changes during inclement weather in 2022, and (3) analyzed whether hormonal ‘stress’ levels or body mass changed after weather events compared to controls. Unlike several species showing increased activity of the stress axis during periods of inclement weather (Bize et al., 2010; Krause et al., 2016; Romero et al., 2000; Wingfield et al., 1983) or food deprivation (Kitaysky et al., 2007, 1999), we predicted that in response to inclement weather, these mountain rodents would adapt by weathering the storm, *i.e.*, saving energy by reducing their overall activity and metabolism.

We expected animals to avoid wet and cold weather conditions by increasing the time spent in sheltered burrow-systems and reducing above-ground foraging activity. We thus expected to observe less individuals foraging during periods of inclement weather, but expected foraging activity to re-increase to higher levels afterwards, perhaps compensating for the inclement periods of lowered resource acquisition. We further expected decreases in metabolic activity during inclement weather to be reflected in overall decreased levels of glucocorticoid levels (Haase et al., 2016) shortly after the period of inclement weather conditions (as measured through fecal glucocorticoid metabolites FCM; Bosson et al., 2009; Sosa et al., 2020), reflecting an overall metabolic state geared towards minimized use of stored energy (for associations between metabolic activity and GCs, see Bonier et al., 2009; Haase et al., 2016). In turn, we predicted such adaptations to result in minimal loss of body mass during periods of detrimental weather.

Columbian ground squirrels are an ideal model for testing the effects of acute inclement weather on animal condition and stress, and the hypothesis of adaptation. These hibernating herbivorous, and diurnally active rodents inhabit open meadows in the Rocky Mountains (Elliott and Flinders, 1991) that are honeycombed with communal and individual burrows in which the animals sleep and raise their young, and in which they may take shelter from inclement weather conditions and predators. They hibernate from August to April of the following year (about 70 % of the year, Dobson et al., 1992; Murie and Harris, 1982). Their active period, during which reproduction and fattening for subsequent hibernation occur, is thus notably short. During the active season, they spend most of their daily time-budget foraging on vegetation, being inactive in their burrows at night. Their daily time-budget varies during the season, with variations according to sex and breeding status (MacWhirter, 1991; Ritchie, 1990). Columbian ground squirrels rely strongly on current foraging conditions to sustain reproduction, although their stored energy capital at the start of the breeding season is also important (Broussard et al., 2005; Dobson et al., 1999; Rubach et al., 2016).

During their short active period, unfavorable weather conditions might be expected to negatively impact above-ground squirrel activity and thus the time they spend foraging. Rainfall and snow cover can render the animals wet, decreasing fur insulation, and inducing high energy losses (Lovegrove, 2003; Webb and King, 1984). Additionally,

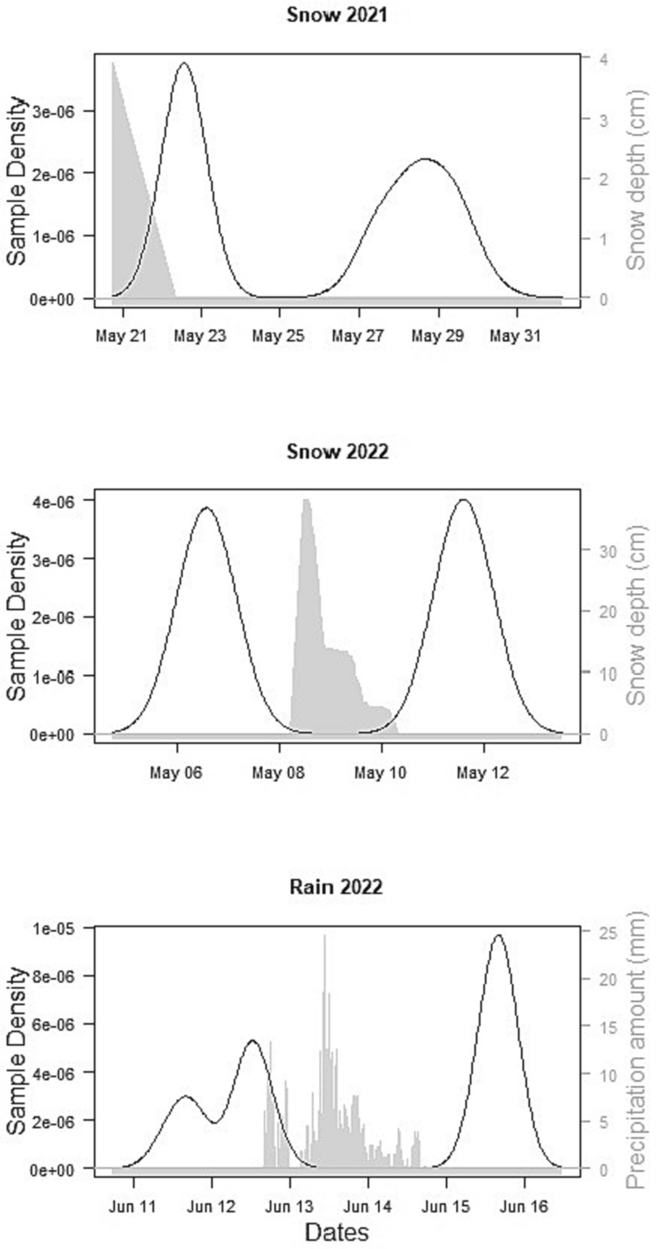

Fig. 1. The density of fecal sampling times and dates compare to snow and rain events are presented for each weather event (grey filled area, snow depth in 2021 and 2022, and rain in 2022).

vegetation is not accessible when covered with snow (Korslund and Steen, 2006), and prolonged periods of snow cover during the active season (*e.g.* 2 consecutive weeks of snow storm – more than half of the mating season in normal years) are known to negatively affect male survival and female breeding success (Neuhaus et al., 1999). However, for shorter spells of inclement weather, little is known on whether the animals are able to adapt or not.

2. Materials & methods

2.1. Data collection

The study was conducted during the 2021 and 2022 active seasons of Columbian ground squirrels in the Sheep River Provincial Park in Alberta, Canada (50°38′N, 114°39′W, 1500-1570 m elevation), located in the foothills of the Rocky Mountains. The study area included three meadows with different ground squirrel populations: meadow A (MA), meadow B (MB), and meadow C (MC). Individuals were trapped (using live-traps National Live Traps; Tomahawk Co., WI, USA: 13 × 13 × 40 cm^3 baited with peanut butter) and permanently marked as juveniles, or when they first appeared in the meadow as immigrant adults, with application of unique metal numbered ear tags (Monel no. 1, National Band & Tag Co.). Sex was determined based on visual inspection of genitalia (Murie and Harris, 1982). Each year, the population was monitored daily from before the first emergences from hibernation (early April each year) to the end of lactation for breeding females. At the first capture of the season, each ground squirrel was given a unique individual black hair-dye mark (Clairol® Hydrience hair dye N°52 Black Pearl, Clairol Inc., New York, USA) on their dorsal pelage for visual identification in the field. At each capture, individuals were weighed to the nearest 5 g using a Pesola® spring-slide scale.

Table 1
Number of samples analyzed (fecal samples with known body mass and individual characteristics) for each weather event, condition (control and after), and age/sex category. In total, 547 fecal samples were obtained from 272 different individuals.

		Yearlings	2+ males	2+ females
Snow 2021	Control	58	24	58
(MA, MB, MC)	After weather event	38	23	63
Snow 2022	Control	27	20	53
(MA, MB, MC)	After weather event	33	24	47
Rain 2022	Control	16	9	12
(MB)	After weather event	17	9	16

In 2021 and 2022, we checked the weather forecast for the Sheep River area (Alberta, Canada) to anticipate possible periods of inclement weather occurring in our populations. We were able to anticipate 2 periods of inclement weather in 2022: one late spring snow storm, and one period of summer rainfall. We target-trapped and weighed the animals, and collected fecal samples just before (control) and after (treatment) these events occurred, *i.e.*, typically the next day within 24 h (average 6.8 ± (SD) 5.9 h, min = 0.25 h, max = 22.9 h) following the end of the period of weather deterioration (see Fig. 1). In 2021, we were not able to anticipate a sudden snow storm, and thus only acquired fecal samples after the event occurred. Thus, we collected control samples roughly one week after the event had passed. In 2021, animals were weighed and feces were collected just after a snow storm in May (treatment, between 11:00 am and 3:37 pm on 22 May 2021), and around a week after this event (control, between 10:43 am on 27 May 2021 and 10:10 am on 30 May 2021). In 2022, animals were weighed and feces were collected just before a snow storm in May (control, between 10:50 am and 6:55 pm on 6 May 2022), and just after (treatment, between 11:15 am and 7:11 pm on 11 May 2022), before a rainfall in June (control, between 09:54 am on 11 June 2022 and 6:23 pm on 12 June 2022, only on MB) and just after (treatment, between 11:01 am and 7:02 pm on 15 June 2022, only on MB). Given that FCM concentrations reflect circulating glucocorticoid levels *ca.* 7 h before sampling (Bosson et al., 2009), the fecal samples collected thus reflected the activity of the stress axis immediately after (or towards the end of) respective storms. On a few occasions, individuals were not weighed and the sample was not considered in further statistical analyses. We ensured that traps were clean before being deployed, and fecal samples were collected within minutes of capture of animals. Fecal samples were most often collected either directly into 2 ml sterile vials as the female defecated, or from the floor of the trap. In this latter case, the female was always observed defecating in the trap and the feces collected immediately. We insured no fecal sample was contaminated by urine upon collection. Contaminated samples were systematically discarded. Fecal samples were stored on ice packs in the field, transferred to a −20 °C freezer within the following hours of sampling, and at the end of the 2022 field season, all samples were transported on dry ice to the University of Toronto and analyzed during summer 2022. Overall, we acquired 547 fecal samples for 272 individuals of known age, but see Table 1 for details of the number of observations per meadow and event.

2.2. Analysis of fecal cortisol metabolites (FCMs)

Fecal cortisol metabolites were estimated as previously validated and described for Columbian ground squirrels (Bosson et al., 2009). Briefly, lyophilized fecal samples were frozen in liquid nitrogen, and pulverized with a small grinding pestle. We weighed 0.050 ± 0.005 g of the sample, recorded the exact weight, and vortexed it in 1 ml of 80 % methanol to extract FCMs (30 min at 2500 g). FCM amounts (in ng/g of dried feces) were determined using a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA), which measures metabolites with a 5α-3β,11β-diol structure (Touma et al., 2003). All samples were run in duplicate (except 3 samples with one of the measures out of the range, and thus only the other one was kept) on eighteen 96 well plates, showing a high repeatability ($R = 0.896$, SE $= 0.008$, CI $= [0.878, 0.910]$, p-value <0.001, $n = 1251$ observations, using the *rpt* function from 'rptR' package). Pooled samples with low value (~60 % binding) and high value (~30 % binding) were run on each plate as controls. Mean intra-assay coefficient of variation was 9.7 %, and the mean inter-assay coefficients of variation based on the pools were 12.42 % (low pool) and 13.74 % (high pool).

2.3. Behavioral sampling & analyses

2.3.1. Behavioral observations

From May 4th to 15th 2022 (*i.e.*, 5 days before, 2 days during and 5 days after the snow event), behavioral observations were performed daily for 2 h in the morning (from 8:30 am for the earliest start, until 11:40 am for the latest end) from the top of 3 high observation towers (1 observer per tower, the allocated tower to an observer changing each day). Visual scans of meadow B were performed every 15 min, recording foraging *versus* other behaviors of all individuals present. From these scans, we calculated the proportion of foraging behavior (main behavior of Columbian ground squirrels), which represented 54 % of their time on average, and between 38 % and 68 % of their total time budget over the entire active season. Individuals were identified from their back hair dye mark. Finally, the location of each individual was recorded along with its behavior within 1-m on a 10 m × 10 m Cartesian grid system that covered the meadow with color-flagged wire pins.

From these observations, we estimated 4 daily behavioral variables: the mean number of observations per scan, the daily percentage of individuals seen above-ground (compared to the actual number of individuals alive and emerged from hibernation on the meadow as of the particular day), the percentage of time spent foraging compared to other behaviors, and the mean total area used by each individual (in m^2). For each individual, area use was estimated from the minimum convex polygon of all observations on a given day (with *mcp* function from 'adehabitatHR' package, with a minimum of five observations per individual).

2.3.2. Above-ground activity from loggers

From June 10th to June 16th 2022 (*i.e.*, 3 days before, 2 days during and 2 days after) we equipped 16 individuals (4 yearlings, 6 older females, and 6 older males) at MB with bio-logging collars that were specifically designed for the ground squirrels. The collars were fitted with a light sensor, microcontroller and internal memory chip. The collars continuously recorded ambient light from three red, blue, green (RGB) channels that were summed and combined *in-situ* into a binary variable 1 (light detected)/0 (no light) every 2 s (Mamtag collars, Sextant Technology Ltd., Marton, New Zealand). Thus, we were able to continuously determine if animals were present above (light =1) or below ground, in their burrow systems (light = 0). From these data, we determined the above-ground activity of equipped animals between 8 am and 6 pm. Between these hours, we calculated the hourly proportion of time spent out of the burrow. The duration of data logging varied among animals depending on logger battery-life and our success at recapturing the animals. In total, we collected 1,516,780 records, *i.e.*, 13,543 records per day per individual, on average, over a period of 7 days.

2.4. Characterization of weather events

2.4.1. Observed snow & rain events

To quantify snow and rain events, we used several climate sources. Local rainfall (in 2022) was recorded at a local weather station (Davis, Vantage Pro2) installed on meadow B. However, because the weather station did not record snow, we relied on another weather station situated in Pekisko (closest available data, located 32 km south of the study site, 50°22′N, 114°25′W, 1341 m elevation, data provided by Agriculture and Irrigation, Alberta Climate Information Service, ACIS, https://acis.alberta.ca/) to assess snow. In 2022, to obtain more detailed local data, we combined records from this weather station with 4 camera traps (photos taken every 30 min) installed on meadow B. The cameras faced wooden poles that were graduated every 5 cm. This set-up provided us with continuous records of snow depth at various locations on the meadow.

In 2021, it snowed up to 15 cm between the 19-20th of May. Snow remained on the ground until the 22nd of May. In 2022, it snowed during the night between 8th and 9th May up to 38 cm, and the snow melted on the 11th of May. It rained continuously on the 13th and 14th of June 2022 (up to 9.8 mm/h, 110 mm in total over the two days). Because weather events could not be controlled and happened at different biological periods in the season (*i.e.*, during the mating season for earlier events *vs.* during lactation for later events), further analyses on biological measures and samples were conducted separately for each weather event (Snow 2021, Snow 2022, Rain 2022).

2.4.2. Extreme events? Assessment of long-term trends

We tested whether the observed events could be characterized as 'extreme' from a climatology perspective, compared to the past climate in the study area. To access past and long-term local weather conditions, we used the Kearney et al. (2020) microclimate model to estimate past snow events on the studied meadow. The modelling function (*micro_ncep* from 'NicheMapR' package; Kearney et al., 2020) downscales global atmospheric climate-forcing data using terrain-specific corrections, including spatial variations in slopes, soil composition and hydrological properties, orientation, and hill shade (NCEP Reanalysis, historical data from the National Center for Environmental Predictions, provided by the NOAA/OAR/ESRL PSL, Boulder, CO, USA, from their website at https://psl.noaa.gov/). Local precipitation events (from a weather station situated in Sheep River Provincial Park from 2009, 50°39′N, 114°37′W, 1525 m elevation, data provided by Agriculture and Irrigation, Alberta Climate Information Service, ACIS, https://acis.alberta.ca/) were available starting in 2009. We used this data as input in the model to increase its accuracy, and ran the model from 2009 to 2022. The microclimate model, combined with local precipitation data, increases the resolution of large-scale weather data and has been empirically validated (Kearney et al., 2020; Lembrechts and Lenoir, 2020; Maclean, 2020; Saleeba et al., 2020; Tamian et al., 2022). We estimated hourly climate conditions at 4 different points on meadow B, estimating the snowfalls and snow depth on the ground (in centimeters).

From the modelled snow data and recorded precipitation, we calculated the number of snowfalls and rainfalls (uninterrupted snow/rain events), the duration of snow and rain events (in hours), and the mean snow depth of the snow events (in cm) or the total precipitation amount of the rain event (in mm) from the 15th of April each year (average day of first hibernation emergences, typically by older males) until the beginning of August (in the period of immergences into hibernation, Neuhaus, 2000; Young, 1990).

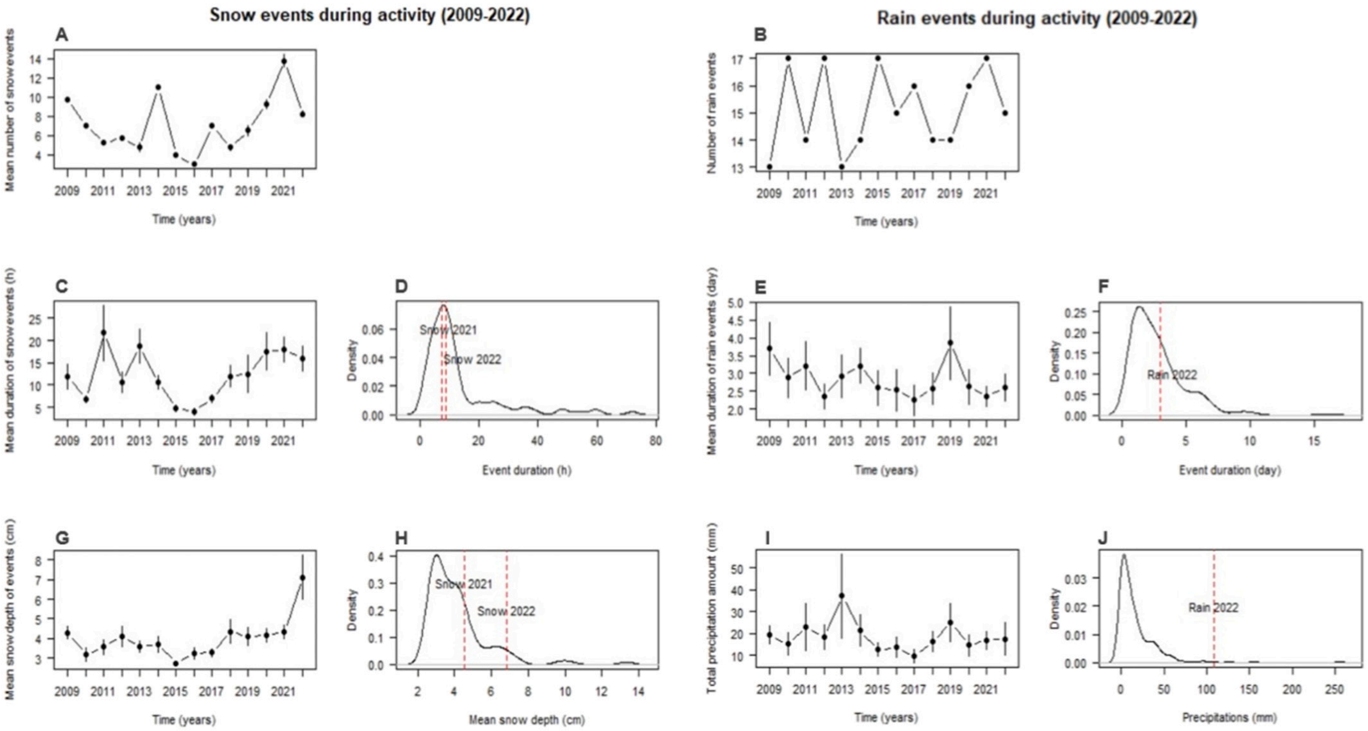

Fig. 2. Weather events characterization: long-term trends in climate regarding past snow (days with snow on the ground) and rain (continuous rainfall) events from 2009 to 2022: (A) and (B) yearly number of snow and rain events, (C & E) yearly mean duration of snow and rain events, (D) duration of 2021 and 2022 snow events (in hours), (F) duration of 2022 rain event (in days), (G) mean yearly snow depth of events, (H) snow depth of 2021 and 2022 snow events (in cm), (I) mean yearly total precipitation of events, (J) total precipitation of 2022 rain event (in mm).

2.5. *Statistical analyses*

All data analyses and statistical procedures were conducted using R version 4.0.3 (2020−10−10). Although we report statistical tests at a probability error threshold of 5 %, results are discussed with regards to biological effect sizes rather than threshold *p*-values, which is more meaningful (Halsey et al., 2015; Nakagawa and Cuthill, 2007), especially considering ecological results. Results presented are means ± SE, along with the number of observations (n). Where appropriate (*i.e.* for linear models), we ensured that model residuals were normally distributed by visual inspection of density distributions, Q-Q plots, cumulative distribution functions, and P-P plots using the ‘fitdistrplus’ package in R (Delignette-Muller and Dutang, 2015).

2.5.1. *Age & sex considerations*

Because the sampled animals differed in terms of sex and reproductive characteristics, we examined separately reproductive males and reproductive females (mature individuals), and one-year-old individuals, usually non-reproductive (immature individuals), resulting in three sex/age categories: ‘Yearlings’, ‘2+ Females’, and ‘2+ Males’.

2.5.2. *Weather effects on physiology (FCMs & body mass)*

For each weather event (Snow 2021, Snow 2022, and Rain 2022), we ran a linear mixed effects model (LMM) with the FCM levels as the dependent variable, and tested for an interaction between the period at which the sample occurred, hereafter called treatment (control *vs* after weather event) and the sex/age category. We included body mass as a covariate in the analyses and controlled for plate, individual, and meadow effects as random terms. Because sampling hour did not significantly affect FCM levels, we did not consider it in the models (LMM, $t = 0.837$, $p = 0.403$, $n = 547$ observation, $N = 272$ individuals). The ranges of trapping times compared to the occurrence of weather events are shown Fig. 1. We compared the models with and without the interactions, and chose the final model according to Akaike's information criterion (lowest AIC and for ΔAIC <2, we chose the most parsimonious model; Burnham and Anderson, 2004). When the interaction was retained within the best model, we ran LMMs for each sex/age category separately to test for treatment effects on FCM levels.

To test whether there was a difference in body mass between the control period and after the weather event, we ran similar linear mixed effects models (for each of the 3 weather events and testing the interaction of the treatment with the sex/age category, controlling for individual and meadow effects, set as random terms) but with body mass as the response variable.

Because individuals were expected to fatten-up during their short activity period, we further examined whether the weather events impacted their mass gain. During the 2022 active season, we weighed individuals on Meadow B (several individuals of each individual category every week) and calculated the average weekly mass when trapped (yearlings: $n = 348$ captures and 39 individuals in total, 2+ females: $n = 456$ captures and 39 individuals, 2+ males: $n = 299$ captures and 19 individuals). We then compared these patterns to patterns in mean weekly body mass from the long-term monitoring of the same population (same trapping and weighing methods as described previously). This represented 2067 captures of yearlings ($n = 664$ individuals), 5487 captures of 2+ females ($n = 320$ individuals), and 1481 captures of 2+ males ($n = 186$ individuals) spanning 24 years (1994, 1999–2021).

2.6. *Ethics statement*

Authorizations for conducting research and collecting samples in Sheep River Provincial Park were obtained from Alberta Environment and Parks and Alberta Tourism, Parks, and Recreation. Animal care was carried out in accordance with Auburn University IACUC protocols, with additional approvals from the University of Calgary.

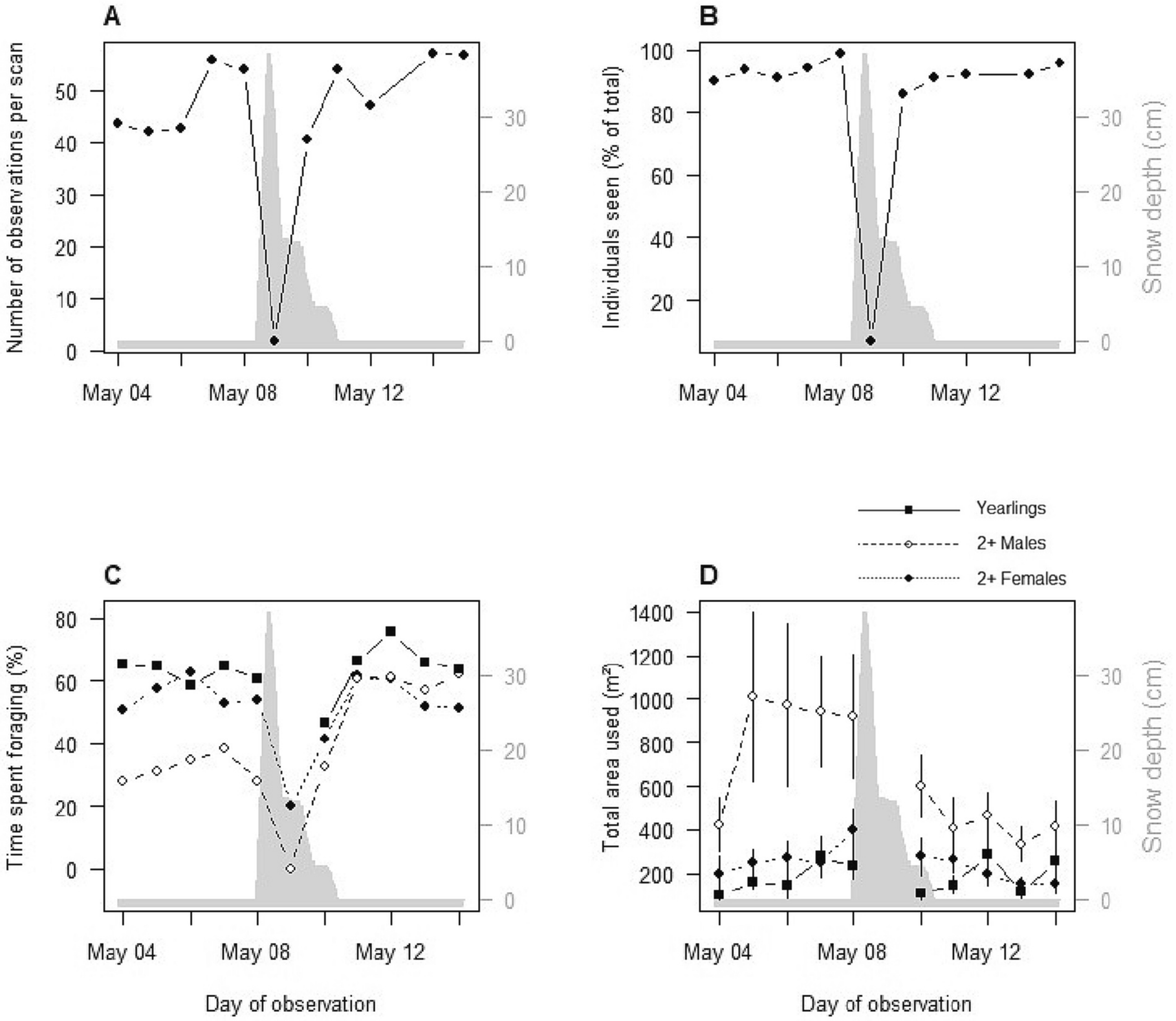

Fig. 3. From behavioral observations during the snow event in 2022, we calculated the number of observations per scan (A), the percentage of individuals seen compared to the theoretical number of individuals alive and having already emerged from hibernation (B), the percentage of time spent foraging (C), and the total area used by individual (D). The last two were calculated independently for each sex/age category (yearlings in black squares, older females in black circles, older males in white circles). The grey filled area in the background corresponds to the snow depth on the meadow during the weather event.

3. Results

3.1. Long-term trends in weather events

Based on the microclimate model, during the 2009–2022 period, the meadows experienced an average of 7.1 ± 0.4 snowfall events during the active periods of the ground squirrels. There was important interannual variability in the number of events, their duration and the snow depth, with lowest values recorded in 2016 (only a couple of very short events) and an increasing trend since (Fig. 2A, C, G). These snow events usually lasted 12.3 ± 1.5 h and spread from only a few millimeters up to 13 cm (Fig. 2C, H). Compared to all other weather events, the two snow events studied here lasted an average duration, but the amount of snow on the ground was quite different between the two, with a moderate amount in 2021 (4.5 cm *vs* 4.1 cm on average) and a large amount in 2022 (6.8 cm *vs* 4.1 cm on average, above the 90th percentile) (Fig. 2H).

From the weather data in the provincial park that were recorded from 2009 to 2022, there were on average 15.1 ± 0.4 rainfall events (13 to 17) during the active period of ground squirrels (Fig. 2B). The number, duration and amount of rain events were also characterized by an important interannual variability, without displaying longer-term trends. These rainfalls usually lasted 2.8 ± 0.1 days and ranged from only a few millimeters up to 255 mm in total (Fig. 2E, I). Compared to all past rainfalls, the event in June 2022 was only slightly longer than the average (3 days *vs* 2.8 days on average, Fig. 2F) and relatively extreme (110 mm *vs* 18 mm on average, Fig. 2J).

3.2. Behavioral responses to weather event

During the May 2022 snow event, the total number of observations per scan and the percentage of individuals seen above ground dropped drastically after the snowfall (when the meadow was snow-covered), on May 9th (from 49 observations par scan on average to 2 observations per scan, and from >92 % of individuals seen on average to 7 %) (Fig. 3A and B). The percentage of time spent foraging by those active above ground was <20 % on May 9th, coincident with the low number of observations (Fig. 3C). In comparison, before the snow event (between May 4th and 8th), yearlings spent 63 ± 1 % of their time foraging, 2+ females 56 ± 2 %, and 2+ males 32 ± 2 %. However, after snow had melted (between May 11th and 15th), males foraged 88 % more than they did before, but females and yearlings did not (LMs, males: $p < 0.001$, $t = 11.44$, females: $p = 0.82$, $t = 0.236$, yearlings: $p = 0.103$, $t =$

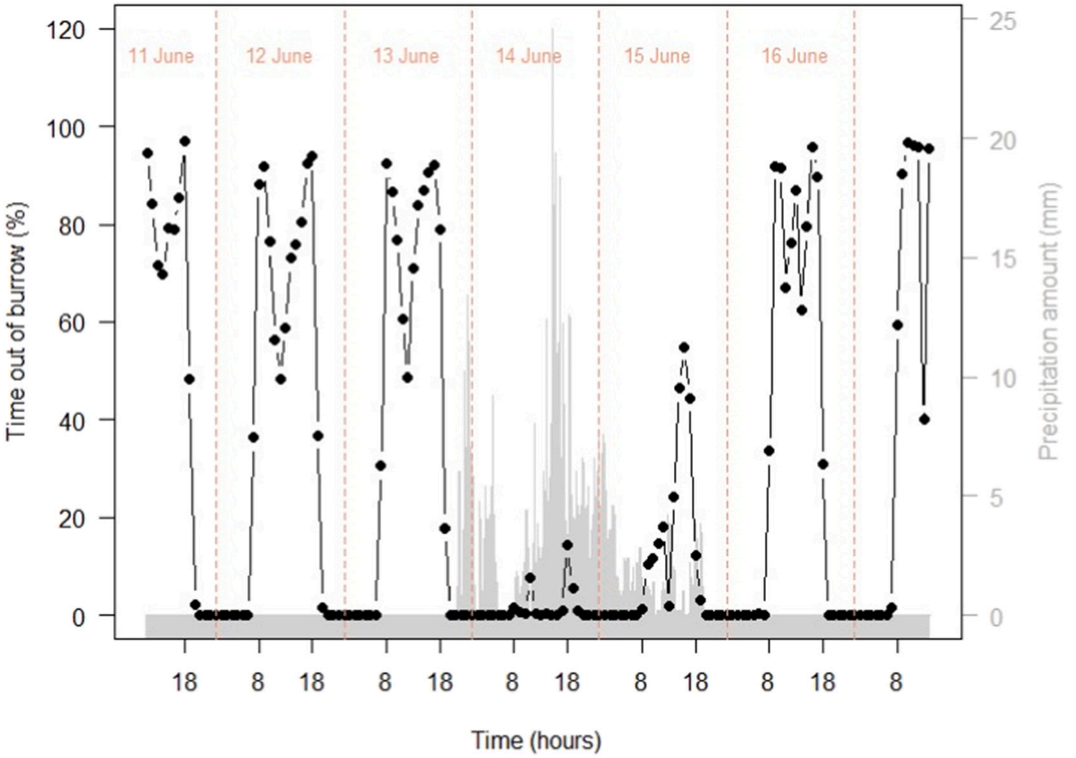

Fig. 4. Hourly percentage of time spent out of the burrow, or diurnal above-ground activity of all individuals during the period of the rain event in 2022. The above-ground activity decreased during hours and days with rain (13th and 14th of June 2022, strong precipitation presented in grey in background).

1.871, $n = 9$ observation sessions for all). Finally, we were not able to calculate the area used by individuals on May 9th because of too few observations of animals being active. However, older males and females covered a 53 % and 31 % larger area before the snowfall (males: 858 ± 127 m^2, females: 278 ± 35 m^2) than after (LMMs, males: 403 ± 54 m^2, $p = 0.001$, $t = -3.273$, $n = 91$ observations, females: 192 ± 24 m^2, $p = 0.056$, $t = -1.922$, $n = 202$ observations, Fig. 3D). The area used by yearlings did not seem to change before and after the snowfall (209 ± 34 m^2 before and 197 ± 30 m^2 after, $p = 0.776$, $t = -0.286$, $n = 135$ observations).

During the rainfall in June 2022, the above-ground activity during the day (8 am-6 pm) decreased significantly for all sex/age categories (LMs, yearlings: $p < 0.001$, $t = -583.2$, females: $p < 0.001$, $t = -474.1$, males: $p < 0.001$, $t = -805.7$, Fig. 4). Indeed, between June 10th–12th, yearlings, 2+ females, and 2+ males spent 82 ± 0.09 %, 67 ± 0.09 %, and 88 ± 0.06 % of their time outside of their burrow respectively, compared to 11 ± 0.07 %, 14 ± 0.07 %, and 11 ± 0.07 % during the rainfall (June 13th and 14th). After the rainfall, the above-ground activity increased to similar levels to 75 %, 67 %, and 82 % of their time outside of their burrow respectively.

3.3. *Physiological responses to weather events*

When testing for snowfall and rainfall effects on fecal cortisol metabolites and on body mass, the interaction between treatment (control/after the snow event) and sex/age category was always retained in the best models (LMMs, $3.5 < \Delta AIC < 8.7$), except for FCM levels in 2021 ($\Delta AIC = 0.2$, see sample sizes in Table 1).

For the snow event of 2021, there was no difference in FCM levels between the control (a week after the weather event, Fig. 5A in red) and the treatment (just after the event, Fig. 5A in blue, $p = 0.067$, $t = -1.845$, $n = 264$ observations). When examining changes in mass, weather effects differed depending on the sex/age category (LMM, $\Delta AIC = 6.9$). Whereas yearlings and older males tended to be 5 % and 8 % heavier a week after the snow event respectively, than just after the event (yearlings: 28 ± 6 g heavier, $p < 0.001$, $t = 4.890$, $n = 96$ observations, 2+ males: 30 ± 13 g heavier, $p = 0.036$, $t = 2.314$, $n = 47$ observations), the body mass of older females did not change (0.4 % difference, −13 ± 11 g, $p = 0.249$, $t = -1.161$, $n = 121$ observations, Fig. 5B). Because the control was sampled 1 week after the treatment, conclusions cannot be drawn easily, since changes in mass could simply reflect the typical mass gain of individuals at this time of the season (see typical mass gain between week 20 and 21 on the blue line, Fig. 6).

For the snow event in 2022, the weather effects on FCM levels and body mass depended on the sex/age category (LMMs, FCM: $\Delta AIC = 8$, mass: $\Delta AIC = 3.9$). All individuals had lower FCM levels after the snowfall than before, but the effect was stronger in adult males: 48 % lower FCM levels after the event for older males *versus* 43 % and 34 % lower FCM levels for older females and yearlings, respectively (yearlings: −162 ± 40 ng/g, $p < 0.001$, $t = -4.075$, $n = 60$ observations, 2+ females: −163 ± 33 ng/g, $p < 0.001$, $t = -5.003$, $n = 100$ observations, 2+ males: −426 ± 138 ng/g, $p = 0.004$, $t = -3.093$, $n = 44$ observations, Fig. 5C). Whereas the body mass of adult males did not change ($p = 0.856$, $t = 0.184$, $n = 44$ observations, Fig. 5D), yearlings and older females had 3 % higher body mass after the event than before (yearlings: 14 ± 4 g, $p = 0.002$, $t = 3.620$, $n = 60$ observations, 2+ females: 17 ± 6 g, $p = 0.008$, $t = 2.809$, $n = 100$ observations).

For the rain event in 2022 on MB individuals, weather effects on FCM levels and body mass again depended on the sex/age category (LMMs, FCM: $\Delta AIC = 3.5$, mass: $\Delta AIC = 8.7$). Only yearlings had statistically significant lower FCM levels after the rainfall than before (27 % lower, −155 ± 60 ng/g, $p = 0.017$, $t = -2.606$, $n = 33$ observations, Fig. 5E), but older females had lower FCM levels that approached significance (2+ females: 17 % lower, −48 ± 22 ng/g, $p = 0.077$, $t = -2.196$, $n = 28$ observations, 2+ males: $p = 0.972$, $t = -0.036$, $n = 18$ observations). In terms of body mass, there were no significant changes before and after the weather event for any sex/age category (yearlings: 33 ± 21 g, $p = 0.136$, $t = 1.532$, $n = 33$ observations, 2+ females: −28 ± 22 g, $p =$

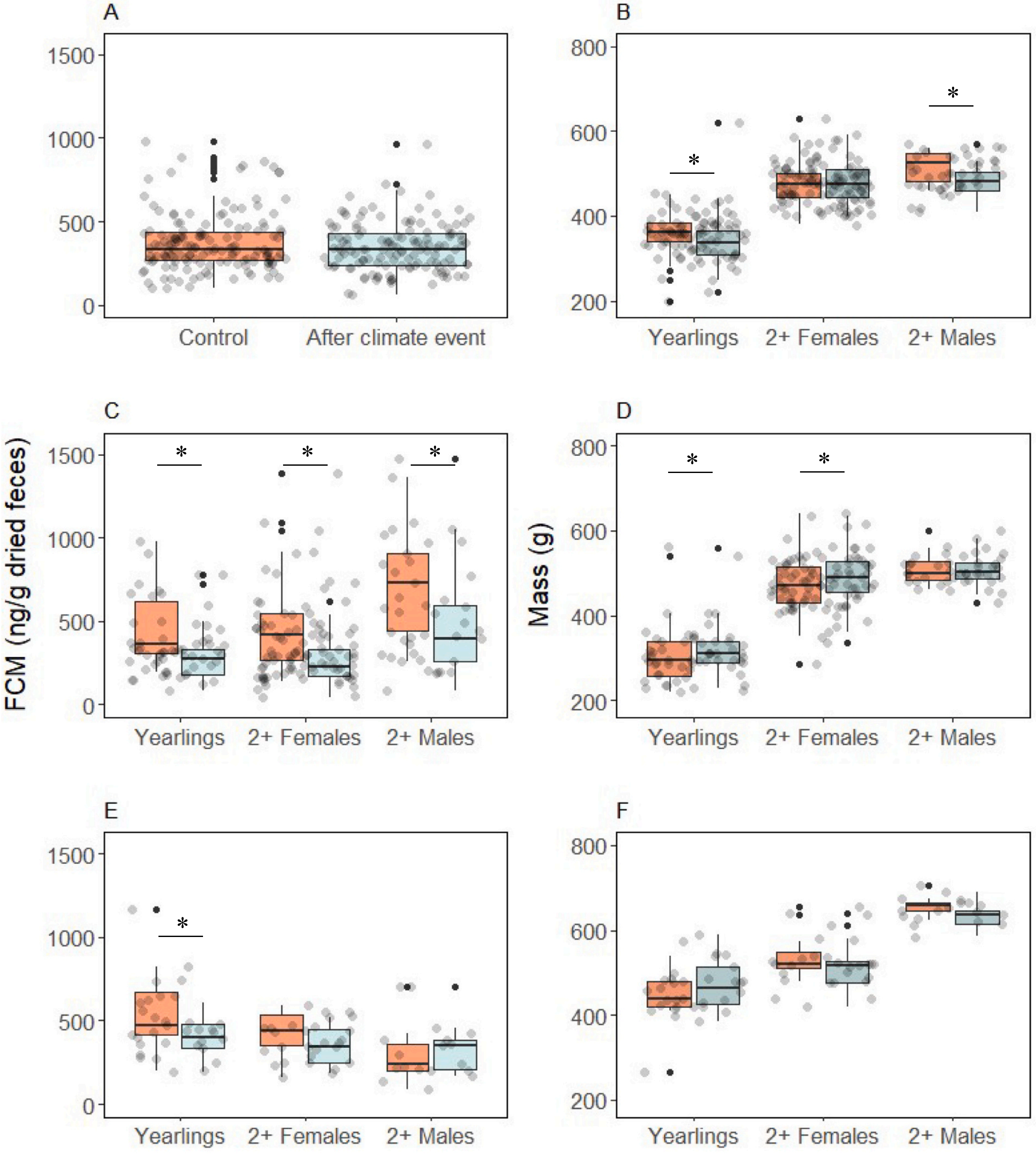

Fig. 5. Fecal cortisol metabolite concentrations (FCM, left) and mass (right) comparisons between the control (orange) and after the climatic event (light blue), for each climatic event (A and B: snow in 2021, C and D: snow in 2022; E and F: rain in 2022) and for each sex/age category (yearlings, older females, older males). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

0.220, $t = -1.255$, n = 28 observations, 2+ males: −24 ± 13 g, $p = 0.090$, $t = -1.808$, n = 18 observations, Fig. 5F).

Finally, the trend in body mass through the active season did not seem to differ greatly in 2022 compared to previous years of monitoring ($n = 23$ years, Fig. 6), for any of the sex/age categories. During the 2022 snow event, all individuals gained mass at a similar rate as in past records (first interval of dashed lines, Fig. 6). During the period of rain in 2022, although older females seemed to always lose mass, the mass of older males stayed constant compared to other years (second interval of dashed lines, Fig. 6). Finally, only yearling individuals seemed to experience a decreased body mass after the rain in 2022 compared to a slight increase in other years, but this trend was not statistically significant when testing for weather effects on yearling mass (see above).

4. Discussion

We examined the effects of periods of inclement weather on the behavior, mass change, and physiology of Columbian ground squirrels, a species inhabiting mountain regions with pronounced weather variation (Zammuto and Millar, 1985). Consistent with our predictions, we found that behavioral activity and foraging decreased during events of inclement weather. Following these events, fecal cortisol metabolites decreased in most individuals, or did not change, likely reflecting an

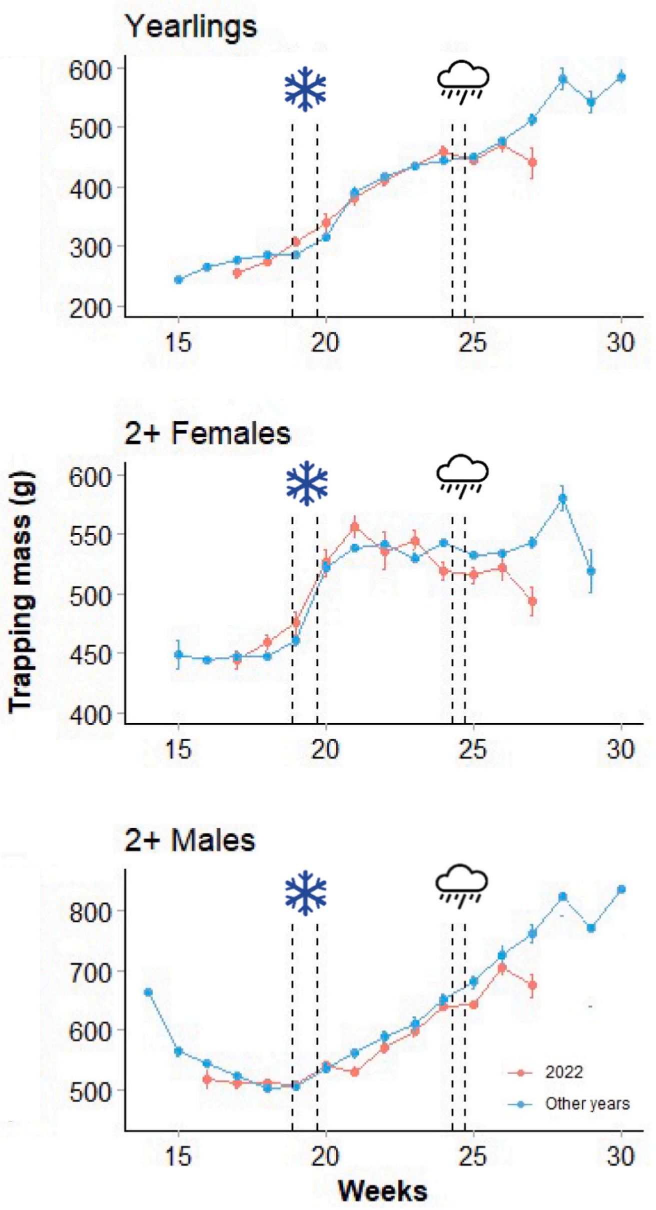

Fig. 6. Comparison between theoretical (blue, calculated from other years) and observed (red, in 2022) weekly body mass (given in weeks since 1 January; week 15 = beginning of April, week 30 = end of July) during the active season of ground squirrels for each individual category (yearlings, older females, older males). The mean body mass (in g) along with standard errors is plotted for each week during active season. The vertical dashed lines represent the occurrence and duration of 2022 weather events (snow and rain). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

overall decrease in metabolic activity and metabolic rate (Haase et al., 2016), and lower use of stored energy resources (*i.e.* carbohydrates and fat). Thus, inclement weather did not strongly impact the body mass of individuals, despite decreased foraging activity during the weather events. Taken together, these results confirm the hypothesis that these mountain rodents have evolved to cope with short periods of inclement weather both through behavioral and metabolic adaptations.

For small mammals, high precipitation and humidity in the environment, combined with low temperatures, can impose substantial thermoregulatory energy losses by decreasing body insulation through wet fur (Lovegrove, 2003; McCafferty et al., 2017; Webb and King, 1984). A way for animals to minimize such costs is to modify behavior (Levy et al., 2019; Williams et al., 2016). Indeed, during snowfalls and rainfalls, we observed that ground squirrels spent less time foraging above-ground, but rather increased the time spent in their burrows. The few observations we made of ground squirrels briefly emerging from their burrows during the rainy/snowy periods showed that their fur was dry (AT, CS, VAV, *personal observations*), confirming that burrows were indeed efficient shelters against the elements.

Due to reduced foraging, energy intake during inclement weather periods was necessarily reduced as well. In our study, the costs of missed foraging opportunities might have been somewhat higher for males than females. We found that older males, but not females, tended to compensate and forage more just after the snow melt in 2022. Similarly, the activity of older males, which exhibited a large activity range prior to the snowfall during the mating season, appeared to be restricted to smaller areas during and after the snow melt, spending more time foraging and potentially avoiding areas with remaining snow (Korslund and Steen, 2006; Stokes et al., 2001). In ground squirrels, the mating season is a period of intense territoriality and aggression for males (Manno and Dobson, 2008; Murie and Harris, 1988, 1978), which do not gain, but at best maintain their body mass through daily foraging activities (Raveh et al., 2010; see Michener and Locklear, 1990 for similar results on Richardson's ground squirrels). Thus, it would make sense that males have more at stake than females in terms of energy acquisition during this period, and that the costs of missed foraging opportunities may rapidly accumulate. For instance, during a prolonged period of snow cover (2 weeks) during the mating season in 1996, Neuhaus et al. (1999) found male survival and mass changes to be more strongly impacted than female survival. Yet, if there was some immediate cost to decreased foraging activity in the present study, this was not clear, at least in terms of changes in body mass. Individuals did not exhibit decreased body mass after inclement weather, and some of them even gained mass over the few days (yearlings and older females in 2022 snow event). Nor did individuals appear to gain less mass than usual when compared with past records of body mass gain at similar periods of the year, and when compared with results in the earlier study (males lost up to 96 g of mass between 30 April and 14 May 1996, Neuhaus et al., 1999).

Our hypothesis to explain the lack of effects of detrimental weather conditions on body mass is that the animals have generally adapted to cope with the fluctuating environments characteristic of their mountain habitat, and geared behavioral and physiological responses towards saving energy in times of hardship. Whereas changes in weather conditions have been found to induce increased HPA activity in various species (Bize et al., 2010; Krause et al., 2016; Wingfield and Kitaysky, 2002), we found the opposite: individuals emerging from their burrows following a period of inclement weather had lower (or similar) fecal cortisol metabolite levels as compared to before the weather event. Because FCM levels reflect circulating cortisol levels some 7 h before (Bosson et al., 2009), the glucocorticoid levels measured in our study would have coincided with the physiological status of the animals shortly after, rather than during, the respective periods of inclement weather. These results suggest a general hypo-responsiveness of the HPA axis which may have persisted shortly after storms had passed, quite possibly related to a general hypometabolic response aimed at saving energy during periods of inclement weather (see Haase et al., 2016 for cortisol – metabolic rate relationships in mammals). Whereas it would have been interesting to know whether such a hypometabolic response was even more pronounced during the inclement weather events, this was unfortunately impossible since ground squirrels were mostly sheltered below ground and could not be trapped.

To conclude, we were able to combine behavioral and physiological examinations to assess the effects of inclement weather on a species well-adapted to variable and unpredictable environments. Whereas our results suggest that these mountain rodents have adapted to life in a stochastic climatic environment, the question remains whether such events will increase in terms of frequency or duration in the future with climate change (*i.e.* real 'extreme weather events' opposed to inclement weather; McPhillips et al., 2018; Seneviratne et al., 2021; van de Pol et al., 2017). Past research (Neuhaus et al., 1999) shows that even these highly adapted animals may suffer in terms of reproduction or survival if periods of inclement weather last for more than a few days. If the amplitude of observed events in our study was high (high snow depth and high precipitation amount), their duration was average compared to past climate records. This corroborates the idea that animals have adapted to 'short' detrimental weather events without direct consequences on their stress levels or body condition, but consequences could well be different in the case of more frequent and prolonged storms (Harris et al., 2018; Morton and Sherman, 1978). If the frequency of weather events increases with global change, individuals might not be able to compensate, with negative consequences on survival and population viability (Neuhaus et al., 1999).

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data supporting this publication are available on Figshare: 10.6084/m9.figshare.24080688.

Acknowledgements

We are grateful to Edward A. Johnson and Steven Vamosi (Directors, Biogeosciences Institute, University of Calgary), Judy Mappin-Buchannan and Adrienne Cunnings (Managers, Kananaskis Field Stations), and Kathreen Ruckstuhl (faculty member responsible for the R.B. Miller Field Station) for housing and facilities during fieldwork. We are grateful to Alberta Parks, and Alberta Environment, Fish & Wildlife for granting us access to the study sites and support with the long-term research. We are particularly grateful to Edward A. Johnson and Kathreen Ruckstuhl for their continued support and friendship throughout the years. We are specifically indebted to Jan O. Murie for initiating the long-term research on Columbian ground squirrels and for his continued advice and friendship, and to David A. Boag for his earlier work on the species. We wish to thank two anonymous reviewers for insightful comments on a previous version of the paper. This research was supported by an Initiative d'Excellence (IDEX attractivité) research grant to C.S., a CNRS Projet International de Coopération Scientifique grant (PICS-07143) to V.A.V., a research grant from the Fondation Fyssen to V.A.V., a USA National Science Foundation grant (DEB-0089473) to F.S.D., and a fellowship grant from the Institute of Advanced Studies of the University of Strasbourg to F.S.D. and V.A.V. A. T. was supported by a PhD scholarship from the Ministère de l'Enseignement supérieur, de la Recherche et de l'Innovation. F.S.D. thanks the Région Grand Est and the Eurométropole de Strasbourg for the award of a Gutenberg Excellence Chair.

Credit authorship contribution statement

Anouch Tamian, Claire Saraux and Vincent A. Viblanc conceived the ideas and designed methodology; Anouch Tamian, Anna Neuhaus Ruckstuhl, Patience Emmanuel, Sylvia Pardonnet, Peter Neuhaus, F. Stephen Dobson, Dominique Filippi, Claire Saraux, and Vincent A. Viblanc collected the data; Anouch Tamian, Phoebe D. Edwards, and Rudy Boonstra did the lab work. Rupert Palme provided antibodies and expertise on FCM measurements. Anouch Tamian analyzed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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