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1 **Weathering the storm: decreased activity and glucocorticoid levels in**
2 **response to inclement weather in breeding Columbian ground squirrels**

3
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21 Highlights

- 22 • Columbian ground squirrels are montane rodents that occupy habitats in rapidly
23 changing environments.
- 24 • Activity, foraging, and space utilization decreased during inclement weather during
25 the breeding season.
- 26 • Fecal cortisol metabolite levels were lower after inclement weather than during
27 control periods.
- 28 • Body mass and body mass gain were not affected by days of inclement weather.
- 29 • These ground squirrels appeared well adapted to inclement weather.

30

31 Abstract

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

50 **Keywords:** Behavioural shifts, energy mobilization, extreme climate events, hibernating
51 sciurid, HPA activity, precipitation-modified behavior, weather-induced stress responses

52

53 Introduction

54 With global change, the frequency of extreme weather events is increasing along with
55 their effects on organisms, which are predicted to continue increasing in the future (Quante et
56 al., 2021; Seneviratne et al., 2021; van de Pol et al., 2017). Such events can induce marked
57 changes in animal phenology, physiology, and behavior, consequently affecting survival and
58 breeding success (Krause et al., 2016; Kucheravy et al., 2021; van de Pol et al., 2017). Even for
59 animals adapted to harsh climate conditions, the occurrence of extreme heat, long freezing
60 events, or heavy precipitation can threaten individual survival and reproductive success, and as
61 a result population dynamics (see Frederiksen et al., 2008; Ropert-Coudert et al., 2015;
62 Wingfield et al., 2017 in birds). Energy regulation is a key factor in animal life histories (Brown
63 et al., 2004). Energy acquisition and expenditure can be strongly influenced by weather
64 conditions either via effects on foraging resources (modifications of resource availability and
65 acquisition; Allison and Conway, 2022) or via effects on animal behavior (*e.g.* foraging
66 behavior) and metabolism (*e.g.* thermoregulation) (Levy et al., 2019; Schweiger and Frey,
67 2021).

68 From a climatology perspective, extreme weather events may be characterized as
69 unusual weather events, that contribute to climate variability, that are at the extremes of
70 historical records in a given place (*e.g.* heat and cold waves, heavy rainfalls, and snow storms,
71 Matthews et al., 2021). Another perspective defines extreme weather events from a biological
72 point of view, an event being considered as extreme when it significantly impacts individuals,
73 populations, or ecosystem functions (Ummenhofer and Meehl, 2017; van de Pol et al., 2017).
74 Thus, from an animal's perspective, the extent to which events of inclement weather constitute
75 extremes, depends on their effects on the organism, especially on body condition and stress
76 physiology, and on whether and how animals cope with these environmental changes (Bize et
77 al., 2010; Krause et al., 2016; Wingfield et al., 2017). Assessing the extent to which various

78 species are able to cope (behaviorally and physiologically) with inclement weather conditions
79 is necessary for discerning the scope of plasticity that they might exhibit in the current context
80 of rapid global change (Harris et al., 2018; Ummenhofer and Meehl, 2017).

81 Assessing behavioral and physiological modifications to inclement weather should be
82 particularly relevant for animals inhabiting mountainous temperate ecosystems where
83 variations in thermal conditions are high, favorable living conditions are constrained temporally
84 (viz. to spring and summer months), and the occurrence and intensity of snowstorms and
85 rainfalls is projected to increase with ongoing climate change (Quante et al., 2021; Seneviratne
86 et al., 2021). Many species rely strongly on foraging conditions during the spring/summer
87 period to sustain their reproduction. This short temporal window is especially challenging for
88 hibernating species, that not only rely on energy income for reproduction, but also for
89 replenishing fat stores in anticipation of the following hibernation (Humphries et al., 2003).
90 Thus, resource acquisition and storage during the active period may have strong influences on
91 survival and reproductive success (Carrier et al., 2022; Murie and Boag, 1984; Zervanos et al.,
92 2014). Inclement weather that occurs during the short spring/summer period can have direct
93 consequences on the mortality of individuals (*e.g.* flooding; Golet et al., 2013, Viblanc et al.,
94 *personal observations*), or indirect consequences through food consumption, reflected in
95 reduced body mass (Lenihan and Vuren, 1996; Neuhaus et al., 1999). As an example, Belding's
96 ground squirrels survival, reproduction, and behavior was strongly impacted by a long spring
97 snowstorm inducing sharp mass loss, decreased reproduction, and increased mortality in the
98 population (Morton and Sherman, 1978). What remains unclear however, is how animals that
99 live in fluctuating environments react to inclement weather: their hormonal, physiological, and
100 behavioral responses (Wingfield et al., 2011).

101 When conditions are beyond those normally experienced, *e.g.* stressful weather events,
102 vertebrate behavior and physiology is modified through the hypothalamic-pituitary-adrenal axis

103 (HPA; Boonstra, 2004; Wingfield et al., 2011). Several studies showed that the activity of HPA
104 axis increases when conditions become more stressful, which can be measured in
105 glucocorticoids concentrations (hormonal mediators of allostasis that trigger a “stress
106 response”, Baker et al., 2013; Boonstra et al., 2020; King et al., 2023; McEwen and Wingfield,
107 2003; Romero and Wingfield, 2015; Walker et al., 2015). Even though the stress response
108 allows individuals to quickly respond to unpredictable stressful events and is considered
109 adaptive (Angelier and Wingfield, 2013; Boonstra et al., 2001; McEwen, 2019), long exposure
110 to stressful stimuli can also have deleterious effects on individuals and affect their long-term
111 survival (Boonstra et al., 1998; Romero, 2004; Sapolsky et al., 2000; Wingfield and Kitaysky,
112 2002).

113 Glucocorticoids are responsible for energy mobilization and fat and protein catabolism,
114 which can ultimately lead to changes in body condition (Angelier et al., 2007; Sapolsky et al.,
115 2000). In case of inclement weather and limited access to food, nutritional stress usually triggers
116 the HPA axis (Jenni-Eiermann et al., 2008; Pravosudov and Kitaysky, 2006) and the response
117 is reflected in increased circulating cortisol concentrations, an important glucocorticoid in
118 mammals (Haase et al., 2016; Vijayan et al., 2010; Zhang and Buck, 2022). In contrast, one
119 hypothesis would be that species adapted to unpredictable environments, such as mountainous
120 ones, could save energy by shutting down the HPA axis and decreasing energy mobilization.
121 This can be the case for hibernating species, which already rely on shelters (e.g. burrows, dens)
122 as part of their natural history, and seasonally limit their metabolism. One non-invasive way to
123 assess HPA activity is to examine fecal cortisol metabolites (FCMs, Gormally and Romero,
124 2020; Palme, 2019; Sheriff et al., 2011; Zhang and Buck, 2022).

125 We tested the hypothesis that animals inhabiting mountainous ecosystems have adapted
126 to cope with short periods of inclement weather. For this test, we studied Columbian ground
127 squirrel (*Uroditellus columbianus*), a model species that is regularly subjected to highly variable

128 and unpredictable weather conditions in its montane habitat (Zammuto and Millar 1985). To do
129 so, we examined the effect of inclement weather on activity patterns, foraging behavior,
130 glucocorticoid levels, and body mass of ground squirrels during two late snowfall events in
131 2021 and 2022 and one rainfall event in 2022. Specifically, we (1) tested whether these weather
132 events were considered as ‘extreme’ from a climatological point of view, (2) described
133 behavioral changes during inclement weather in 2022, (3) analyzed whether hormonal ‘stress’
134 levels or body mass changed after weather events compared to controls. Unlike several species
135 showing increased activity of the stress axis during periods of inclement weather (Bize et al.,
136 2010; Krause et al., 2016; Romero et al., 2000; Wingfield et al., 1983) or food deprivation
137 (Kitaysky et al., 2007, 1999), we predicted that in response to inclement weather, these
138 mountain rodents would adapt by weathering the storm, *i.e.*, saving energy by reducing their
139 overall activity and metabolism.

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

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

166 During their short active period, unfavorable weather conditions might be expected to
167 negatively impact above-ground ground squirrels activity and thus the time they spend foraging.
168 Rainfall and snow cover can render the animals wet, decreasing fur insulation, and inducing
169 high energy losses (Lovegrove, 2003; Webb and King, 1984). Additionally, vegetation is not
170 accessible when covered with snow (Korslund and Steen, 2006), and prolonged periods of snow
171 cover during the active season (*e.g.* 2 consecutive weeks of snow storm – more than half of the
172 mating season in normal years) are known to negatively affect male survival and female
173 breeding success (Neuhaus et al., 1999). However, for shorter spells of inclement weather, little
174 is known about how the animals adapt.

175

176 Materials & Methods

177 *Data collection*

178 The study was conducted during the 2021 and 2022 active seasons of Columbian ground
179 squirrels in the Sheep River Provincial Park in Alberta, Canada (50°38'N, 114°39'W, 1500-
180 1570m elevation), located in the foothills of the Rocky Mountains. The study area included
181 three meadows with different ground squirrel populations: meadow A (MA), meadow B (MB),
182 and meadow C (MC). Individuals were trapped (using live-traps National Live Traps;
183 Tomahawk Co., WI, USA: 13 x 13 x 40 cm³ baited with peanut butter) and permanently marked
184 as juveniles, or when they first appeared in the meadow as immigrant adults, with application
185 of unique metal numbered ear tags (Monel no. 1, National Band & Tag Co.). Sex was
186 determined based on visual inspection of genitalia (Murie & Harris, 1982). Each year, the
187 population was monitored daily from before the first emergences from hibernation (early April
188 each year) to the end of lactation for breeding females. At the first capture of the season, each
189 ground squirrel was given a unique individual black hair-dye mark (Clairol® Hydrience hair
190 dye N°52 Black Pearl, Clairol Inc., New York, USA) on their dorsal pelage for visual
191 identification in the field. At each capture, individuals were weighed to the nearest 5g using a
192 Pesola® spring-slide scale.

193 In 2021 and 2022, we checked the weather forecast for the Sheep River area (Alberta,
194 Canada) to anticipate possible periods of inclement weather occurring in our populations. We
195 were able to anticipate 2 periods of inclement weather, one late spring snow storm (in 2022)
196 and one period of summer rainfall in 2022. We target-trapped and weighed the animals, and
197 collected fecal samples just before (control) and after (treatment) these events occurred, i.e.,
198 typically the next day within 24h (average $6.8 \pm$ (SD) 5.9 hours, min = 0.25 hours, max = 22.9

199 hours) following the end of the period of weather deterioration (see Fig. 1). In 2021, we were
200 not able to anticipate a sudden snow storm, and were thus only able to acquire fecal samples
201 after the event occurred. Thus, we collected control samples roughly one week after the event
202 had passed. In 2021, animals were weighed and feces were collected just after a snow storm in
203 May (treatment, between 11:00am and 3:37pm on 22 May 2021), and around a week after this
204 event (control, between 10:43am on 27 May 2021 and 10:10am on 30 May 2021). In 2022,
205 animals were weighed and feces were collected just before a snow storm in May (control,
206 between 10:50am and 6:55pm on 6 May 2022), and just after (treatment, between 11:15am and
207 7:11pm on 11 May 2022), before a rain fall in June (control, between 09:54am on 11 June 2022
208 and 6:23pm on 12 June 2022, only on MB) and just after (treatment, between 11:01am and
209 7:02pm on 15 June 2022, only on MB). Given that FCM concentrations reflect circulating
210 glucocorticoid levels ca. 7 hours before sampling (Bosson et al., 2009), the fecal samples
211 collected thus reflected the activity of the stress axis immediately after (or towards the end of)
212 respective storms. On a few occasions, individuals were not weighed and the sample was not
213 considered in the further statistical analyses. We ensured that traps were clean before being
214 deployed, and fecal samples were collected within minutes of capture of animals. Fecal samples
215 were most often collected either directly into 2mL sterile vials as the female defecated or from
216 the floor of the trap. In this latter case, the female was always observed defecating in the trap
217 and the feces collected immediately. We insured no fecal sample was contaminated by urine
218 upon collection. Samples that were contaminated were systematically discarded. Fecal samples
219 were stored on ice packs in the field, transferred to a -20°C freezer within the following hours
220 of sampling, and at the end of the 2022 field season, all samples were transported on dry ice to
221 the University of Toronto and analyzed during summer 2022. Overall, we acquired 547 fecal
222 samples for 272 individuals of known age, but see Table 1 for details of the number of
223 observations per meadow and event.

224

225 ***Analysis of fecal cortisol metabolites (FCMs)***

226 Fecal cortisol metabolites were estimated as previously validated and described for
227 Columbian ground squirrels (Bosson et al., 2009). Briefly, lyophilized fecal samples were
228 frozen in liquid nitrogen, and pulverized with a small grinding pestle. We weighed $0.050 \pm$
229 0.005 g of the sample, recorded the exact weight, and vortexed it in 1ml of 80% methanol to
230 extract FCMs (30 min at 2500g). FCM amounts (in ng/g of dried feces) were determined using
231 a 5α -pregnane- 3β , 11β , 21 -triol- 20 -one enzyme immunoassay (EIA), which measures
232 metabolites with a 5α - 3β , 11β -diol structure (Touma et al., 2003). All samples were run in
233 duplicate (except 3 samples with one of the measures out of the range, and thus only the other
234 one was kept) on eighteen 96 well plates, showing a high repeatability ($R = 0.896$, $SE = 0.008$,
235 $CI = [0.878, 0.910]$, p -value < 0.001 , $n = 1251$ observations, using the *rpt* function from ‘rptR’
236 package). Pooled samples with low value (~60% binding) and high value (~30% binding) were
237 run on each plate as controls. Mean intra-assay coefficient of variation was 9.7%, and the mean
238 inter-assay coefficients of variation based on the pools were 12.42% (low pool) and 13.74%
239 (high pool).

240

241 ***Behavioral sampling & analyses***

242 *Behavioral observations*

243 From May 4th to 15th 2022 (*i.e.*, 5 days before, 2 days during and 5 days after the snow
244 event), behavioral observations were performed daily for two hours in the morning (from
245 8:30am for the earliest start until 11:40 am for the latest end) from the top of 3 high observation

246 towers (1 observer per tower, the allocated tower to an observer changing each day). Visual
247 scans of meadow B were performed every 15 minutes, recording the foraging versus other
248 behaviors of all individuals present, and estimate the proportion of foraging (main behavior of
249 Columbian ground squirrels, which represents 54% of their time on average, and between 38%
250 and 68% of their total time budget over the entire active season). Individuals were identified
251 from their back hair dye mark. Finally, the location of each individual was recorded along with
252 its behavior within 1-m on a 10 m x 10 m Cartesian grid system that covered the meadow with
253 color-flagged wire pins.

254 From these observations, we estimated 4 daily behavioral variables: the mean number
255 of observations per scan, the daily percentage of individuals seen above-ground (compared to
256 the actual number of individuals alive and emerged from hibernation on the meadow as of the
257 particular day), the percentage of time spent foraging compared to other behaviors, and finally
258 the mean total area used by each individual (in m²). For each individual, area use was estimated
259 from the minimum convex polygon of all observations on a given day (with *mcp* function from
260 ‘adehabitatHR’ package, with a minimum of five observations per individual).

261

262 *Above-ground activity from loggers*

263 From June 10th to June 16th 2022 (*i.e.*, 3 days before, 2 days during and 2 days after) we
264 equipped 16 individuals (4 yearlings, 6 older females, and 6 older males) at MB with bio-
265 logging collars that were specifically designed for the ground squirrels. The collars were fitted
266 with a light sensor, microcontroller and internal memory chip. The collars recorded to
267 continuous recording of the presence of light from three red, blue, green (RGB) channels that
268 were summed and combined *in-situ* into a binary variable 1 (light detected) / 0 (no light) every
269 2 seconds (Mamtag collars, Sextant Technology Ltd., Marton, New Zealand). Thus, we were

270 able to continuously determine if animals were present above ground (light =1) or remained
271 below in their burrow systems (light = 0). From these data, we were able to determine above-
272 ground activity of the equipped animals between 8am and 6pm. Between these hours, we
273 calculated the hourly proportion of time spent out of the burrow. The duration of data logging
274 varied among animals depending on logger-battery life and our success at recapturing the
275 animals. In total, we collected 1,516,780 records, *i.e.*, 13,543 records on average per day per
276 individual over a period of 7 days.

277

278 ***Characterization of weather events***

279 *Observed snow & rain events*

280 To quantify snow and rain events, we used several climate sources. Local rainfall (in
281 2022) was recorded at a local weather station (Davis, Vantage Pro2) that was installed on
282 meadow B. However, because the weather station did not record snow, we relied on another
283 weather station situated in Pekisko (closest available data, located 32-m south of the study site,
284 50°22'N, 114°25'W, 1341m elevation, data provided by Agriculture and Irrigation, Alberta
285 Climate Information Service, ACIS, <https://acis.alberta.ca/>) to assess snow. In 2022, to obtain
286 more detailed local data, we combined records from this weather station with 4 camera traps
287 (photos taken every 30 min) installed on meadow B. The cameras faced wooden poles that were
288 graduated every 5cm, which provided continuous records of snow depth at various locations on
289 the meadow.

290 In 2021, it snowed up to 15 cm between the 19-20th of May. Snow remained on the
291 ground until the 22nd of May. In 2022, it snowed during the night between 8th and 9th May up
292 to 38 cm, and the snow melted on the 11th of May. It rained continuously on the 13th and 14th

293 of June 2022 (up to 9.8 mm/hour, 110 mm in total over the two days). Because weather events
294 could not be controlled and happened at different biological periods in the season (*i.e.*, during
295 the mating season for earlier events *vs.* during lactation for later events), further analyses on
296 biological measures and samples were conducted separately for each weather event (Snow
297 2021, Snow 2022, Rain 2022).

298

299 *Extreme events? Assessment of long-term trends*

300 We tested whether the observed events could be characterized as ‘extreme’ from a
301 climatological perspective, compared to the past climate in the study area. To access past and
302 long-term local weather conditions, we used the Kearney et al. (2020) microclimate model to
303 estimate past snow events on the studied meadow. The modelling function (*micro_ncep* from
304 ‘NicheMapR’ package; Kearney et al., 2020) downscales global atmospheric climate-forcing
305 data using terrain-specific corrections, including spatial variations in slopes, soil composition
306 and hydrological properties, orientation, and hill shade (NCEP Reanalysis, historical data from
307 the National Center for Environmental Predictions, provided by the NOAA/OAR/ESRL PSL,
308 Boulder, CO, USA, from their website at <https://psl.noaa.gov/>). Because local precipitation
309 events (from a weather station situated in Sheep River Provincial Park from 2009, 50°39’N,
310 114°37’W, 1525m elevation, data provided by Agriculture and Irrigation, Alberta Climate
311 Information Service, ACIS, <https://acis.alberta.ca/>) were available starting in 2009 and used as
312 input in the model to increase accuracy, the model was run from 2009 to 2022. The
313 microclimate model, combined with local precipitation data, increases the resolution of large-
314 scale weather data and has been empirically validated (Kearney et al., 2020; Lembrechts and
315 Lenoir, 2020; Maclean, 2020; Saleeba et al., 2020; Tamian et al., 2022). We estimated hourly

316 climate conditions at 4 different points on meadow B, estimating the snowfalls and snow depth
317 on the ground (in centimeters).

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

324

325 *Statistical analyses*

326 All data analyses and statistical procedures were conducted using R version 4.0.3 (2020-
327 10-10). Although we report statistical tests at a probability error threshold of 5%, results are
328 discussed with regards to biological effect sizes rather than threshold p-values, which is more
329 meaningful (Halsey et al., 2015; Nakagawa and Cuthill, 2007), especially considering
330 ecological results. Results presented are means \pm SE, along with the number of observations
331 (n). Where appropriate (i.e. for linear models), we ensured that model residuals were normally
332 distributed by visual inspection of density distributions, Q-Q plots, cumulative distribution
333 functions, and P-P plots using the ‘fitdistrplus’ package in R (Delignette-Muller and Dutang,
334 2015).

335

336 *Age & sex considerations*

337 Because the sampled animals differed in terms of sex and reproductive characteristics,
338 we examined separately reproductive males and reproductive females (mature individuals), and

339 one-year-old individuals, usually non-reproductive (immature individuals), resulting in three
340 sex/age categories: ‘Yearlings’, ‘2+ Females’, and ‘2+ Males’.

341

342 *Weather effects on physiology (FCMs & body mass)*

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

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

359 Because individuals were expected to fatten-up during their short activity period, we
360 further examined whether the weather events impacted their mass gain. During the 2022 active
361 season, we weighed individuals on Meadow B (several individuals of each individual category
362 every week) and calculated the average weekly mass when trapped (yearlings: $n = 348$ captures

363 and 39 individuals in total, 2+ females: n = 456 captures and 39 individuals, 2+ males: n = 299
364 captures and 19 individuals). We then compared these patterns to patterns in mean weekly body
365 mass from the long-term monitoring of the same population (same trapping and weighing
366 methods as described previously). This represented 2067 captures of yearlings (n = 664
367 individuals), 5487 captures of 2+ females (n = 320 individuals), and 1481 captures of 2+ males
368 (n = 186 individuals) spanning 24 years (1994, 1999-2021).

369

370 *Ethics statement*

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

375

376 Results

377 *Long-term trends in weather events*

378 Based on the microclimate model, during the 2009-2022 period, the meadows
379 experienced an average of 7.1 ± 0.4 snowfall events during the active periods of the ground
380 squirrels. There was important interannual variability in the number of events, their duration
381 and the snow depth, with lowest values recorded in 2016 (only a couple of very short events)
382 and an increasing trend since (Fig. 2.A, C, G). These snow events usually lasted 12.3 ± 1.5
383 hours and spread from only a few millimeters up to 13 cm (Fig. 2.C, H). Compared to all other
384 weather events, the two snow events studied here lasted an average duration, but the amount of

385 snow on the ground was quite different between the two, with a moderate event in 2021 (4.5
386 cm vs 4.1 cm on average) and a large one in 2022 (6.8 cm vs 4.1 cm on average, above the 90th
387 percentile) (Fig. 2.H).

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

396

397 ***Behavioral responses to weather event***

398 During the May 2022 snow event, the total number of observations per scan and the
399 percentage of individuals seen above ground dropped drastically after the snowfall (when the
400 meadow was snow-covered), on May 9th (from 49 observations per scan on average to 2
401 observations per scan, and from more than 92% of individuals seen on average to 7%) (Fig. 3.A
402 and 3.B). The percentage of time spent foraging by those active above ground was less than
403 20% on May 9th, coincident with the low number of observations (Fig. 3.C). In comparison,
404 before the snow event (between May 4th and 8th), yearlings spent $63 \pm 1\%$ of their time foraging,
405 2+ females $56 \pm 2\%$, and 2+ males $32 \pm 2\%$. However, after snow had melted (between May
406 11th and 15th), males foraged 88% more than they did before, but females and yearlings did not
407 (LMs, males: $p < 0.001$, $t = 11.44$, females: $p = 0.82$, $t = 0.236$, yearlings: $p = 0.103$, $t = 1.871$,
408 $n = 9$ observation sessions for all). Finally, we were not able to calculate the area used by

409 individuals on May 9th because of too few observations of animals being active. However, older
410 males and females covered a 53% and 31% larger area before the snowfall (males: $858 \pm 127\text{m}^2$,
411 females: $278 \pm 35\text{m}^2$) than after (LMMs, males: $403 \pm 54\text{m}^2$, $p = 0.001$, $t = -3.273$, $n = 91$
412 observations, females: $192 \pm 24\text{m}^2$, $p = 0.056$, $t = -1.922$, $n = 202$ observations, Fig. 3.D). The
413 area used by yearlings did not seem to change before and after the snowfall ($209 \pm 34\text{m}^2$ before
414 and $197 \pm 30\text{m}^2$ after, $p = 0.776$, $t = -0.286$, $n = 135$ observations).

415 During the rainfall in June 2022, the above-ground activity during the day (8am-6pm)
416 decreased significantly for all sex/age categories (LMs, yearlings: $p < 0.001$, $t = -583.2$,
417 females: $p < 0.001$, $t = -474.1$, males: $p < 0.001$, $t = -805.7$, Fig. 4). Indeed, between June 10th-
418 12th, yearlings, 2+ females, and 2+ males spent $82 \pm 0.09\%$, $67 \pm 0.09\%$, and $88 \pm 0.06\%$ of
419 their time outside of their burrow respectively, compared to $11 \pm 0.07\%$, $14 \pm 0.07\%$, and $11 \pm$
420 0.07% during the rainfall (June 13th and 14th). After the rainfall, the above-ground activity
421 increased to similar levels to 75%, 67%, and 82% of their time outside of their burrow
422 respectively.

423

424 *Physiological responses to weather events*

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

429 In the context of the snow event of 2021, there was no difference in FCM levels between
430 the control (a week after the weather event, Fig. 5.A in red) and the treatment (just after the
431 event, Fig. 5.A in blue, $p = 0.067$, $t = -1.845$, $n = 264$ observations). When examining changes

432 in mass, weather effects differed depending on the sex/age category (LMM, $\Delta\text{AIC} = 6.9$).
433 Whereas yearlings and older males tended to be 5% and 8% heavier a week after the snow event
434 respectively, than just after the event (yearlings: $28 \pm 6\text{g}$ heavier, $p < 0.001$, $t = 4.890$, $n = 96$
435 observations, 2+ males: $30 \pm 13\text{g}$ heavier, $p = 0.036$, $t = 2.314$, $n = 47$ observations), body mass
436 of older females did not change (0.4% difference, $-13 \pm 11\text{g}$, $p = 0.249$, $t = -1.161$, $n = 121$
437 observations, Fig. 5.B). Because the control was sampled 1 week after the treatment,
438 conclusions cannot be drawn easily as the mass changes could simply reflect the usual mass
439 gain of individuals at this time of the season (see typical mass gain between week 20 and 21 on
440 the blue line, Figure 6).

441 For the snow event in 2022, the weather effects on FCM levels and body mass depended
442 on the sex/age category (LMMs, FCM: $\Delta\text{AIC} = 8$, mass: $\Delta\text{AIC} = 3.9$). All individuals had lower
443 FCM levels after the snow fall than before but the effect was stronger in adult males: 48% lower
444 FCM levels after the event for older males versus 43% and 34% lower FCM levels for older
445 females and yearlings, respectively (yearlings: $-162 \pm 40\text{ ng/g}$, $p < 0.001$, $t = -4.075$, $n = 60$
446 observations, 2+ females: $-163 \pm 33\text{ ng/g}$, $p < 0.001$, $t = -5.003$, $n = 100$ observations, 2+ males:
447 $-426 \pm 138\text{ ng/g}$, $p = 0.004$, $t = -3.093$, $n = 44$ observations, Fig. 5.C). Whereas the body mass
448 of adult males did not change ($p = 0.856$, $t = 0.184$, $n = 44$ observations, Fig. 5.D), yearlings
449 and older females had 3% higher body mass after the event than before (yearlings: $14 \pm 4\text{ g}$, p
450 $= 0.002$, $t = 3.620$, $n = 60$ observations, 2+ females: $17 \pm 6\text{ g}$, $p = 0.008$, $t = 2.809$, $n = 100$
451 observations).

452 For the rain event in 2022 on MB individuals, the weather effects on FCM levels and
453 body mass again depended on the sex/age category (LMMs, FCM: $\Delta\text{AIC} = 3.5$, mass: $\Delta\text{AIC} =$
454 8.7). Only yearlings had statistically significant lower FCM levels after the rainfall than before
455 (27% lower, $-155 \pm 60\text{ ng/g}$, $p = 0.017$, $t = -2.606$, $n = 33$ observations, Fig. 5.E), but older
456 females had lower FCM levels that approached significance (2+ females: 17% lower, $-48 \pm$

457 22 ng/g, $p = 0.077$, $t = -2.196$, $n = 28$ observations, 2+ males: $p = 0.972$, $t = -0.036$, $n = 18$
458 observations). In terms of body mass, there were no significant changes before and after the
459 weather event for any sex/age category (yearlings: 33 ± 21 g, $p = 0.136$, $t = 1.532$, $n = 33$
460 observations, 2+ females: -28 ± 22 g, $p = 0.220$, $t = -1.255$, $n = 28$ observations, 2+ males: -24
461 ± 13 g, $p = 0.090$, $t = -1.808$, $n = 18$ observations, Fig. 5.F).

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

471

472 Discussion

473 We examined the effects of periods of inclement weather on the behavior, mass change,
474 and physiology of Columbian ground squirrels, a species inhabiting mountain regions with
475 pronounced weather variation (Zammuto and Millar, 1985). Consistent with our predictions,
476 we found that behavioral activity and foraging decreased during events of inclement weather,
477 and that following these events FCM decreased in most individuals, or did not change, likely
478 reflecting an overall decrease in metabolic activity and metabolic rate (Haase et al., 2016), and
479 lower use of stored energy resources (*i.e.* carbohydrates and fat). Thus, inclement weather and
480 decreased behavioral activity did not strongly impact the body mass of individuals, despite

481 expected decreases in activity and foraging during the weather events. Taken together, these
482 results confirm the hypothesis that these mountain rodents have evolved to cope with short
483 periods of inclement weather both through behavioral and metabolic adaptations.

484 For small mammals, high precipitation and high humidity in the environment, combined
485 with low temperatures, can impose substantial thermoregulatory energy losses by decreasing
486 body insulation through wet fur (Lovegrove, 2003; McCafferty et al., 2017; Webb and King,
487 1984). A way for animals to minimize such costs is to modify behavior (Levy et al., 2019;
488 Williams et al., 2016). Indeed, during snowfalls and rainfalls, we observed that ground squirrels
489 spent less time foraging in the above-ground habitat, but rather increased the time spent in their
490 burrows. The few observations we made of ground squirrels briefly emerging from their
491 burrows during the rainy/snowy periods showed that their fur was dry (AT, CS, VAV, personal
492 observations), suggesting that burrows were indeed efficient shelters against the elements.

493 Due to reduced foraging, energy intake during inclement weather periods was
494 necessarily reduced as well. In our study, the costs of missed foraging opportunities might have
495 been somewhat higher for males than females. We found that older males, but not females,
496 tended to compensate and forage more just after the snow melt in 2022. Similarly, the activity
497 of older males, which exhibited a large activity range prior to the snowfall during the mating
498 season, appeared to be restricted to smaller areas during and after the snow melt, spending more
499 time foraging and potentially avoiding areas with remaining snow (Korslund and Steen, 2006;
500 Stokes et al., 2001). In ground squirrels, the mating season is a period of intense territoriality
501 and aggression for males (Manno and Dobson, 2008; Murie and Harris, 1988, 1978), which do
502 not gain, and at best maintain their body mass through daily foraging activities (Raveh et al.,
503 2010; see Michener and Locklear, 1990 for similar results on Richardson's ground squirrels).
504 Thus, it would make sense that males have more at stake than females in terms of energy
505 acquisition during this period, and that the costs of missed foraging opportunities may rapidly

506 accumulate. For instance, during a prolonged period of snow cover (2 weeks) during the mating
507 season in 1996, Neuhaus et al. (1999) found male survival and mass changes to be more strongly
508 impacted than female survival. Yet, if there was some immediate cost to decreased foraging
509 activity in the present study, this was not clear, at least in terms of changes in body mass.
510 Individuals did not exhibit decreased body mass after inclement weather, and some of them
511 even gained mass over the few days (yearlings and older females in 2022 snow event).Nor did
512 individuals appear to gain less mass than usual when compared with past records of body mass
513 gain at similar periods of the year, and when compared with results in the earlier study (males
514 lost up to 96g of mass between 30 April and 14 May 1996, Neuhaus et al., 1999).

515 Our hypothesis to explain the lack of effects of detrimental weather conditions on body
516 mass is that the animals have generally adapted to cope with the fluctuating environments
517 characteristic of their mountain habitat, and geared behavioral and physiological responses
518 towards saving energy in times of hardship. Whereas changes in weather conditions have been
519 found to induce increased HPA activity and stress levels in various species (Bize et al., 2010;
520 Krause et al., 2016; Wingfield and Kitaysky, 2002), we found the opposite: individuals
521 emerging from their burrows following the period of inclement weather had lower (or similar)
522 fecal cortisol metabolite levels as compared to before the weather event. Because FCM levels
523 reflect circulating cortisol levels some 7 hours before (Bosson et al., 2009), the glucocorticoid
524 levels measured in our study would have coincided with the physiological status of the animals
525 shortly after, rather than during, the respective periods of inclement weather. These results
526 suggest a general hypo-responsiveness of the HPA axis which may have persisted shortly after
527 storms had passed, quite possibly related to a general hypometabolic response aimed at saving
528 energy during periods of inclement weather (see Haase et al., 2016 for cortisol – metabolic rate
529 relationships in mammals). Whereas it would have been interesting to know whether such a
530 hypometabolic response was even more pronounced during the inclement weather events, this

531 was unfortunately impossible since ground squirrels were mostly sheltered below ground and
532 could not be trapped.

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

549

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567

568 Conflict of Interest

569 The authors declare no conflict of interest.

570 Author Contributions

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

578

579 Data Availability Statement

580 Data supporting this publication will be made available on Figshare upon acceptance of the
581 paper.

582

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854 Table and figure captions

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

858 **Figure 1.** The density of fecal sampling times and dates compare to snow and rain events are
859 presented for each weather event (grey filled area, snow depth in 2021 and 2022, and rain in
860 2022).

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

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

875 **Figure 4.** Hourly percentage of time spent out of the burrow, or diurnal above-ground activity
876 of all individuals during the period of the rain event in 2022. The above-ground activity

877 decreased during hours and days with rain (13th and 14th of June 2022, strong precipitation
878 presented in grey in background).

879 **Figure 5.** Fecal cortisol metabolite concentrations (FCM, left) and mass (right) comparisons
880 between the control (orange) and after the climatic event (light blue), for each climatic event
881 (A and B: snow in 2021, C and D: snow in 2022; E and F: rain in 2022) and for each sex/age
882 category (yearlings, older females, older males).

883 **Figure 6.** Comparison between theoretical (blue, calculated from other years) and observed
884 (red, in 2022) weekly body mass (given in weeks since 1 January; week 15 = beginning of
885 April, week 30 = end of July) during the active season of ground squirrels for each individual
886 category (yearlings, older females, older males). The mean body mass (in g) along with standard
887 errors is plotted for each week during active season. The vertical dashed lines represent the
888 occurrence and duration of 2022 weather events (snow and rain).

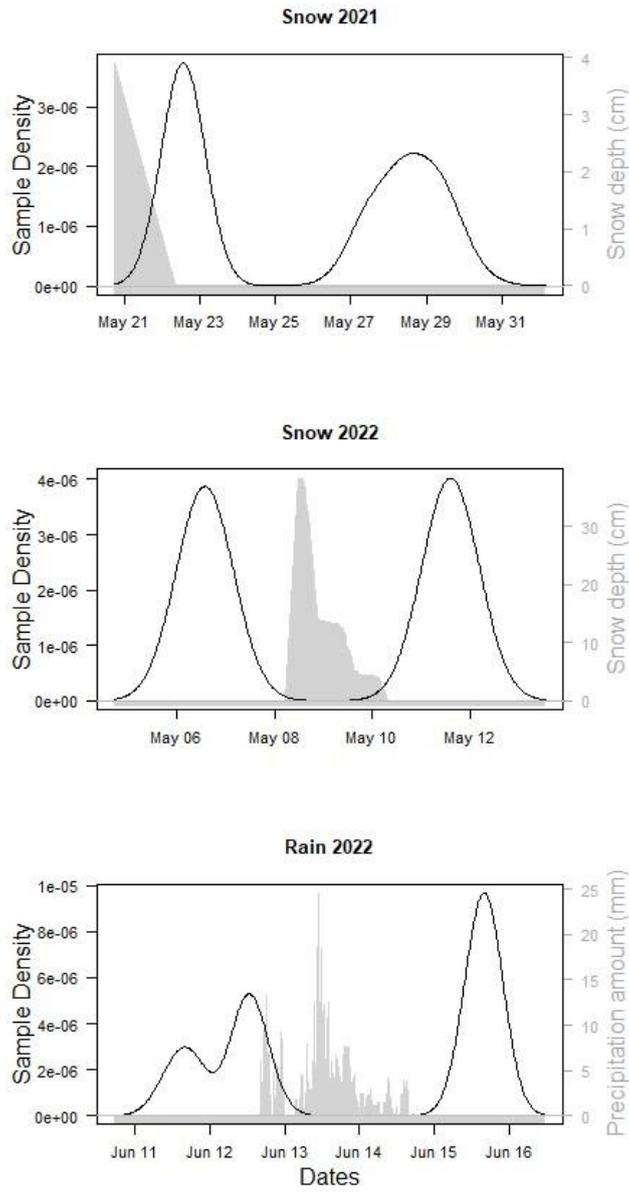
889

890 Table 1.

		Yearlings	2+ Males	2+ Females
Snow 2021 <i>(MA, MB, MC)</i>	<i>Control</i>	58	24	58
	<i>After weather event</i>	38	23	63
Snow 2022 <i>(MA, MB, MC)</i>	<i>Control</i>	27	20	53
	<i>After weather event</i>	33	24	47
Rain 2022 <i>(MB)</i>	<i>Control</i>	16	9	12
	<i>After weather event</i>	17	9	16

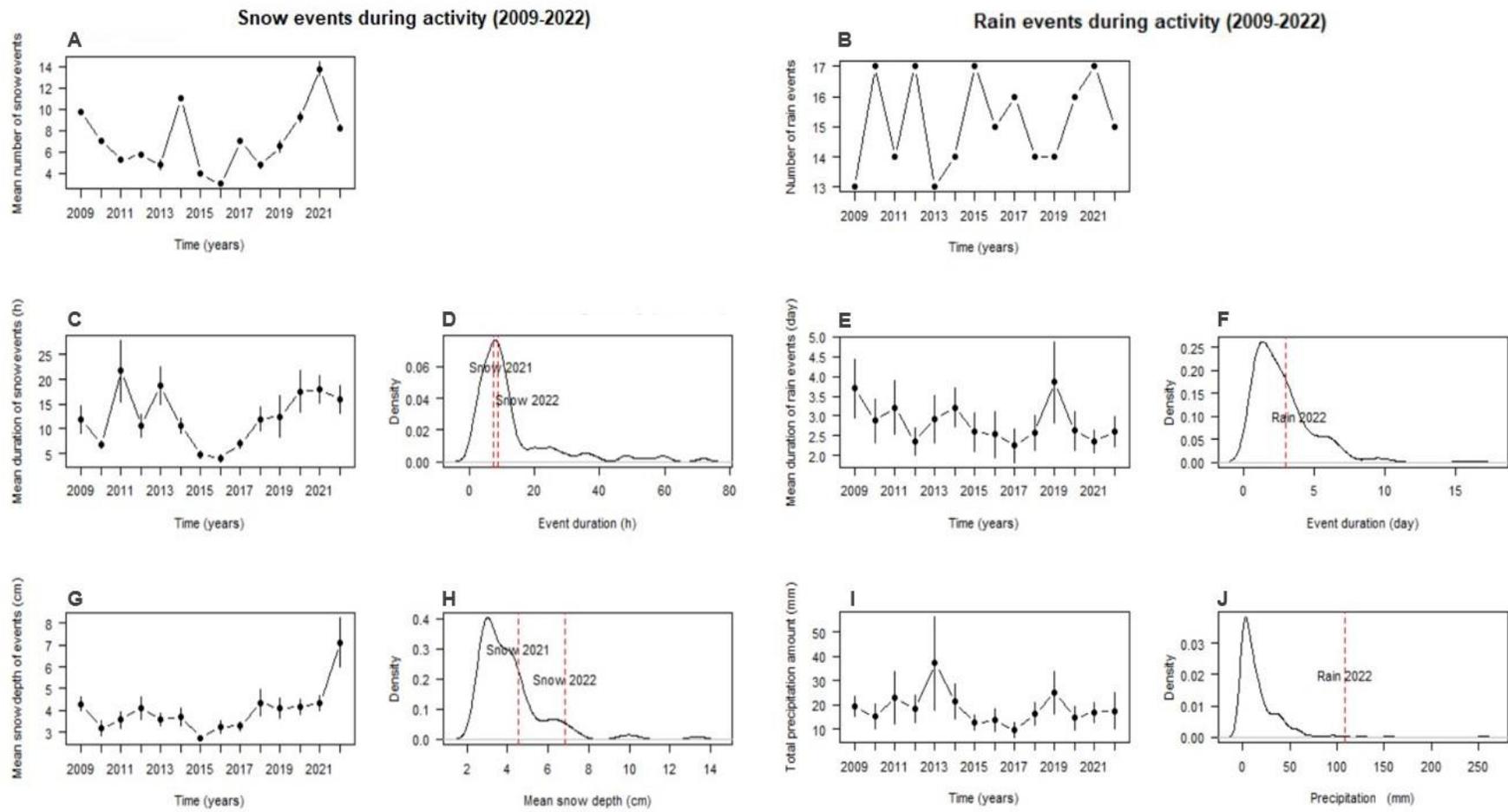
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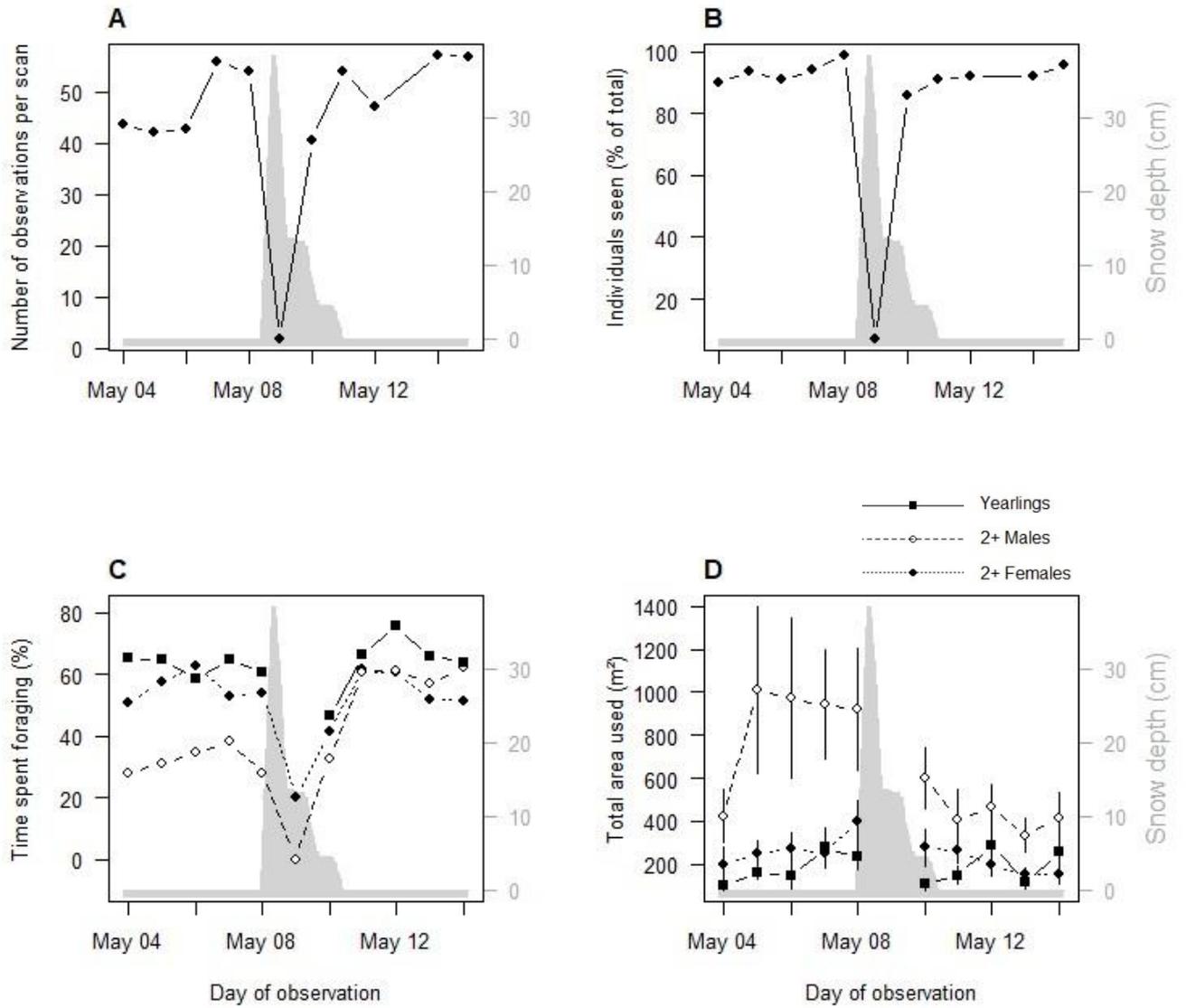
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894 Figure 1.



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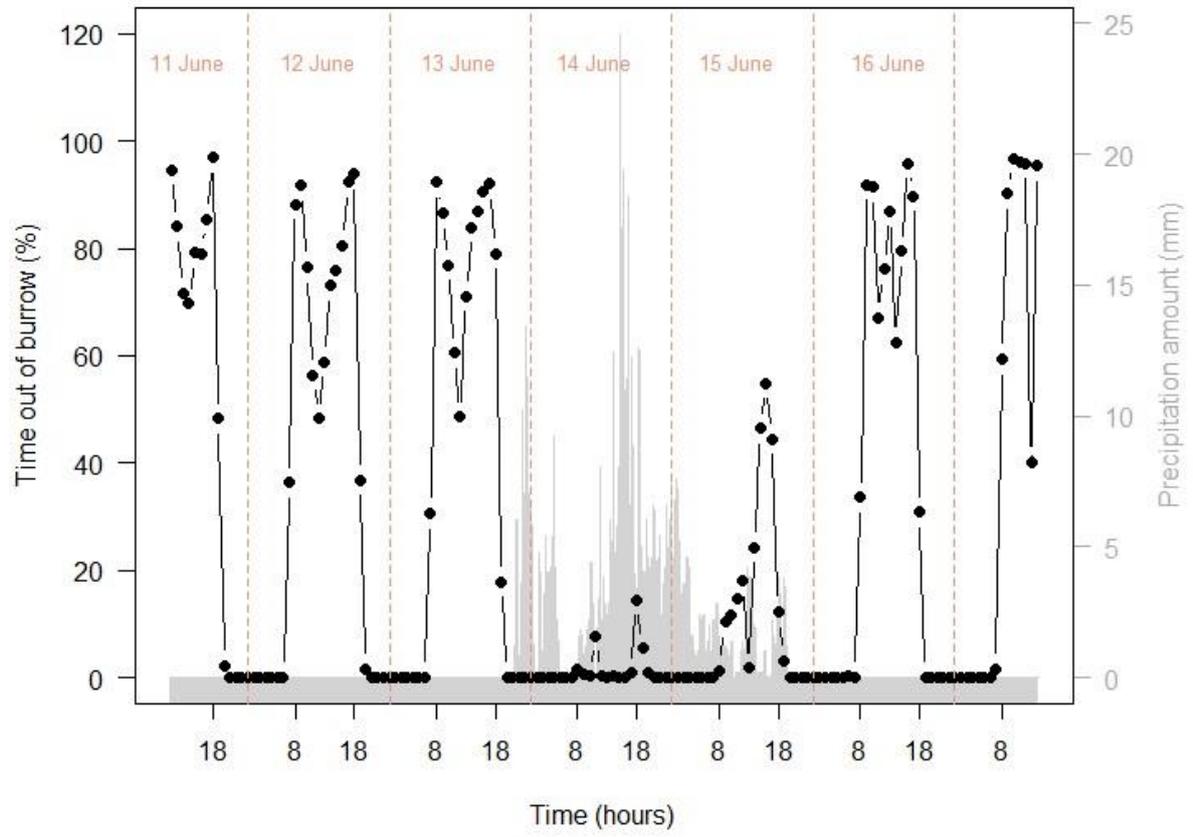
896 Figure 2.



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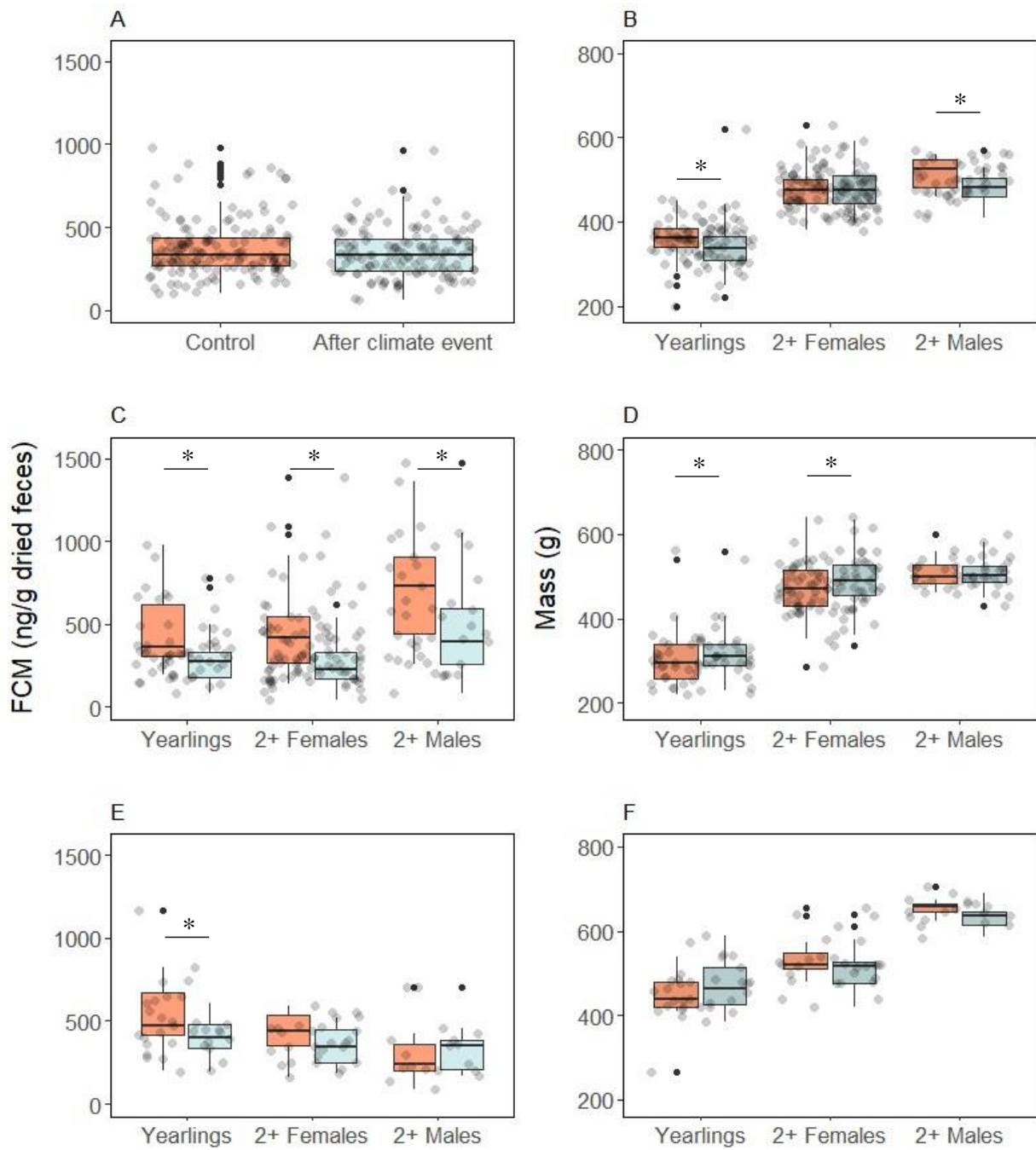
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899 Figure 3.



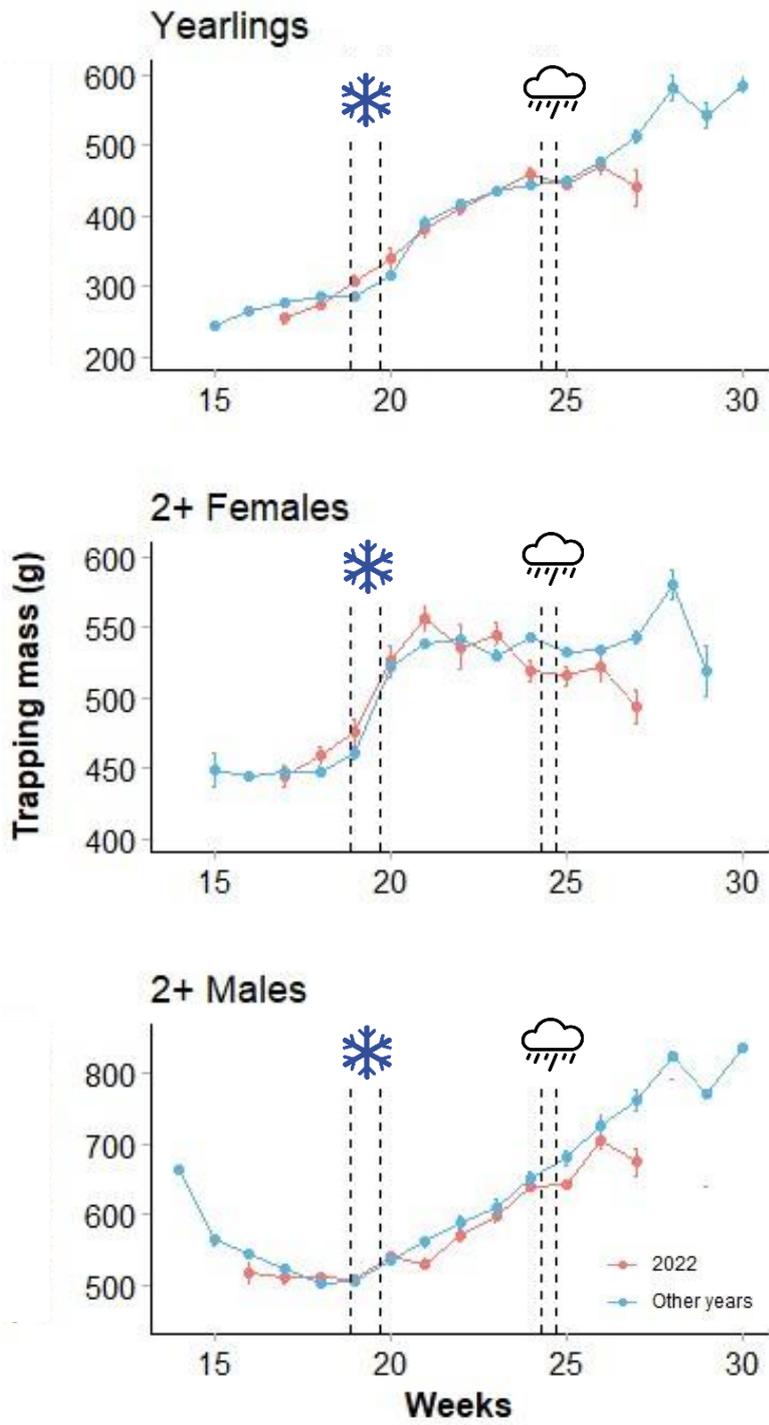
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901 Figure 4.



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903 Figure 5.



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905 Figure 6.