

# Climatic variation and risk assessment in a highly seasonal mammal

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## Abstract

Climate change and its resulting effects on seasonality are known to alter a variety of animal behaviors including those related to foraging, phenology, and migration. Although many studies focus on the impacts of phenological changes on physiology or fitness enhancing behaviors, fewer have investigated the relationship between variation in weather and phenology on risk assessment. Fleeing from predators is an economic decision that incurs costs and benefits. As environmental conditions change, animals may face additional stressors that affect their decision to flee and influence their ability to effectively assess risk. Flight initiation distance (FID)—the distance at which animals move away from threats—is often used to study risk assessment. FID varies due to both internal and external biotic and physical factors as well as anthropogenic activities. We asked whether variation in weather and phenology is associated with risk-taking in a population of yellow-bellied marmots (*Marmota flaviventris*). As the air temperature increased marmots tolerated closer approaches, suggesting that they either perceived less risk or that their response to a threat was thermally compromised. The effect of temperature was relatively small and was largely dependent upon having a larger range in the full data set that permitted us to detect it. We found no effects of either the date that snow disappeared or July precipitation on marmot FID. As global temperatures continue to rise, rainfall varies more and drought becomes more common, understanding climate-related changes in how animals assess risk should be used to inform population viability models.

**Key words:** climate change, flight initiation distance, phenology, temperature, yellow-bellied marmots.

One of the greatest threats to plant and animal populations today is a rapidly changing climate and the environmental changes that follow. The Intergovernmental Panel on Climate Change predicts drastic changes to biodiversity levels, phenology, seasonality, and snow cover even with global warming limited to 1.5 °C (IPCC 2023). Human-driven climate change is responsible for a variety of negative environmental effects not limited to extreme heatwaves (Coumou and Rahmstorf 2012), drought (Cook et al. 2018), and severe winter weather (Cohen et al. 2021). Such changes put many populations at risk, especially those in high-elevation regions with highly seasonal life histories. Climate change modifies selection pressures to which a species' response depends on both its phenotypic plasticity and its genetic variation (Roff 2002). Already, climate change is known to affect life history traits in a variety of animals including mammals (Wells et al. 2022), birds (Both and Visser 2005; Dunn and Møller 2019), fishes (Jensen et al. 2008), insects (Gomi et al. 2007), and reptiles (Le Galliard 2012).

For animals, escaping from a predator is an economic decision. Optimal escape theory predicts that animals will not flee an area with resources until the cost of staying outweighs the cost of fleeing (Ydenberg and Dill 1986). Prey animals face risks and costs simultaneously and must adjust their risk assessment and escape behavior to reflect this tradeoff

(Cooper 2003; Lagos et al. 2009; Díaz and Møller 2023). Risk assessment extends beyond simply deciding whether to stay or flee in the presence of a predator. Prey animals must also determine at which speed they will flee, where they will flee to, how far they will flee, whether they will enter a refuge, and what path they will take to reach that refuge (Cooper 2003). There are a variety of factors that influence risk assessment (Stankowich and Blumstein 2005). The chance of immediate survival during an encounter with a predator is increased by fleeing, but there is an associated cost of reducing foraging opportunities. However, by not fleeing, and subsequently being preyed upon, prey sacrifice their future fitness (Cooper 2015).

Antipredator behavior is a key life history trait for which we have not developed a comprehensive understanding of how it covaries with weather and seasonality. There are reasons to believe that weather and seasonality should affect risk assessment. Associations between antipredator behavior and environmental changes have been found in birds. In a study of over 200 species of European birds, Diaz et al. (2021) showed that FID decreased with increases in precipitation and temperature which they attributed to diminished foraging success. In reptiles, body temperature has been shown to profoundly affect an individual's flight behavior with higher body temperature being correlated with a higher

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likelihood to flee (Hertz, Huey, Nevo 1982). Ambient temperature also has significant effects on antipredator behavior with studies involving snakes demonstrating a positive correlation between temperature and aggression (Schieffelin and De Queiroz 1991). Additionally, high ambient temperatures drive mid-sized African mammalian herbivores to experience heat stress while foraging because they must forage during the day to avoid their nocturnal predators (Veldhuis et al. 2020).

Flight initiation distance (FID)—the distance at which an animal initiates flight from an approaching threat—is a common metric used to study escape behavior. A variety of internal and morphological factors such as pregnancy status (Braña, 1993), coloration (Møller, Liang and Samia 2019), and body size (Møller, 2015) affect FID. As climate conditions change more drastically, escape behavior is likely to be influenced by both environmental stressors as well as animals' internal physiological responses to those environmental stressors. Indeed, as noted above, Díaz et al. (2021) found that European birds tolerated closer approaches as the temperature increased, and time of day effects reported in studies of tropical birds' FIDs may be a function of temperature (Ekanayake et al. 2022).

Yellow-bellied marmots (*Marmota flaviventris*; hereafter, "marmots") make an excellent study system to investigate the relationship between variation in seasonality and FID. Marmots have a highly seasonal life history with mortality in the summer primarily attributed to predation (Van Vuren 2001) and mortality in the winter associated with starvation during hibernation (Armitage 2014). Their summer active season is characterized by reproduction and foraging to gain mass for the winter hibernation period (Cordes et al. 2020). In species that live in regions with harsh winters, hibernation is key to survival. Individuals use this period to save energy and avoid predation although environmental conditions are unfavorable. During hibernation, marmots rely exclusively on fat stores accumulated in the summer to survive (Geiser 2013). Previous studies have demonstrated that earlier emergence from hibernation is resulting in longer growing seasons for pups, and marmots are entering hibernation with larger body masses (Ozgul et al. 2010). Additionally, yellow-bellied marmots live in high-elevation regions that have been demonstrably changing because of climate change (Beniston, Diaz, Bradley 1997; Inouye et al. 2000; Diaz, Grosjean, and Graumlich 2003; Trew and Maclean 2021).

Importantly, previous marmot studies have found an association between temperatures and rainfall and other aspects of marmot life history. Using a long-term predictive model, Glad and Mallard (2022) found that up to 54% of alpine marmot (*Marmota marmota*) habitat loss would be due to climate change assuming the changes reported in the IPCC's RCP 8.5 model. Additionally, Cordes et al. (2020) found a generally negative association between climatic factors (including winter snowfall and summer rainfall) and winter survival and a positive association between climate change and summer survival in yellow-bellied marmots. Increases in spring temperatures were associated with earlier emergence from hibernation. Earlier emergence times result in marmots coming aboveground although there is still snow on the ground and require them to draw on residual fat reserves to begin reproduction and resume digestive activities (Inouye et al. 2000). The persistence of snow cover beyond marmot spring emergence reduces marmot survival and reproductive success (Armitage 2013). However, the presence of

heavy snow cover during the hibernation period is crucial for winter survival, presenting the need for winters with heavy snowfall and springs with low temperatures to be maintained (Armitage 2013).

We focused on 3 environmental factors that might influence marmot risk assessment: temperature, the timing of spring snowmelt, and summer rainfall, and made 3 predictions. 1) If high temperatures created physiological stress (as has been reported in other taxa), we expected that marmots might tolerate closer approaches when the ambient temperature was greater. We recognize that it is also conceivable that higher temperatures may reduce food needs and hence could be associated with longer FIDs (sensu Díaz et al. 2021). 2) Since late Spring snowmelt decreases the amount of time available to gain body fat and reproduce (Ozgul et al. 2010), we predicted that in years with later spring snowmelt, FID would decrease because individuals would have to maximize energy intake during a shorter season and therefore may tolerate greater risks. 3) Summer drought impedes the ability of marmots to gain sufficient body mass to survive the winter (Cordes et al. 2020), and thus, in years with less summer precipitation we expected that marmots would tolerate closer approaches because the cost of flight was increased.

## Materials and Methods

### Study system and site

Yellow-bellied marmots are social sciurid rodents that inhabit regions within the western United States (Frase and Hoffmann 1980). This project used data collected from a population of marmots that live in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado, United States (38°57'N, 106°59'W). In the montane region, marmots face predators including hawks (*Buteo* spp.), golden eagles (*Aquila chrysaetos*), badgers (*Taxidea taxus*), weasels (*Mustela frenata*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) (Van Vuren 2001).

### Trapping and observations

Following Armitage (1982), we trapped marmots using walk-in live traps baited with horse feed set close to burrow entrances and known locations. Once animals were trapped, we transferred them to cloth handling bags to record body mass, sex, and reproductive status. Marmots are individually marked with unique ear tag numbers and dye marks on their dorsal pelage to permit identification from afar.

### Quantifying flight initiation distance

Using a standard protocol (e.g., Blumstein et al. 2015), relaxed marmots (i.e., those not alarmed by the researcher presence and not actively watching the researcher) were approached in the field at a rate of 0.5 m/s. Marmots were not studied when it was raining or snowing, or when it was excessively windy (i.e., Beaufort > 3). We marked the researcher's starting location by dropping a flag and dropped flags at the location where the marmot became alert and the location where the marmot initiated flight. We continued walking to the marmot's initial location and dropped a fourth flag. Using a meter tape, we measured (to the nearest 0.01 m) the distance of each flag from the marmot's starting location. We recorded starting distance (SD; the distance between animal and the observer's starting point), alert distance (AD; the distance between observer and animal at which the animal oriented toward the

observer), the distance at which the marmot initiates flight (FID), and the marmot's distance from the nearest burrow when it fled. We also recorded the marmot's starting substrate (low vegetation, high vegetation, talus (a patch of loose rocks), dirt, stones), starting behavior (sit, forage, look, stand look), slope of approach (measured in degrees), slope of flight (measured in degrees), and method of escape (run or walk).

### Quantifying the environment

To estimate temperature at the time of each FID experiment, we used the Gothic Research Meadow weather station (38.96, −106.99), a United States Environmental Protection Agency Clean Air Status and Trends Network (EPA CASTNET, station ID GTH-161) data collection location, to obtain hourly temperatures. The Gothic Research Meadow weather station is located within our study site with marmot colonies ranging from 100 m to 2.5 km away from the weather station. Because the temperature at a given moment is relatively consistent in the valley it allowed us to use the information from this weather station for all of our FID observations regardless of the exact location where the data were collected. FIDs are recorded to the minute but we rounded these to the nearest hour to pair each datapoint with a temperature from the weather station.

We calculated the date of snow disappearance for each colony site using RMBL's spatial data platform (<https://www.rmbl.org/scientists/resources/spatial-data-platform/>, Breckheimer et al. 2021). This tool used MODIS and Landsat remotely sensed data to calculate daily estimates of fractional snow covered area (fSCA). We extracted the data using the `rSDP` R packages (Breckheimer 2023) and estimated the date of snow disappearance (referred to as snow melt date hereafter) at each colony site by taking the average day of snow disappearance across all pixels of each marmot colony.

To study summer rainfall's effects on FID, we focused on the month of July. This is because vegetation may rely on soil moisture throughout June, even in relatively dry years (Berkelhammer et al. 2020). We used average daily July precipitation data taken from a private weather station from the CoCoRaHS (Community Collaborative Rain, Hail and Snow network, station CO-GN-18) immediately next to the RMBL (38.96°, −106.99 °) and located between 100 m and 2.5 km from marmot colonies. Summer precipitation did not vary substantially across the study site.

### Statistical analysis

To test the first 2 questions, we fitted a linear mixed effects model to explain variation in log transformed FID as a function of summer air temperatures at the time of FID and winter snow melt. The fixed effects for this model included air temperature when the FID was conducted, the log of the alert distance for the FID experiment, FID trial number (to account for habituation), time at which the FID was conducted (converted to radians; see Bulla et al., 2016), valley position (up valley sites have a systematically shorter growing season than down valley sites, and this is associated with a variety of life history traits—e.g., Heissenberger et al. 2020), the log distance to burrow + 1, day of year of snow disappearance, and day of the year when the FID was conducted. We did not include age and sex in these models because prior work has shown these effects to have a negligible impact on FID (e.g., Uchida and Blumstein 2021). All independent variables were scaled for analysis using the function “scale” from the base R package. Random effects were the marmot's identity, colony, and the year. This model

included 1584 observations from 545 individuals across 17 years (2003–2022, no observations in 2006–2007).

To test the third question, we used only observations conducted in July and fitted the same linear mixed effects model with the addition of average daily July rainfall. This model included 694 observations from 332 individuals across 17 years.

Models were fitted using the function ‘lmer’ (Bates et al. 2015) and evaluated using the package `lmerTest` (Kuznetsova et al. 2017) in the R programming environment (R Core Team 2023). We used the package performance (Lüdtke et al. 2021) to evaluate model assumptions. Residuals were roughly normal, q-q plots straight, and VIF values were less than 5 which suggests that we were not violating distributional assumptions. To address a reviewer's concern that these relationships could have been non-linear, we fitted gamm models and found that the results did not change and that significant relationships were indeed linear. We do not report these exploratory results here, but include the code (and results) with the paper's code at OSF (<https://osf.io/68z9n/>).

### Results

We used our full data set to test the first 2 hypotheses. In this full data set the temperature range was from −0.5 °C to 24.1 °C. There was a significant, but slight, negative association between FID and temperature in the first model (estimate = −0.043,  $P = 0.004$ ). Marmots tolerated closer approaches as temperature increased (Table 1) with FIDs at 24 °C being 10 m shorter than at 0 °C (Fig. 1). There was no relationship between the date of snow disappearance and FID (estimate = −0.008,  $P = 0.79$ ). As expected from other studies of marmot FID, some other measured factors (alert distance, trial number, and distance to burrow) explained significant variation in FID (Table 1).

In the substantially smaller July only dataset, the temperature range was 6.33 °C to 24.1°C. We used this smaller dataset to test our third hypothesis about July precipitation. We found no relationship between temperature and FID (estimate = −0.008,  $P = 0.71$ ), no relationship between the date on which snow disappeared on FID (estimate = −0.06,  $P = 0.25$ ), and no effect of July precipitation on FID (estimate = 0.04,  $P = 0.28$ ). Here too, some other measured factors (alert distance, trial number, distance to burrow) explained significant variation in FID (Table 1).

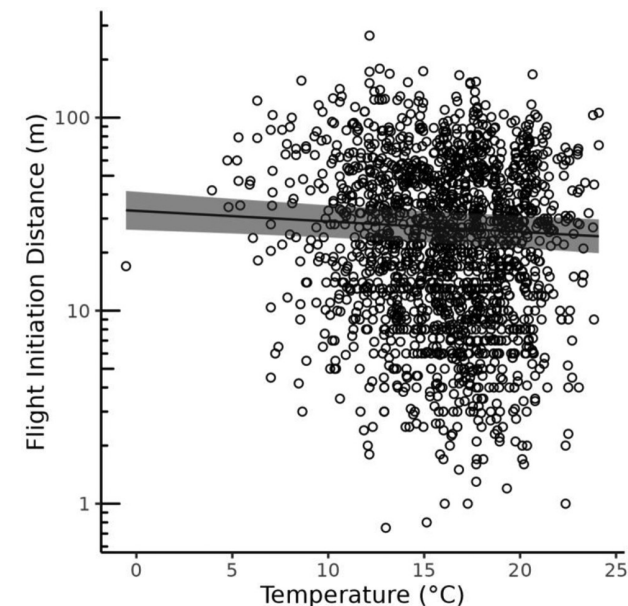
### Discussion

In a rapidly heating world, it is important to document and understand how temperature, rainfall, and seasonality influence risk assessment in animals. In the Southwestern United States, long-term climate models predict increased temperatures and increased drought severity (Cook et al. 2018; US EPA, 2024) 2 factors that increased risk taking in marmots. Overall, our results showed that marmot antipredator behavior varied as a function of air temperature, but not 2 other key variables (the date of snowmelt and July precipitation) that are associated with climate change in our study site.

As temperature increased, free-living marmots tolerated closer approaches, which suggests that they either perceived lower risks or that they were thermally stressed and their escape behavior was compromised. For marmots the effect of temperature on FID was small and our ability to detect it depended upon both the range of temperatures in the data and sample size which were substantially larger in the full data set than the substantially smaller July only data set. Temperature effects on risk taking was

**Table 1.** Results from 2 complementary linear mixed effects models explaining variation in (log-transformed) flight initiation distance (FID) in yellow-bellied marmots. The first used the entire data set to test the hypotheses that the date of snow disappearance and temperature were associated with FID. The second focused on observations made in July to test the hypothesis that July rainfall was associated with FID. Repeatability was measure as the ration of the among-individual variance ( $V_{\text{individual}}$ ) divided by the total variance (sum of the variance components). Significant,  $P$ -values ( $< 0.05$ ) are bolded.

| Predictors                                          | Full data set |                |        | July data set |                |        |
|-----------------------------------------------------|---------------|----------------|--------|---------------|----------------|--------|
|                                                     | Estimates     | CI             | P      | Estimates     | CI             | P      |
| (Intercept)                                         | 2.93          | 2.75 to 3.12   | <0.001 | 2.83          | 2.60 to 3.06   | <0.001 |
| Alert distance (log)                                | 0.66          | 0.62 to 0.70   | <0.001 | 0.65          | 0.60 to 0.71   | <0.001 |
| Date of snow disappearance                          | -0.01         | -0.07 to 0.06  | 0.796  | -0.07         | -0.17 to 0.04  | 0.235  |
| Trial number                                        | -0.08         | -0.13 to -0.04 | <0.001 | -0.06         | -0.10 to -0.01 | 0.011  |
| Valley position [up-valley]                         | 0.25          | -0.02 to 0.52  | 0.073  | 0.21          | -0.12 to 0.54  | 0.214  |
| Day of year                                         | 0.01          | -0.03 to 0.04  | 0.688  | 0.04          | -0.01 to 0.09  | 0.112  |
| Temperature                                         | -0.04         | -0.07 to -0.01 | 0.004  | -0.01         | -0.05 to 0.04  | 0.713  |
| Time (in radians)                                   | 0.02          | -0.01 to 0.05  | 0.281  | -0.00         | -0.05 to 0.04  | 0.858  |
| Distance to burrow (log(x + 1))                     | 0.13          | 0.10 to 0.16   | <0.001 | 0.12          | 0.07 to 0.17   | <0.001 |
| Average daily July rainfall                         |               |                |        | 0.04          | -0.03 to 0.12  | 0.263  |
| <b>Random effects</b>                               |               |                |        |               |                |        |
| V <sub>residual</sub>                               | 0.24          |                |        | 0.25          |                |        |
| V <sub>individual</sub>                             | 0.04          |                |        | 0.03          |                |        |
| V <sub>year</sub>                                   | 0.01          |                |        | 0.02          |                |        |
| V <sub>Colony</sub>                                 | 0.04          |                |        | 0.06          |                |        |
| Repeatability                                       | 0.27          |                |        | 0.30          |                |        |
| Marginal R <sup>2</sup> /conditional R <sup>2</sup> | 0.632/0.731   |                |        | 0.579/0.706   |                |        |
| <b>Sample size</b>                                  |               |                |        |               |                |        |
| Individuals                                         | 545           |                |        | 332           |                |        |
| Years                                               | 17            |                |        | 17            |                |        |
| Colonies                                            | 11            |                |        | 11            |                |        |
| Observations                                        | 1584          |                |        | 694           |                |        |



**Figure 1.** Relationship between flight initiation distance (in meters) and temperature (in °C) in yellow-bellied marmots. Open circles represent raw observations, the line and shaded area represent the back-transformed predictions with 95% confidence intervals from the model using the entire dataset. Flight initiation distance axis is log-scaled.

similar to the results of a number of laboratory studies of fishes where warmer temperatures enhanced risk taking. For instance, Mexican livebearing fish (*Pseudoxiphophorus jonesii*) moved more and took greater risks when experimentally exposed to hotter water (Culumber 2020). Similarly, guppies (*Poecilia reticulata*) spent more time closer to their natural cichlid predator as temperature and turbidity increased (Zanghi et al. 2023), and lemon damselfish (*P. moluccensis*) emerged from refugia sooner at higher temperatures suggesting that they took greater risks as temperature increased (Biro et al. 2010). By contrast, European birds decreased their FID as temperature increased (Díaz et al. 2021); a finding consistent with a reduced metabolic need in higher temperatures, thermal constraints on escape, as well as decreased foraging success at higher temperatures. However, many of these data were collected during the breeding season when avian species become more insectivorous to feed their young. Higher temperatures may decrease foraging ability because insect prey are able to escape better in warmer temperatures. Marmots, however, are vegetarians and thus we expect there should not be differences in foraging efficiency when it is hotter. In the Kalahari desert, arid zone birds studied during the summer also decreased their FID, but this was most pronounced when it was  $>35^{\circ}\text{C}$  (Pistrorius 2016) a finding consistent with thermal stress.

Neither rainfall at a key time of the year, nor a key measure of seasonality, the date at which the snow disappeared,

explained significant variation in marmot risk assessment. Both of these measures can affect body condition in marmots (Armitage 2014) and other species (Rhind and Bradley 2002; Parrott et al. 2007). But for marmots at least, they were not significantly associated with FID. King penguins (*Aptenodytes patagonicus*) tolerated closer human approaches to their nests when it was actively windy and raining (Hammer et al. 2022).

Prior marmot work has focused on both the extreme plasticity in marmot FID (e.g., Uchida and Blumstein 2021) as well as identifying a heritable basis of FID (Skurka et al. in revision). Here we have shown phenotypic plasticity in how FID varies as a function of natural variation in ambient temperature whereby marmots take greater risks as temperature increased. This suggests that there is a heat stress response that compromises their antipredator behavior. This is particularly important given that, between 1976 and 2008, marmot average body mass in the summer has increased by nearly 10% (Ozgul et al. 2010). Such an increase in body mass associated with an increase in temperature might further increase heat stress and further compromise FID. However, because marmot FID is significantly heritable, it may be possible that there could be an evolutionary response to increased temperatures to reduce risk taking. Such a response assumes that this FID response was not otherwise physiologically constrained because large-bodied animals are less efficiently able to lose body heat (the heat dissipation model: e.g., Dyer et al. 2023). Historically, mammalian body size decreased during both the Paleocene–Eocene thermal maxima and the Eocene thermal maxima-periods characterized by increased global temperatures (D'Ambrosia et al. 2017) which would ultimately influence the FID–temperature relationship. However, cold-tolerance evolves more rapidly than heat tolerance in both endotherm and ectotherms (Bennett et al. 2021). In the short term, it appears that increased temperatures combined could make marmots (and likely other animals) more vulnerable to their predators (assuming that predators themselves are not heat stressed). Such increased vulnerability should be factored into demographic models that are used to model population persistence to understand the relative importance of these behavioral responses on population viability.

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## Authors' Contributions

M.S. and D.T.B. conceived the idea. J.G.A.M. led the data analysis. J.G.A.M. and D.T.B. interpreted the data. M.S. and D.T.B. wrote the first draft of the paper. All authors edited the final draft.

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## Conflict of Interest

The authors declare no conflicts of interest.

## Ethics Statement

Data were collected under the UCLA Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permission from Colorado Parks and Wildlife (TR917, renewed annually).

## Data Availability

Analyses reported in this article can be reproduced using the data and code available on OSF: <https://osf.io/68z9n/>

## References

- Armitage KB, 1982. Yellow-bellied marmot. In: Davis DE, editor. *CRC Handbook of Census Methods for Terrestrial Vertebrates*. Boca Raton, FL: CRC Press, Inc., 148–149.
- Armitage KB, 2013. Climate change and the conservation of marmots. *Nat Sci* 05:36–43.
- Armitage KB, 2014. *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. Cambridge, United Kingdom: Cambridge University Press.
- Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48.
- Beniston M, Diaz HF, Bradley RS, 1997. Climatic change at high elevation sites: An overview. In: Diaz HF, Beniston M, Bradley RS, editors. *Climatic Change at High Elevation Sites*. Dordrecht, Netherlands: Springer, 1–19.
- Bennett JM, Sunday J, Calosi P, Villalobos F, Martínez B et al., 2021. The evolution of critical thermal limits of life on Earth. *Nat Commun* 12:1198.
- Berkelhammer M, Still CJ, Ritter F, Winnick M, Anderson L et al., 2020. Persistence and plasticity in conifer water-use strategies. *J Geophys Res Biogeosci* 125:e2018JG004845.
- Biro PA, Beckmann C, Stamps JA, 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc Biol Sci* 277:71–77.
- Blumstein DT, Flores G, Munoz NE, 2015. Does locomotor ability influence flight initiation distance in yellow-bellied marmots? *Ethology* 121:434–441.
- Both C, Visser ME, 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biol* 11:1606–1613.
- Braña F, 1993. Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66:216–222.
- Breckheimer I, 2023. *rSDP: discover, query, and subset data from the RMBL spatial data platform*. Available from: <https://github.com/rmbld-sdp/rSDP>, <https://rmbld-sdp.github.io/rSDP>.
- Breckheimer I, Blonder B, Carroll R, Petry W, Still C et al., 2021. Integrative remote sensing to promote environmental discovery: The RMBL spatial data platform. *AGU Fall Meeting Abstracts*, 2021, GC22E-05. <https://ui.adsabs.harvard.edu/abs/2021AGUFMGC22E..05B/abstract>
- Bulla M, Valcu M, Dokter AM, Dondua AG, Kosztolányi A et al., 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature* 540:109–113.

- Cohen J, Agel L, Barlow M, Garfinkel CI, White I, 2021. Linking Arctic variability and change with extreme winter weather in the United States. *Science* 373:1116–1121.
- Cook BI, Mankin JS, Anchukaitis KJ, 2018. Climate change and drought: From past to future. *Curr Clim Change Rep* 4:164–179.
- Cooper WE Jr, 2003. Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology* 109:617–626.
- Cooper WE Jr, 2015. Theory: models of escape behavior and refuge use. In: Cooper WE Jr, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge UK: Cambridge University Press, 88–112.
- Cordes LS, Blumstein DT, Armitage KB, CaraDonna PJ, Childs DZ et al., 2020. Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc Natl Acad Sci USA* 117:18119–18126.
- Coumou D, Rahmstorf S, 2012. A decade of weather extremes. *Nat Clim Change* 2:491–496.
- Culumber ZW, 2020. Thermal stress increases activity and risk-taking behavior but not anxiety in a livebearing fish. *Environ Biol Fishes* 103:313–317.
- D'Ambrosia AR, Clyde WC, Fricke HC, Gingerich PD, Abels HA, 2017. Repetitive mammalian dwarfing during ancient greenhouse warming events. *Sci Adv* 3:e1601430.
- Diaz HF, Grosjean M, Graumlich L, 2003. Climate variability and change in high elevation regions: Past, present and future. *Climate Change* 59:1–4.
- Díaz M, Grim T, Markó G, Morelli F, Ibáñez-Alamo JD et al., 2021. Effects of climate variation on bird escape distances modulate community responses to global change. *Sci Rep* 11:12826.
- Díaz M, Möller AP, 2023. Lockdown effects on fear revealed direct and indirect effects of human presence on perceived predation risk. *Sci Tot Environ* 872:162122.
- Dunn PO, Möller AP, editors. 2019. *Effects of Climate Change on Birds*. Oxford: Oxford University Press.
- Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR, 2023. The travel speeds of large animals are limited by their heat-dissipation capacities. *PLoS Biol* 21:e3001820.
- Ekanayake KB, Gnanapragasam JJ, Ranawana K, Vidanapathirana DR, Abeyawardhana UT et al., 2022. Ecological and environmental predictors of escape among birds on a large tropical island. *Behav Ecol Sociobiol* 76:31.
- Frase BA, Hoffmann RS, 1980. *Marmota flaviventris*. *Mamm Species* 135:1–8.
- Geiser F, 2013. Hibernation. *Curr Biol* 23(5):R188–R193.
- Glad A, Mallard F, 2022. Alpine marmot (*Marmota marmota*) distribution evolution under climate change: The use of species distribution models at a local scale in the western Pyrenees massif (France). *Ecol Inf* 69:101646.
- Gomi T, Nagasaka M, Fukuda T, Hagihara H, 2007. Shifting of the life cycle and life-history traits of the fall webworm in relation to climate change. *Entomol Exp Appl* 125:179–184.
- Hammer TL, Bize P, Saroux C, Gineste B, Robin JP et al., 2022. Repeatability of alert and flight initiation distances in king penguins: Effects of colony, approach speed, and weather. *Ethology* 128:303–316.
- Heissenberger S, Pinho GM, Martin JGM, Blumstein DT, 2020. Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal. *Behav Ecol* 31:826–833.
- Hertz PE, Huey RB, Nevo E, 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Anim Behav* 30:676–679.
- Inouye DW, Barr B, Armitage KB, Inouye BD, 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proc Natl Acad Sci USA* 97:1630–1633.
- IPCC. 2023. *Synthesis report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.
- Jensen LF, Hansen MM, Pertoldi C, Holdensgaard G, Mensberg K-LD et al., 2008. Local adaptation in brown trout early life-history traits: implications for climate change adaptability. *Proc R Soc B Biol Sci* 275:2859–2868.
- Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. lmerTest package: Tests in linear mixed effects models. *J Stat Softw* 82:1–26.
- Lagos PA, Meier A, Tolhuysen LO, Castro RA, Bozinovic F et al., 2009. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Can J Zool* 87:1016–1023.
- Le Galliard JF, Massot M, Baron JP, Clobert J, 2012. Ecological effects of climate change on European reptiles. In: Post E, Doak D, Brodie J, editors. *Wildlife Conservation in a Changing Climate*, Chicago: University Chicago Press, 179–203.
- Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D, 2021. Performance: An R package for assessment, comparison and testing of statistical models. *J Open Source Softw* 6:3139.
- Møller AP, 2015. Birds. In: Cooper WE Jr, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge: Cambridge University Press, 88–112.
- Møller AP, Liang W, Samia DSM, 2019. Flight initiation distance, color and camouflage. *Curr Zool* 65:535–540.
- Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT et al., 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482–485.
- Parrott ML, Ward SJ, Temple-Smith PD, Selwood L, 2007. Effects of drought on weight, survival and breeding success of agile antechinus (*Antechinus agilis*), dusky antechinus (*A. swainsonii*) and bush rats (*Rattus fuscipes*). *Wildl Res* 34:437–442.
- Pistrouis P, 2016. *How Air Temperature Affects Flight Initiation Distance in Arid-Zone Birds*. MS Thesis, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, South Africa.
- R Development Core Team, 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rhind SG, Bradley JS, 2002. The effect of drought on body size, growth and abundance of wild brush-tailed phascogales (*Phascogale tapoatafa*) in south-western Australia. *Wildl Res* 29:235–245.
- Roff DA, 2002. *Life History Evolution*. Sunderland, Mass: Sinauer Associates.
- Schieffelin CD, de Queiroz A, 1991. Temperature and defense in the common garter snake: warm snakes are more aggressive than cold snakes. *Herpetol* 47:230–237.
- Skurka MA, Martin JGA, Blumstein DT, in revision. The heritability of fear: decomposing sources of variation in marmot flight initiation distance. *Anim Behav*.
- Stankowich T, Blumstein DT, 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc Biol Sci* 272:2627–2634.
- Trew BT, Maclean IMD, 2021. Vulnerability of global biodiversity hotspots to climate change. *Global Ecol Biogeogr* 30:768–783.
- Uchida K, Blumstein DT, 2021. Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behav Ecol* 32:668–678.
- US EPA, 2024. A closer look: Temperature and drought in the southwest. Available from: <https://www.epa.gov/climate-indicators/southwest>. Accessed: 3 June 2024.
- Van Vuren DH, 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). *Am Midl Nat* 145:94–100.
- Veldhuis MP, Hofmeester TR, Balme G, Druce DJ, Pitman RT et al., 2020. Predation risk constrains herbivores' adaptive capacity to warming. *Nat Ecol Evol* 4:1069–1074.
- Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM, 2022. Life history consequences of climate change in hibernating mammals: A review. *Ecography* 2022:e06056.
- Ydenberg R, Dill L, 1986. The economics of fleeing from predators. *Adv Study Behav* 16:229–249.
- Zanghi C, Munro M, Ioannou CC, 2023. Temperature and turbidity interact synergistically to alter anti-predator behaviour in the Trinidadian guppy. *Proc. Biol Sci* 290:20230961.