Climate Influences on Male Golden-Mantled Ground Squirrel Reproductive Phenology

Paola Villanueva Astilleros

Caitlin Wells and Travis Rainey

Independent Research & Course / REU

Summer 2026

Abstract

Successful sexual reproduction requires both sexes to be reproductive at the same time. A variety of internal and external factors, such as climatic events, cue reproduction. Changes in climatic cues can cause reproductive phenology to shift, potentially affecting each sex differently and causing a phenological mismatch. Golden-mantled ground squirrels (GMGS; *Callospermophilus lateralis*) are a short-lived, hibernating species with a brief reproductive window. Female GMGS reproductive phenology is advancing with climate change, but changes in male reproductive phenology remain unknown. We used 29 years of male reproductive data from annual censuses to assess whether male reproductive phenology in GMGS is correlated with snowmelt. We found that snowmelt date is a significant predictor of reproductive status at both the individual and population level. We found that earlier snowmelt dates correlated with lower proportions of reproductive males, and later snowmelt dates correlated with higher proportions of reproductive males. These findings indicate that male reproductive phenology is responsive to climate cues, suggesting that male and female GMGS reproductive phenologies likely remain matched. However, more research is needed to determine the relative rates of their shifts to confirm there is no phenological mismatch between the sexes and to determine whether reproductive synchrony will be maintained in the long term as the climate continues to shift.

Introduction

Many species have adapted the timing of important life history events (i.e., phenology) to match favorable environmental conditions (Bronson 2009, Carey 2014). Seasonal cues, such as changes in photoperiod, help regulate reproduction across a variety of taxa (Nakane and Yoshimura 2019). Environmental rhythms such as food and water availability can serve as supplementary cues for reproduction (Tolla and Stevenson 2020), the phenological event that drives population dynamics (Lambin et al. 2025). As climate change progresses (Jones et al. 2001), environmental cues like temperature are changing, causing shifts in reproductive phenology (Schaper et al. 2012, Aubry and Williams 2022).

Successful sexual reproduction requires the reproductive windows, or the time when females are fertile and males are capable of contributing sperm, of both sexes to be aligned with each other (Thompson et al. 2023). The cues that regulate reproduction, and changes in these cues, can have different effects on males and females within the same species (Williams et al. 2017, 2022). The sexual match/mismatch hypothesis is a framework that describes how climate change can alter reproductive phenology in a sex-dependent manner, which can influence the emergence and successful recruitment in sexually reproducing animal species (Nakazawa et al. 2023). In some small mammal species, the reproductive windows of males and females shift in opposite directions (Sipari et al. 2014, Sarli et al. 2016) while only one sex shifts in others (Kucheravy et al. 2021). Studying how changes in climatic cues affect both male and female reproductive phenology can help us determine when sex-specific shifts are expected.

A mismatch in male and female reproductive phenology has previously been reported for some Arctic ground squirrel (*Urocitellus parryii*) populations (Sheriff et al. 2013, Williams et al. 2017). In female ground squirrels, hibernation emergence advanced in response to earlier snowmelt dates, indicating that they follow climatic cues, while males had no change, indicating they follow an annual cycle instead (Chmura et al. 2023). Consequently, years with early snowmelt might lead to reduced population-level fitness.

Golden-mantled ground squirrels (GMGS; *Callospermophilus lateralis*) are a short-lived, hibernating species with an annual breeding cycle. Male GMGS at high elevation emerge from hibernation before snowmelt, spend three weeks foraging before developing testes (i.e., male reproductive window), which remain for about 30 days (Bronson 1980). Females emerge from hibernation shortly after snowmelt and enter estrus (i.e., female reproductive window) for just one day (Kenagy et al. 1989). This relatively short estrus duration (Hayssen et al. 1993) increases the sexual mismatch if the male and female windows shift at different rates.

Within GMGS, female estrous is correlated with emergence from hibernation and snowmelt, leading to the female reproductive window shifting earlier along with average snowmelt (Bronson 1980, Wells and Van Vuren 2025). Changes in male reproductive phenology remain unstudied, so it is unknown whether a reproductive mismatch exists with GMGS populations. Understanding whether male reproductive phenology follows climatic cues or an annual cycle can help us determine whether climate change can be causing a reproductive mismatch in GMGS reproduction, which can reduce population-level fitness.

Therefore, we investigated whether male reproductive phenology is trending earlier, like snowmelt and female reproductive phenology, to determine if climate change is causing a sexual mismatch for GMGS. Specifically, we tested whether the proportion of reproductive males during the breeding season correlates with snowmelt. We hypothesized that the proportion of reproductive male GMGS will remain unchanged and follow an annual cycle instead of being correlated with climatic cues, as is the case with arctic ground squirrels (Chmura et al. 2023).

Methods

We studied the GMGS population at the Rocky Mountain Biological Laboratory townsite (2900 m), in the East River Valley, Gunnison County, Colorado (38°580N, 106°590W), from 1996 to 2026. We live-trapped squirrels each year between June 1 and 15 using Tomahawk model 201 traps baited with a black-oil sunflower seed and peanut butter mixture. Individual squirrels were marked with numbered eartags (Model 1005-1, National Band and Tag Company, Newport, Kentucky) for permanent identification. During each capture, the mass of the squirrel was taken to the nearest gram with a Pesola spring scale, along with anogenital distance (AG) to determine sex and reproductive status. “Scrotal” was defined as darkly pigmented and swollen genital tissue indicating scrotal testes. “Non-scrotal” was defined as the lack of obviously darkened tissues or distended testicles. We assessed only male squirrels who were two years or older, as yearling males are rarely reproductively mature (Wells et al. 2017). For males whose age was unknown, only those weighing at least 180 grams were included, as this is the threshold for adult male body mass (Howland et al. 2024).

Because the reproductive status of males was not consistently recorded in 1996-2002, 2004-2010, and 2012-1015, we used AG distance as a proxy to determine reproductive status during analysis. We compiled all trapping events where the AG distance and reproductive status were recorded and calculated the average AG distance for scrotal and non-scrotal males. We used these averages as the cutoff for determining the reproductive status of males whose statuses were unknown. We determined that males were non-scrotal if they had an AG distance of 22 or less and scrotal if they had an AG distance of 27 or more, while excluding males with AG distances in between. Using this approach, we calculated an error rate of 8% for known non-scrotal males, and 15% for known scrotal males.

We calculated the percentage of males that were reproductive, or scrotal, between June 1 and 15 each year. For individuals who were captured multiple times during a single year, we randomly selected one entry to include in our analysis. The data were standardized using a Z-score, which we calculated as [(proportion of scrotal males that year - mean proportion of scrotal males) / standard deviation].

We used the first day of bare ground as our date of snowmelt. The first day of bare ground was defined as the first day with 0 cm of snow on the ground, as recorded in long-term snow data from the Rocky Mountain Biological Laboratory (barr 2026).

After a pre-modeling check for bias related to yearly sample size with a simple linear regression, we conducted our primary data analyses at the population and individual level. The individual-level model was a binomial logistic generalized linear mixed model using the lme4 package in RStudio and included a random effect of male identity, along with the fixed effect of snowmelt, serving to check for the non-independence of males who were present in multiple years. The population-level model was a simple linear regression to test if the first day of bare ground significantly predicted the Z-Score for the proportion of scrotal males in RStudio.

Results

Pre-modeling

In the simple linear regression, we found that the yearly sample size did not significantly predict the proportion of scrotal males and does not bias the model based on sample size (β = -0.134 ± 0.142, p = 0.355; R^2 = 0.033; Figure 1).

Individual-level model

In the generalized linear mixed model, we found that the snowmelt date significantly predicted the male reproductive status (β = 0.108 ± 0.049, p = 0.027), with later snowmelt dates associated with a higher probability of reproductive males in early June. The random intercept for individual squirrels accounted for variation in their baseline reproductive status (variance = 1.175, SD = 1.084). The model was based on 69 observations from 58 individuals (Figure 2).

Population-level model

In the simple linear regression, we found that the snowmelt date significantly predicted the proportion of scrotal males (β = 0.039 ± 0.016, p = 0.018; R^2 = 0.196), with later snowmelt dates associated with more reproductive males in early June (Figure 3).

Discussion

Contrary to our expectation, we found that the date of snowmelt, or bare ground, is a statistically significant predictor in our individual-level and population-level models and is correlated with the proportion of scrotal males during our annual census. Later snowmelt dates led to higher proportions of scrotal males during our annual census, while earlier snowmelt dates led to lower proportions of scrotal males. The lower proportion of scrotal males during the annual census suggests that more males entered their reproductive window earlier, and hence, were no longer reproductive during the June 1 to 15 annual census.

The plasticity in male reproductive timing suggests that GMGS males may be responding to climatic cues, instead of following an annual cycle. While previous research on arctic ground squirrels indicates that male hibernation emergence is not shifting with climatic shifts (Chmura et al. 2023), research on Columbian ground squirrels (Urocitellus columbianus) suggests that male hibernation emergence is shifting with climatic cues (Thompson et al. 2023). One explanation for why male arctic ground squirrels are not responding to changing climate cues (Chmura et al. 2023) is that the timing between torpor termination and hibernation emergence is around 15-25 days in arctic ground squirrels (Williams et al. 2017) and only about 8 days in Columbian ground squirrels (Thompson et al. 2023). Additionally, differences in snowpack duration may contribute to differences between our findings and those of arctic ground squirrels.

Our research does not incorporate hibernation emergence due to logistical constraints, but the timing of male hibernation emergence likely also shifts with snowmelt, as the timing of male hibernation emergence and reproductive windows are highly linked (Kenagy et al. 1989). If this is not the case, then there may be a decoupling of phenological stages with a shift in reproductive timing. The decoupling of phenological stages has previously been suggested as a response to phenological mismatch, such as the mistiming of optimal temperatures or food abundance

(Visser and Gienapp 2019). A decoupling in phenological stages has previously been reported in female European ground squirrels (*Spermophilus citellus*), where the time between hibernation emergence and becoming reproductively receptive is increasing due to the need for more time to gain sufficient body mass for reproduction (Millesi et al. 1999). Further research is needed to investigate whether there is a decoupling of hibernation emergence and reproductive readiness timing in male GMGS.

Unlike our expectation, our study does not provide clear support for the sexual match/mismatch hypothesis within our population, as both male and female reproductive phenology appears to correlate with snowmelt dates (Wells and Van Vuren 2025) and the hypothesis only applies to species whose sexes are not in sync (Nakazawa et al. 2023). Our research found that climate change is not causing a sexual mismatch for GMGS, although more research is needed to investigate whether male and female reproductive phenologies are shifting at the same rate. Further research comparing the average rates of male and female reproductive window shifts would confirm our findings. Further research is needed to evaluate potential changes to hibernation emergence timing in male GMGS.

References

Aubry, L. M., and C. T. Williams. 2022. Vertebrate Phenological Plasticity: From Molecular Mechanisms to Ecological and Evolutionary Implications. Integrative And Comparative Biology 62:958–971.

barr, billy. 2026. Long Term Weather Data. Gothic, CO Weather. <https://www.gothicwx.org/long-term-snow.html>. Accessed 26 July 2026.

Bronson, F. H. 2009. Climate change and seasonal reproduction in mammals. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 364:3331–3340.

Bronson, M. T. 1980. Altitudinal Variation in Emergence Time of Golden-Mantled Ground Squirrels (Spermophilus lateralis). Journal of Mammalogy 61:124–126.

Carey, C. 2014. Climate Change, Extinction Risks, and Reproduction of Terrestrial Vertebrates. Pages 35–54 *in* W. V. Holt, J. L. Brown, and P. Comizzoli, editors. Reproductive Sciences in Animal Conservation. Volume 753. Advances in Experimental Medicine and Biology, Springer New York, New York, NY.

Chmura, H. E., C. Duncan, G. Burrell, B. M. Barnes, C. L. Buck, and C. T. Williams. 2023. Climate change is altering the physiology and phenology of an arctic hibernator. Science 380:846–849.

Hayssen, V. D., Ari Van Tienhoven, and Ans Van Tienhoven. 1993. Asdell's Patterns of Mammalian Reproduction: A Compendium of Species-specific Data. Cornell University Press.

Howland, S., C. P. Wells, and D. H. Van Vuren. 2024. Causes and consequences of pre-hibernation body mass in golden-mantled ground squirrels (*Callospermophilus lateralis*). J. Scheibe, editor. Journal of Mammalogy 105:348–357.

Jones, P. D., T. J. Osborn, and K. R. Briffa. 2001. The Evolution of Climate Over the Last Millennium. Science 292:662–667.

Kenagy, G. J., S. M. Sharbaugh, and K. A. Nagy. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269–282.

Kucheravy, C. E., J. M. Waterman, E. A. C. Dos Anjos, J. F. Hare, C. Enright, and C. N. Berkvens. 2021. Extreme climate event promotes phenological mismatch between sexes in hibernating ground squirrels. Scientific Reports 11:21684.

Lambin, X., M. Begon, S. J. Burthe, I. M. Graham, J. L. MacKinnon, S. Telfer, and M. K. Oli. 2025. Density-dependent recruitment but not survival drives cyclic dynamics in a field vole population. Proceedings of the National Academy of Sciences 122:e2509516122.

Millesi, E., S. Huber, L. G. Everts, and J. P. Dittami. 1999. Reproductive Decisions in Female European Ground Squirrels: Factors Affecting Reproductive Output and Maternal Investment. Ethology 105:163–175.

Nakane, Y., and T. Yoshimura. 2019. Photoperiodic Regulation of Reproduction in Vertebrates. Annual Review of Animal Biosciences 7:173–194.

Nakazawa, T., Y. Hsu, and I. Chen. 2023. Why sex matters in phenological research. Oikos 2023:e09808.

Sarli, J., H. Lutermann, A. N. Alagaili, O. B. Mohammed, and N. C. Bennett. 2016. Seasonal reproduction in the Arabian spiny mouse, Acomys dimidiatus (Rodentia: Muridae) from Saudi Arabia: The role of rainfall and temperature. Journal of Arid Environments 124:352–359.

Schaper, S. V., A. Dawson, P. J. Sharp, P. Gienapp, S. P. Caro, and M. E. Visser. 2012. Increasing Temperature, Not Mean Temperature, Is a Cue for Avian Timing of Reproduction. The American Naturalist 179:E55–E69.

Sheriff, M. J., M. M. Richter, C. L. Buck, and B. M. Barnes. 2013. Changing seasonality and phenological responses of free-living male arctic ground squirrels: the importance of sex. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120480.

Sipari, S., M. Haapakoski, I. Klemme, J. Sundell, and H. Ylönen. 2014. Sex-specific variation in the onset of reproduction and reproductive trade-offs in a boreal small mammal. Ecology 95:2851–2859.

Thompson, M. J., F. S. Dobson, D. W. Coltman, J. O. Murie, S. Raveh, and J. E. Lane. 2023. Sexes in sync: phenotypic plasticity, sexual selection and phenological synchrony between the sexes in a wild hibernator. Proceedings of the Royal Society B: Biological Sciences 290:20231113.

Tolla, E., and T. J. Stevenson. 2020. Sex Differences and the Neuroendocrine Regulation of Seasonal Reproduction by Supplementary Environmental Cues. Integrative and Comparative Biology 60:1506–1516.

Visser, M. E., and P. Gienapp. 2019. Evolutionary and demographic consequences of phenological mismatches. Nature Ecology & Evolution 3:879–885.

Wells, C. P., K. M. Tomalty, C. H. Floyd, M. B. McElreath, B. P. May, and D. H. Van Vuren. 2017. Determinants of multiple paternity in a fluctuating population of ground squirrels. Behavioral Ecology and Sociobiology 71:42.

Wells, C. P., and D. H. Van Vuren. 2025. No limit yet to phenological plasticity of reproductive timing in a high-elevation hibernator experiencing earlier springs. Ecology.

Williams, C. T., C. L. Buck, M. J. Sheriff, M. M. Richter, J. S. Krause, and B. M. Barnes. 2017. Sex-Dependent Phenological Plasticity in an Arctic Hibernator. The American Naturalist 190:854–859.

Williams, C. T., H. E. Chmura, C. K. Deal, and K. Wilsterman. 2022. Sex-Differences in Phenology: A Tinbergian Perspective. Integrative and Comparative Biology 62:980–997.

Figures

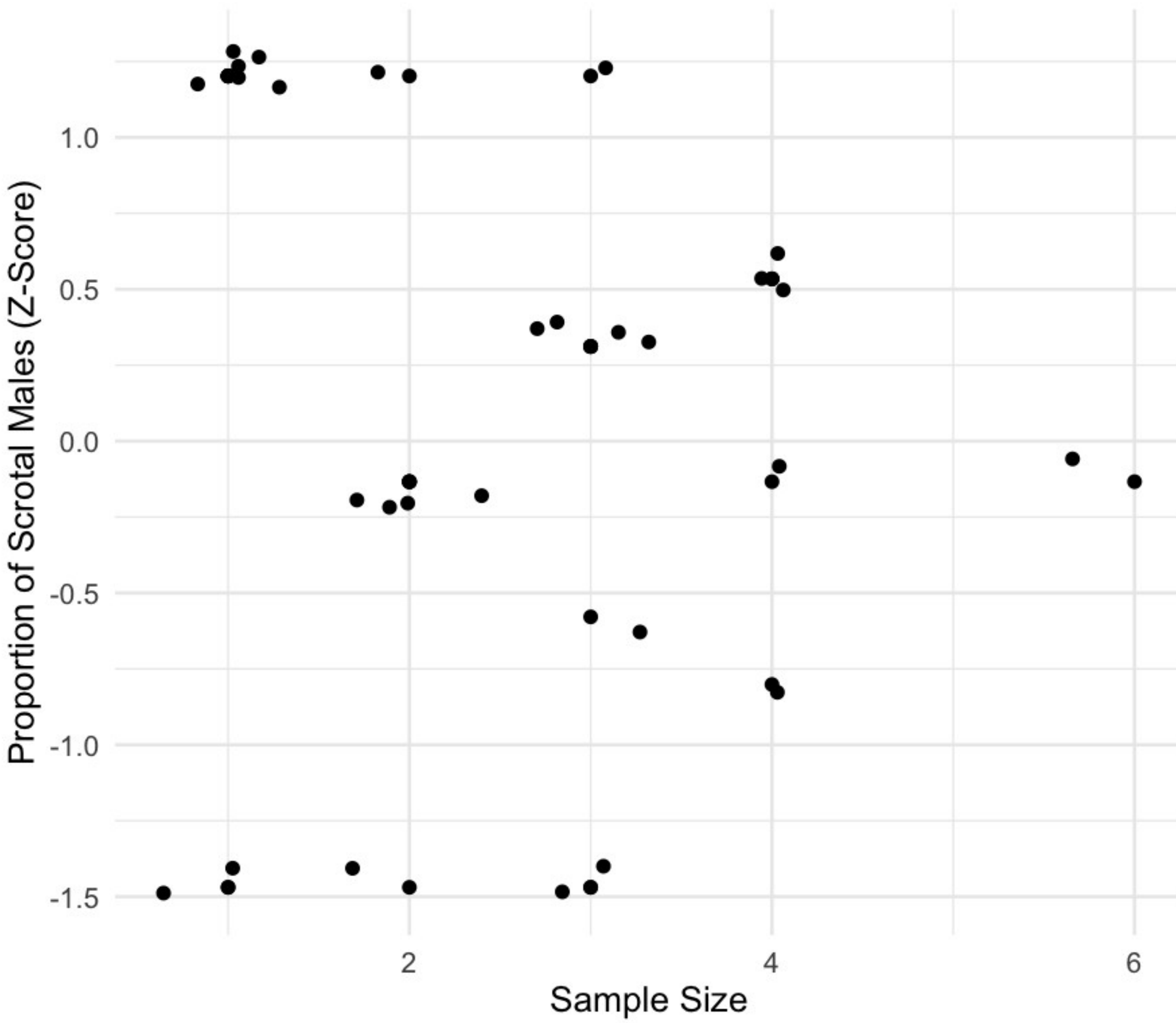

Figure 1: Linear regression of sample size on proportion of scrotal males (Z-Score)

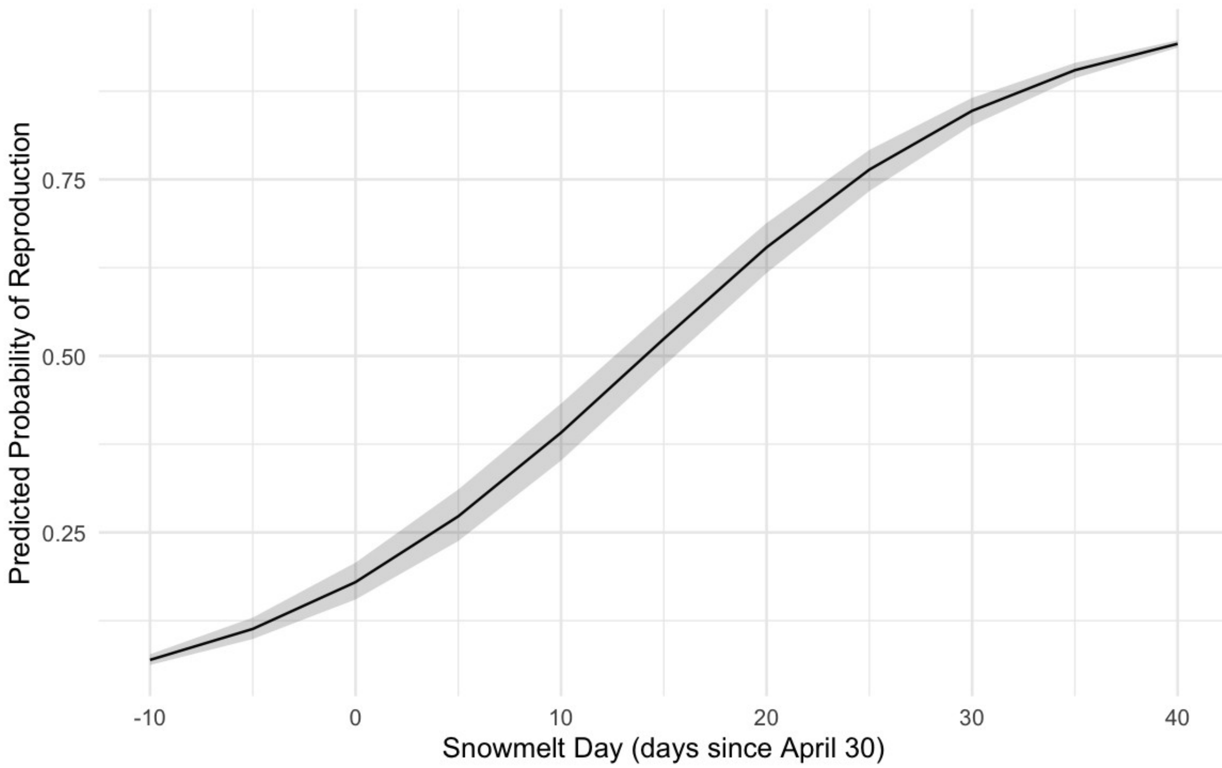

Figure 2: Predicted probability of reproduction as a function of snowmelt date.
Predictions are from a generalized linear mixed-effects model with individual squirrel as a random intercept.
The solid line represents the fitted relationship, and the shaded band shows the 95% confidence interval.

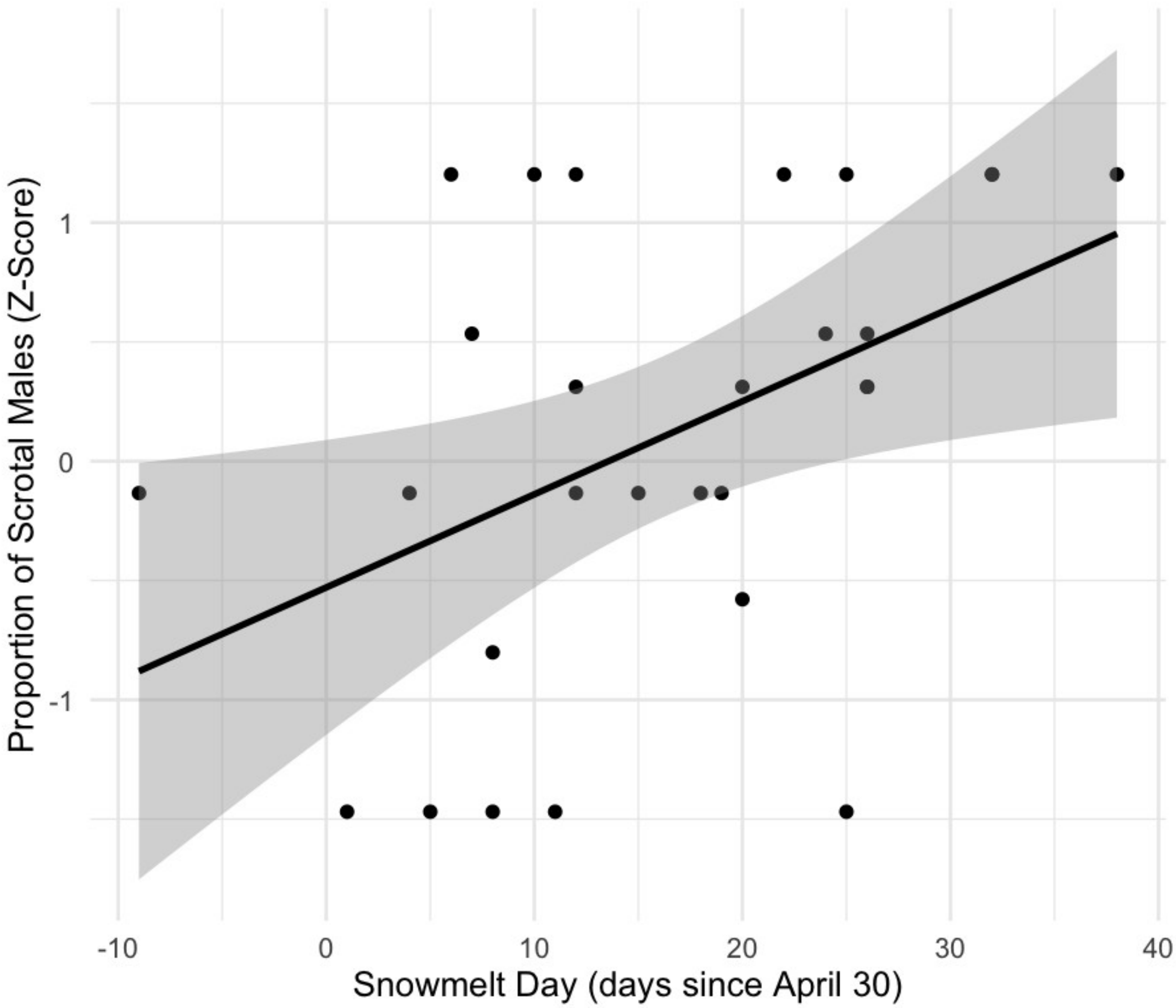

Figure 3: linear regression of snowmelt date on proportion of scrotal males (Z-Score)