

Fear ecology: A brief review on *Tamias* foraging behavior in
response to predatorial pressures

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Abstract

Fear ecology is the study of prey behavioral responses to predatorial influences. Such influences affect the behavior of individual prey, ultimately shaping the spatiotemporal dynamics of ecosystems. Prey can have a range of behavioral responses to predatorial pressures and are often affected by a variety of environmental factors simultaneously. *Tamias ruficaudus* and *Tamias amoenus* served as the model organism in this study in order to observe the effects of various predator influences on their foraging behaviors. We predicted *Tamias* foraging activity would be affected uniquely by individual predator-types (H1) and this gradient-response pattern would be consistent in multiple areas. This study was conducted in the National Bison Range near Charlo, MT. We placed feeding trays with peanuts, scent-treated stakes, and camera trap stakes at sixteen sites (divided into four areas) over the course of four weeks. Across the sixteen sites, there was no significant association between *Tamias* foraging and individual scent-treatments. Foraging was limited to one area, which showed a local association between *Tamias* foraging and individual scent-treatments. The absence of foraging consistency suggests *Tamias* behavior in response to predator pressures is facilitated by local environmental factors.

Keywords: fear ecology, predator pressures, prey behavior, Tamias

Introduction and Review

The relationship between predator and prey is one of the fundamental drivers of an ecosystem. Predation has the ability to influence trophic structures and the behavior of prey (Ripple and Beschta, 2004). It can limit energy up the food chain by inducing stress in prey, in some cases shortening food chains (Trussell *et al.*, 2006). Further, predation can determine spatial ranges of lower trophic levels from the top-down and influence the resource-density of prey species (Willems and Hill, 2009; Preisser *et al.*, 2005). A number of cases show predator presence can have a larger influence on plant communities than on herbivores (Schmitz, 1999). The continuous, unrelenting pressures that predatorial species exert on prey species has created a unique dynamic classified as the ecology of fear.

The primary mechanism of predatorial ecosystem influence is through spatially influencing or decreasing the population numbers of prey species. This influence often results in a negative relationship between the spatial distributions of predator and prey (Laundré, 2010). Because prey are usually only at danger of predators when foraging, predators typically show close associations with a prey's food source (Brown *et al.*, 2001). By following a prey's food source, especially during seasonal changes, predators indirectly influence the amount of foraging done on the lowest trophic levels.

In synchrony with influences on whole populations, predators are drivers of fear ecology on the individual level. Prey foraging behavior is typically the most altered characteristic. Species of rodentia, such as chipmunks (*Tamias*) or mice (*Peromyscus*), have exhibited olfactory foraging changes in response to biotic pressures (Vander Wall, 2000). Moreover, predator induced fear can lead to sustained physiological stress in prey, leading to long-term behavioral changes (Clinchy *et al.*, 2012). Conversely, prey behavior can become laxer in the absence of predator pressures. Reduction in predator numbers engenders less fearful and more catchable prey. Bigger, fiercer predators have been shown to deplete food patches at a faster rate due to fear inducement (Brown *et al.*, 1999).

In many ecosystem, granivores play serve as a trophic bridge between basal flora and tertiary predators. Various rodents forage on tree seeds, caching and converting their energy to be unlocked by predators (Jensen, 1985). Due to their central role in forest and desert ecosystems, rodentia often serve as the study species in fear ecology (Farias and Kittlein, 2008). Their behavioral changes due to environmental influences, such as predator risk, are typically evident (Kotler, 1984). In the montane forests of western Montana, this role is played by a variety of granivores, primarily mice (*Peromyscus maniculatus*) and chipmunks (*Tamias*).

Species of *Tamias* found across the northern edge of the United States include *T. ruficaudus*, *T. amoenus*, *T. townsendii*, *T. minimus*, and *T. striatus* (Bergstrom, 1988). *Tamias* fear behavior can be generalized across multiple species due to their similar niche occupations (Banfield, 1974). In the presence of danger, *Tamias* usually seek the sanctuary of trees or ground holes (Clarke *et al.*, 1993). The means of shelter they prefer are often determined by their familiarity with location. In response to fear, chipmunk physiological changes can include fear bradycardia, fear tachycardia, or increase sinus arrhythmia (Smith *et al.*, 1981). *Tamias*, like most prey species, often exhibit a “landscape of fear” where their spatial ranges are determined by predator pressures (Tolon *et al.*, 2009).

Tamias in the northwestern United States serve as important seed dispersers in forest stands. Both species forage seeds of shrubs and trees, carrying individual seeds and caching them in various spots. In some cases, *Tamias* have been found to be the primary distributors of around eighty percent of an individual shrub’s seeds (Vander Wall 1994). Moreover, chipmunks contribute to the food base of many predators in the northwestern United States including our study area, the National Bison Range. Common predators of *Tamias* include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata*), and various birds of prey. The role of *Tamias* is one of both predator and prey, and they are fundamental to the forest ecosystem.

Species of *Tamias* present at the National Bison Range include the yellow-pine (*T. amoenus*) and the red-tailed (*T. ruficaudus*) chipmunks. The yellow-pine and red-tailed chipmunks primarily inhabits coniferous forests (Hoffman and Pattie, 1968; Good and Sullivan, 2002). However, while *T. amoenus* normally nest in trees, logs, and various crevices for shelter,

T. ruficaudus tend to prefer residence on the ground in burrows or crevices (Sutton, 1992; Best, 1993). As with many chipmunk species, both are diurnal (Howell, 1920; Best, 1993).

Although specific predators of *T. amoenus* and *T. ruficaudus* are documented, little is known of the interactions between the predators and prey. Because *Tamias* play a central role in the trophic structure of their ecosystems, it is important to distinguish the nuances of *Tamias* response to predation pressures. Observing *Tamias* foraging behavior in the presence of predation risk facilitates understanding of the trophic dynamics within a specific habitat. We hypothesize that *Tamias* foraging activity will be affected differently by separate predator presences (H1), because each predator exhibits unique predation methods. Moreover, we expect to see consistency of this gradient-response (H2), suggesting *Tamias* foraging behavior and predator avoidance is an inherent characteristic.

Methods

This study was conducted over the course of four weeks at the National Bison Range (47.3706° N, 114.2571° W) through the University of Notre Dame Environmental Research Center – West (UNDERC-West) in Charlo, Montana. The bison range and research center are located in the Mission Valley of the Rocky Mountains.

In this study, the two species will be generalized as the genus *Tamias* because they inhabit similar forest stands and have similar foraging habits (Banfield, 1974). Because *Tamias* generally inhabit coniferous forests, 16 forested trial sites were found in the National Bison Range (NBR). These sites were located at higher elevations (1189.8 m – 1374.7 m) in forests dominated by Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menzeisii*). Sites in similar forest stands were picked as a means to control for similar population densities (Yahner, 1977). The trial sites were spread across four areas (A1-4), with each area consisting of

four trial sites (**Figure 1**). Each site contained a feeding tray, scent-treated stake, and camera trap stake.

Predators of *Tamias* located in the NBR include coyotes, bobcats, red foxes, badgers, and various birds of prey. Like many other rodents, *Tamias* rely mainly on olfaction to forage and to avoid local predators (Vander Wall, 2000). We used samples of urine from three of these predators (coyote, bobcat, and red fox) to serve as a substitute for predator presence. The predator urine was soaked into a p-wick (ThePeeMart, Sandy Point, ME) and dangled from a wooden stake with fishing line. The first tray type (TT1) served as a control site, with the p-wick and stake left untreated. TT1 was used as a relative measurement of *Tamias* foraging in each area without predator pressures.

The scent-treated trial sites consisted of: TT2) the feeding tray in the presence of a coyote scent treatment, TT3) the feeding tray in the presence of a bobcat scent treatment, and TT4) the feeding tray in the presence of a red fox scent treatment. The scent-treated stakes were placed less than 10 cm from the feeding tray entrances. A camera trap (Bushnell, Overland Park, KS) attached to a wooden stake was placed 1 m from the entrances of the feeding trays to record *Tamias* foraging activity. The inclusion of cameras in this experiment allowed for direct observation and confirmation of chipmunk foraging activity. Cameras also showed whether any non-*Tamias* species were feeding on the food source as well.

We used one type of food source as a means to monitor *Tamias* activity in the areas. The food source consisted of peanuts (in-shell) in a feeding tray. Peanuts serve as a source of high fatty-acid intake for chipmunks and have been found to be favorable when studying *Tamias* foraging behavior (Munro *et al.*, 2005). This was also used as a means of avoiding introducing invasive species to the National Bison Range. To limit the amount of unwanted foraging by other

species, we constructed a mesh wire cover for each tray. The mesh-wire cover contained a 4 in² entrance on one end of the feeding tray, based on the average diameter of a chipmunk burrow entrance (Caines, Unpublished). The cover was intended to reduce the likelihood of birds and larger mammals accessing the peanuts. Moreover, the peanuts were kept in-shell to prevent smaller granivores, such as *Peromyscus*, from accessing and removing the food source.

This study included sixteen trial sites (labeled with geographic coordinates) in four areas. Each trial site group contained one of the four tray types, totaling to four replicates of each tray type. Suitable sample areas included forested habitats that were far enough away from each other (>500 m), so predator scents did not mix. Prior to testing, trays were secured with mesh wire covering (staked to ground) and scent-treated with the proper urine depending on the tray type. Two distinct areas were deliberately picked to avoid scent overlap, while sample sites and scents were randomly chosen. Individual sites and scents were assigned a number (1-4) and selected using a random number generator.

Prior to testing, the individual feeding trays were filled with 100 in-shell peanuts. H1 was tested by placing feeding trays directly in front of camera traps. Trays, scent treatments, and camera traps were placed at approximately 7:00 a.m. because chipmunks are most active during the early morning hours (Howell, 1920). They were collected after twelve hours to give foraging access to multiple individuals. Multiple individuals were expected to visit the feeding trays because *Tamias* tend to forage in a given spot for a relatively short amount of time (Howell, 1920). Moreover, *Tamias* exhibit extensive spatial overlap (Getty, 1981). After feeding trays and camera traps were obtained the remaining peanuts were counted. *Tamias* visitations captured by camera traps were counted for each trial, as well. Trial sites were used two consecutive days to account for predator scent-acclimation by *Tamias*. Feeding trays and camera traps were returned

to the trial site prior to the second trial. Scent treatments were not collected until the end of the second trial.

Predator influence on chipmunk foraging habits were tested by the decrease in number of the food source after each trial. It was assumed that the greatest predator influence would co-occur with tray containing the lowest drop in number after the daily trials. For H1, a one-way ANOVA or Kruskal-Wallis test were to be conducted, depending on normality and distribution of variance across predator scents. If peanut number was to remain even across the trials, it would be assumed individual predator-types had a similar influence on *Tamias* foraging activity.

If a gradient-response was observed in chipmunk foraging habits, H2 would be tested by comparing the ranking of each scent treatment across the four areas. Again, a one-way ANOVA or Kruskal-Wallis test would be run. By testing for consistency within the predator-avoidance gradient, we could observe whether avoidance based on predator-type is an inherent characteristic of *Tamias* or dependent on extrinsic factors such as habitat location. Similarly, if an “all-or-nothing” response was obtained, we could test for consistency depending on extrinsic factors such as location and elevation.

Results

All statistical tests were run on RStudio (Version 1.0.143). Out of the 16 trial sites tested, only 5 sites showed *Tamias* visitations and 2 sites exhibited *Tamias* foraging (**Table 1; Table 2**). A Kruskal-Wallis test run on the documented visitations showed no significant relationship between scent treatments and *Tamias* visitations (Kruskal-Wallis $X^2 = 2.4545$, $df = 3$, $p = 0.4836$). A Kruskal-Wallis test run on the number of peanuts foraged showed no significant relationship between scent treatments and *Tamias* foraging (Kruskal-Wallis $X^2 = 2.0893$, $df = 2$, $p = 0.3518$).

Because all foraging was contained to A2, a Pearson's chi-squared test was run for documented visitations and peanuts foraged. The test ran on documented visitations resulted in significance between the visitations in each trial site ($X^2 = 63.875$, $df = 3$, $p = 8.729e-14$). The test ran on peanuts foraged resulted in significance between foraging that occurred at each trial site ($X^2 = 239.94$, $df = 3$, $p < 2.2e-16$).

Discussion

There were no significant relationships observed between scent treatments and documented visitations. Similarly, there were no significant associations between scent treatments and number of peanuts foraged. The lack of associations, in this case, can be directly attributed to the lack of data across the 16 sites. A2 was the only area to exhibit both visitations and foraging. Visitations experienced in other areas were minimal. It is likely foraging was not temporally affected, because the two instances of foraging occurred nearly one month apart (Jul. 7-8 and Aug. 1-2).

Additionally, lack of consistency across all areas suggests foraging behaviors as a response to predator pressures is not intrinsically driven. *Tamias* foraging responses rely on an amalgam of extrinsic factors. For example, *Tamias* have been found to use coarse woody debris (CWD) as a mechanism of predator protection (Zollner and Crane, 2003). Such habitat "sanctuaries" have been shown to affect the amount of foraging by *Tamias* (Bowers *et al.*, 1993). In an area with a higher CWD abundance, *Tamias* may be more willing to sacrifice temporary safety for high energy-gain. In future studies, taking CWD counts could show a possible association between foraging behavior and predator pressures.

Less locally-restricted extrinsic factors have also been shown to impact granivore foraging success. Competitive foraging advantages are susceptible to change with correlating

changes in weather conditions. During drier conditions, *Tamias* that rely on olfaction have a distinct foraging advantage and higher success rate than in wetter conditions. For the months of June and July, 2018 had over twice the amount of rainfall as 2017 (**Figure 4** – Round Butte, AgriMet Weather Station, Round Butte, MT). It is possible *Tamias* ability of locating feeding trays through olfaction was affected by the wetter conditions this summer. Such an influence would explain the differences in foraging rates between this study and a similar study conducted the previous summer (Nez, Unpublished).

Another explanation for lack of visitations in certain areas could be due to the density of *Tamias*. Less populated areas would result in less visitations and foraging. Chipmunks were observed in 3 of 4 total areas, with a high volume of visitations and all foraging occurrences contained to A2. Moreover, no evidence of competition was recorded in these areas.

Documentations of chipping or chases would point to the existence of neighboring individuals (Yahner, 1977). By analyzing the amount of competition in a particular site, we could estimate the general *Tamias* density in the area.

In trial sites limited to one documented visitation, all visitations occurred on the first day of trials. It is unlikely that individuals forgot the location of the feeding sites on the second day because *Tamias* have exhibited high spatial memory in locating cache sites (Vander Wall, 2000). All controllable environmental factors were kept consistent, suggesting scent-treatments were drivers of foraging-absence on the first day and visitation-absence on the second day.

Foraging was most likely contained to A2 because of various environmental factors. The two sites (A2 S1, A2 S3) that experienced foraging were also the two lowest sites in terms of elevation. However, visitations were experienced across the full range of elevations. It is important to distinguish between visitations and foraging because visitations did not always

result in foraging. This relationship between the two activities highlights a gradient of behavioral risks individuals are willing to take. The number of peanuts foraged at trial site A2 S3 (bobcat-treated) show once the foraging-threshold was broken during visitations, *Tamias* valued energy-gain over sanctuary. Conversely, there were trial sites that experienced visitations without foraging. Although individuals were within foraging-distance of the food source, the close proximity of a predator's presence was incentive enough to drive *Tamias* away. The number of peanuts foraged at trial site A2 S3 (bobcat-treated) show once the foraging-threshold was broken during visitations, *Tamias* valued energy-gain over sanctuary. This was seen in the significant relationships between scents and visitations and foraging in A2 (**Figure 2; Figure 3**). The control site in A2 experienced the most visitations and foraging, which was expected. The scent-treatments exhibited a gradient-response in which *Tamias* would show visitation and foraging in the presence of bobcats, show visitation with out foraging in the presence of red foxes, and show no visitation in the presence of coyotes.

Due to the significant associations between scent-treatments and visitations/foraging, A2 showed a glimpse of possible behavioral separation in the foraging approach of *Tamias*. Spatially, bobcat absence was an unlikely driver of *Tamias* visitations and foraging because the proximity of study areas was less than the home range of a typical bobcat (Elizalde-Arellano, 2012). Temporally, however, it is possible bobcats have not recently been prevalent in A2, resulting in lax-attitude toward the bobcat-treated site. Following that trend, coyotes would have been the most recent predator in A2, followed by red foxes. Although that information was not available during the study, the gradient-response poses a possible means of analyzing predatorial spatiotemporal movement in the NBR through the behavior of related prey.

In conclusion, there were hints of a relationship between predator scent-treatments and *Tamias* peanut foraging behavior. There was no regulation of various environmental factors, such as *Tamias* density or abundance of sanctuaries from predators. Although the four areas contained similar forest stands, they may have been more distinct from one another when considering environmental influences on *Tamias* foraging. Thus, significant differences in foraging were contained to one area. The results of this study point toward possible local influences on prey behavior, but this work requires further replication to be certain. Determined by a multitude of both micro- and macro-environmental interactions, prey have various behavioral reactions to fear from predator pressures. The mix of these subtle spatiotemporal differences in predator-prey interactions facilitates the dynamic aspects of the overall ecosystems.

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Tables and Figures

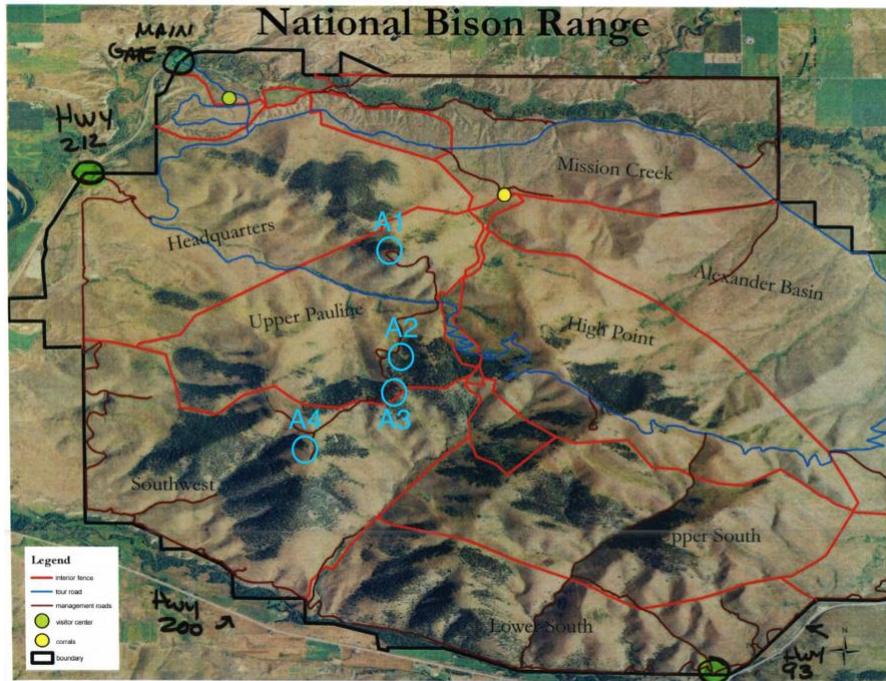


Figure 1: Location of trial areas at the NBR (A1-A4).

Area	Control	Coyote	Bobcat	Red Fox
A1	0	0	0	0
A2	133	0	92	0
A3	0	0	0	0
A4	0	0	0	0

Table 1: Number of peanuts foraged across all four areas in the NBR. Table shows a combination of trial sites in each area.

Area	Control	Coyote	Bobcat	Red Fox
A1	0	0	0	0
A2	37	0	26	1
A3	0	0	0	1
A4	0	0	1	0

Table 2: Number of documented visitations across all four areas in the NBR. Table shows a combination of trial sites in each area.

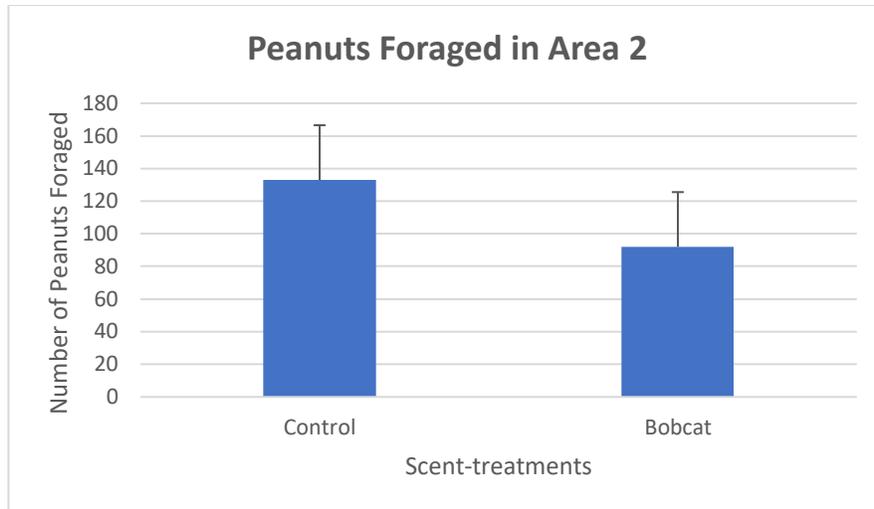


Figure 2: Total *Tamias* foraging at control (133±33.54 peanuts) and bobcat (92±33.54 peanuts) sites in Area 2 ($p = 8.729e-14$).

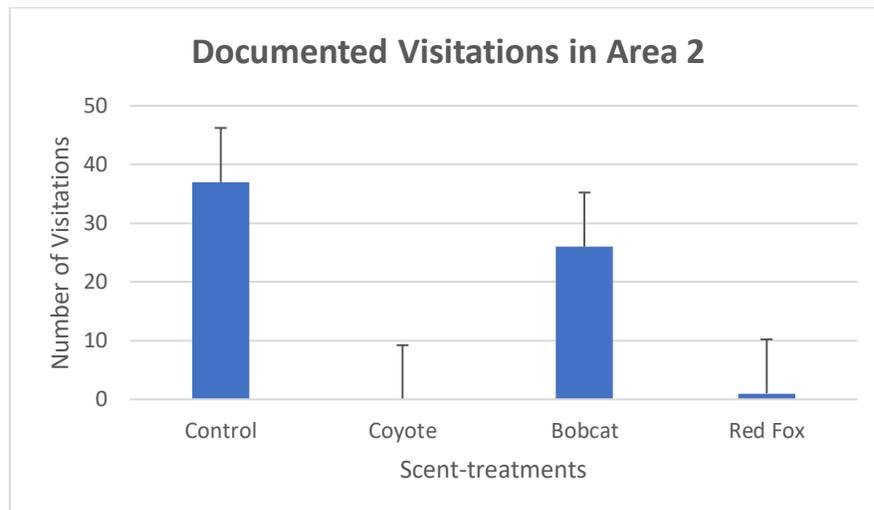


Figure 3: Total *Tamias* foraging at control (37±9.23 visitations), coyote (0±9.23 visitations), bobcat (26±9.23 visitations), and red fox (1±9.23 visitations) sites in Area 2 ($p < 2.2e-16$).

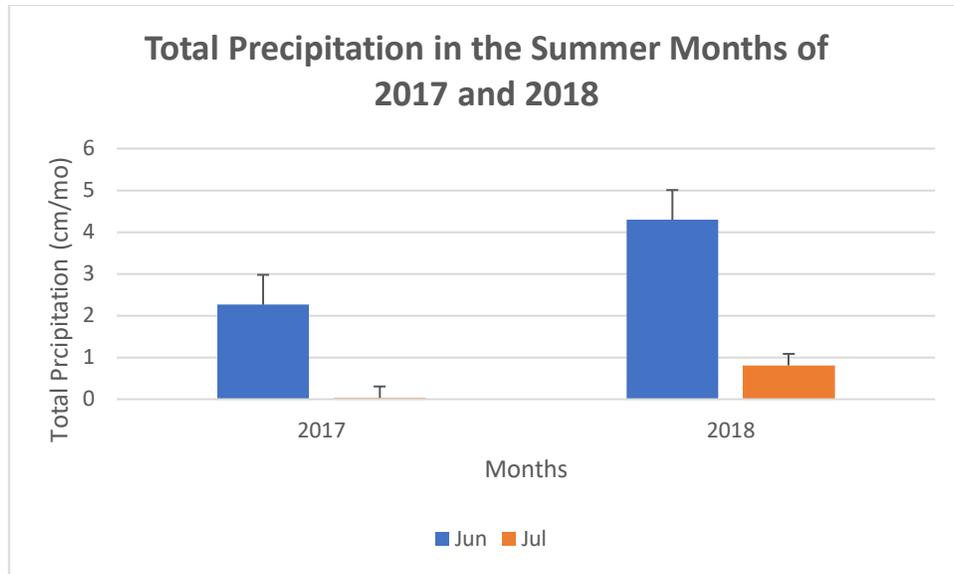


Figure 4: Total precipitation in June 2017 (2.26 ± 0.72), July 2017 (0.03 ± 0.28), June 2018 (4.29 ± 0.72), and July 2018 (0.81 ± 0.28). All data was collected by Round Butte, AgriMet Weather Station, Round Butte, MT.