

**Temperature and Nestling Development: Temporal Variations in
Zonotrichia leucophrys oriantha Feeding Frequency**

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Abstract

Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) are unique in that their nestlings, which require parental care for 9 days before fledging, have a 25% higher metabolic rate than other open-nesting passerines. This unusually high energetic demand requires that parents frequently feed their young; however, female sparrows must balance their time between bouts of foraging and incubating to protect vulnerable nestlings from extreme temperatures. I hypothesized that this tradeoff in parental nest attendance behavior varies on colder versus warmer days. In particular, feeding rates are reduced and/or delayed on cold mornings and on hot afternoons. These patterns would accommodate for incubation during early hours and shading from intense sun during afternoon hours. This was tested by monitoring Mountain White-crowned Sparrow nests with data loggers that recorded temperature every two minutes and a nest camera that revealed the frequency of different behaviors. Analysis showed a significant but extremely weak negative correlation between the frequency of feeding and temperature ($R^2 = 0.063831$, $p = 0.0042$) and between the proportion of time parents were absent from the nest and temperature ($R^2 = 0.047224$, $p = 0.0141$). ANOVAs of both temperature with feeding frequency and temperature with parental absence over 3.5 hour intervals revealed that cold mornings have higher feeding frequency but a lower proportion of parental absence than warm mornings. In cold afternoons, there is a higher feeding frequency but an equivalent proportion of parental absence as warm afternoons. However, only the difference in morning feeding frequency is significant ($p = 0.03$).

Introduction

The cross-generational population dynamics of sexually-reproducing organisms is dependent upon the reproductive success demographics from one breeding season to the next: Fisher's fundamental theorem of natural selection asserts that a population's mean rate of evolutionary change in fitness is equal to the additive genetic variance in fitness (Gustafsson 1986). Reproductive success in birds is defined as the proportion of nests that produce fledglings and the number of fledglings per individual female each year is tied to the demographic trends of overall bird populations (Murray 2000). Two factors that influence nest survival are the availability of food and temperature. The tradeoffs parent birds must make between nest thermoregulation and foraging has been studied in the Yellow-eyed Junco (*Junco phaeonotus*). These birds must balance the conflicting pressures to maintain optimal egg temperatures while still foraging enough to support their own metabolic needs in a high-elevation environment (Sullivan 2016). Furthermore, a study on Great Tits (*Parus major*) revealed that both male and female nest attentiveness during egg stage increased with lower temperatures (Matysiokova and Remes 2010), while Avery and Krebs (1984) found that adult Great Tits caught more spiders on foraging bouts when ambient temperatures were higher. Additionally, a study conducted on tree swallow nestlings found that those reared in artificially heated nest boxes had significantly greater mass and growth rates than those in control nest boxes (Dawson et al. 2005). Thus, parent birds must ultimately divide their time spent foraging for themselves and for their nestlings against the time spent maintaining optimal nest temperature. While many studies have been conducted on this tradeoff for nests in egg stage, there is a comparative lack of information pertaining to the dynamic between temperature and feeding for nestling-stage nests.

Birds that breed at high elevation must overcome a variety of environmental challenges to maintain the balance of nest thermoregulation and feeding. These challenges include hypoxia, fragmented habitats, sporadic and extreme inclement weather, intensified solar radiation, and a

mean 57% shorter breeding season than their low-elevation conspecifics (Martin 2014). Daily temperature fluctuations are particularly dramatic: in a study of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*; hereafter MWCS) at Tioga Pass in the Sierra Nevada Mountains, mean hourly temperature was recorded from June to August 1980 and ranged from 0 °C to 25 °C within a day (Morton 2002). Found throughout elevations of 800m to 3,600m within the Sierra Nevada, Cascade, and Rocky Mountain ranges of the United States, MWCS nestlings have a metabolism rate that is 25% higher than other species of open-nesting passerines and a logistic growth rate constant that is 129% of the predicted allometric model (Morton et al. 1972; Weathers et al. 2003). Furthermore, the nestlings do not develop endothermy until 3-4 days after hatching and are not fully homeothermic until the time they fledge (Morton 2002). This delayed thermoregulatory development places additional pressures on the parent MWCS to provide for their own metabolic needs, the nestlings' elevated metabolic needs, and the nestlings' thermoregulatory needs while surviving the variable temperatures and harsh conditions of a high-elevation environment.

The MWCS's preferred nesting habitat is in dense thickets of mixed willow (*Salix* spp.) species in alpine and subalpine meadows (Morton 2002). These nests are cup shaped, constructed from dry grass, twigs, animal hair, and bark. In many cases, the female will build her nest in the base of a tall shrub, provided that snowpack does not restrict nest site choices (Morton et al. 1972). After MWCS nestlings hatch, they require 9-11 days of parental care prior to fledging (Morton 2002). The nesting season follows the life cycle of local insects, such that MWCS are able to feed their nestlings adult and larval insects (Morton et al. 1972). At day 7 nests, feeding begins around 45 minutes before sunrise and continues at different rates throughout the day until 45 minutes after sunset. At one MWCS nest, researchers observed 186 feeding visits throughout the course of the day. 41.4% of these visits were made by the male parent, while the female made the remaining 58.6% of feedings (Morton 2002). In this same study, the highest frequencies of feeding occurred from 06:00 til 08:00. The researchers believe this trend appears because that nestlings are hungriest and beg most actively in the early morning after not having eaten all night. As the nestlings' thermoregulatory abilities develop, the hours of feeding extend by up to 3 hours into the colder early morning (Morton 2002).

The objectives of this study are to investigate the tradeoff parent birds must make between spending more time insulating the nestlings or making foraging bouts— particularly considering that MWCS nestlings do not hatch with fully-developed thermoregulatory capabilities yet maintain high metabolic levels. Specifically, I studied how the relationship between the frequency at which MWCS parents feed their nestlings and the ambient temperature may change as a result of daily weather fluctuations. I hypothesized that this tradeoff in parental nest attendance behavior varies on colder versus warmer days, such that feeding rates are reduced and/or delayed on cold mornings and on hot afternoons. These patterns would accommodate for incubation during early hours and shading from intense sun during afternoon hours.

Methods

Study sites

This study was conducted in alpine and subalpine meadows surrounding the Rocky Mountain Biological Laboratory in the West Elk Mountain Range of Colorado. I worked eight different sites (Fig. 6) across an elevational gradient: the lowest sites were within the East River Valley starting at 2924m. We had one mid-elevation site in Schofield Park at 3167m, and three high-elevation sites reaching 3465m. Within these sites, we focus on areas with dense thickets of various willow species (*Salix* spp.) or cinquefoil (*Potentilla* spp.). These thickets are typically interspersed with herbaceous vegetation such as larkspur (*Delphinium* spp.), corn lily (*Veratrum* spp.), and mountain bluebell (*Mertensia* spp.) and surrounded by forests composed primarily of engelmann spruce (*Picea engelmannii*) and douglas fir (*Pseudotsuga menziesii*). In this environment, there is a brief and vigorous growing season over the summer; during this time, the MWCS nest and raise young (Inouye et al. 2000; Morton 2002).

Nest searching and monitoring

Nests were located using a rope dragging technique to induce flushing females. This occurred when two people pulled a 12m long rope with attached noisemakers across the top of potential nesting habitat, such as a willow or cinquefoil thicket. The noisemakers were clusters of three empty aluminum cans spaced approximately one meter apart throughout the length of the rope. The sound of the approaching rope drag prompted female MWCS to hop off of their nests, run a short distance, and then fly out of the vegetation. By observing where the female flew out, researchers retraced her steps to find the nest. Nest searching was performed at study sites 1, 2, 4, Schofield, North Pole Basin, Virginia Basin, and Paradise Basin (fig. 6), and nests used in this study were located at sites 2, 4, and Schofield Park. Upon locating a nest, preliminary data gathering and processing occurred. First, the nest was inspected for eggs or nestlings, which were visually aged according to standards for altricial nestling development (Weller 1956; Jongsomjit et al. 2007). The nest was then marked using a hand-held Garmin Etrex GPS unit and orange flagging tape was placed three paces to the north and south of the nest to facilitate quick relocation during monitoring. Temperature data was recorded using iButton Thermochron data loggers camouflaged with flat brown paint on their exposed surface. One was placed within the nest lining and another was placed approximately 15cm outside of the nest. These data loggers were preformatted to record the ambient temperature every two minutes.

Parental nest behavior monitoring

Camouflaged, security-style cameras mounted to a stake were placed approximately 15 cm from a nest and angled directly at the nestlings. The cameras were deployed when the oldest nestling was 5-6 days old. This age range was selected to reduce the chances of nest abandonment and because all nestlings in a multiple-nestling brood are able to thermoregulate by shivering by at least day 6 if not before (Morton 2002). These cameras were connected to a 15m extension cord that lead back to an external battery and micro-DVR setup that was concealed in the vegetation. I used a Digital Prism 7" color monitor, two 1/3-inch weatherproof color CCD IR security video cameras, and a Solid State Micro DVR that recorded onto SD cards. The footage was 352x256 frame size at 30 frames per second. The power converter I used was a Schumacher 410W connected to a 9lb ETX12 battery. The cameras recorded footage from at least 0830 until 1300. Before leaving, researchers monitored live activity at the nest to ensure that the parents returned and the camera's presence did not induce nest abandonment. Nest cameras were used in conjunction with data

loggers to allow comparison of nest temperature, ambient microclimate temperature, and the frequency of feeding visits made by the MWCS parents.

Data analysis

When analyzing video footage, the start and end time for every behavior exhibited by MWCS parents was recorded. The observed behaviors were male parent feeding nestlings, female parent feeding nestlings, unknown parent feeding nestlings, both parents feeding nestlings, male parent feeding female parent, incubation, shading or fussing in nest, fecal sac removal, and no parents present at nest. After cataloguing the start and end times of each behavior from the footage for 10 nests, I calculated the mean duration of each behavior on 30 minute intervals. These 30 minute intervals were coded from 07:00:00 til 14:30:00, with 1 being 07:00:00-07:30:00 and 15 being 14:00:00-14:30:00. I also calculated the mean temperatures recorded by data loggers on the same intervals. The intervals are 30 minutes long because this allows enough time for a whole behavior to begin and end (the longest duration of a behavior from preliminary data gathering is 12 minutes). I then further simplified data by assigning behaviors to codes: 0 = No Parent Present, 1 = Shading/Fussing or Incubate, and 2 = all other behaviors. The behaviors were categorized such that 0 was no parent present to thermoregulate, 1 was parent present and actively thermoregulating, and 2 was parent present but not actively thermoregulating. I then calculated the proportion of time that parents were absent from the nest over each 30 minute period as well as the total number of feedings during each period. The number of nestlings in each nest studied ranged from 1 to 4; thus, to avoid bias, I ran a regression of nestling number as the independent variable and feeding frequency as the dependent variable. The regression line was $y = 37.416667 + 2.958333x$, with an R^2 value of 0.1221 and a p value of 0.3223. Because this was not significant, I included all nests in the ultimate analyses. Finally, it was necessary for some parts of the ultimate analysis to condense data into morning and afternoon categories. To do so, I constructed a plot of all the temperatures recorded while filming (fig. 1). This graph shows variation in daily weather trends at nesting sites, and displays the range of starting temperatures, trends of temperature change during the day, and the main divergence point between morning and afternoon (between time period 7 and 8). Given this information, I assigned time periods 2-8 to be group 1 (morning) and time periods 9-15 to be group 2 (referred to as afternoon, though it includes some late-morning hours). For the final analysis, I ran linear regressions comparing temperature vs feeding frequency and temperature vs parental absence using individual time periods as data points, as well as one-way ANOVAs comparing the same variables over the averaged values for morning and afternoon time groups.

Results

A regression of temperature as the independent variable against feeding frequency as the dependent variable (Fig. 2) revealed a significant but extremely weak negative correlation ($R^2 = 0.063831$, $p = 0.0042$). One-way ANOVAs of these variables were performed for the average values across time periods 2-8 (morning) and 9-15 (afternoon). The morning group ANOVA had an $F_{1,9}$ ratio of 1.66, p value of 0.23, and effect size of 0.17, while the afternoon group had an $F_{1,9}$ -ratio of 6.53, p value of 0.03, and effect size of 0.45. A regression of temperature and proportion of time parents spent off the nest (Fig. 3) was also significant yet weakly negative ($R^2 = 0.047224$, $p = 0.0141$). The ANOVAs of temperature and parental absence had an $F_{1,9}$ -ratio of 0.59, p value of 0.46, and effect size of 0.07 for the morning group and an $F_{1,9}$ -ratio of 1.45, p value of 0.26, and effect size of 0.15 for the afternoon group.

Discussion

This study seeks to address the relationship of daily temperature with parental nest attendance behaviors. I hypothesized that feeding frequency would be reduced on cold mornings and on hot afternoons so that the parent MWCS could spend more time protecting nestlings from the days' most harsh temperatures. This was analyzed by quantifying the frequency of feedings per 30 minute time interval as well as the proportion of time that parents were absent from the nest. A long-term study of MWCS found that, in brood sizes of three or four nestlings aged zero days, adults were recorded making an average of 3.5 feeding trips per hour. This rate quickly grew to a mean of 16.5 trips per hour once nestlings reached nine days old (Morton 2002). My data was collected on days 5-6 of nestling development, when feeding frequencies can range from 13 to 16 trips per hour (Morton 2002). By filming only when nestlings are within a set age range ensures some consistency of parental fitness because the nests will have already progressed to at least day 17 of development since clutch initiation; furthermore, the thermoregulatory capabilities of the nestlings are standardized. Despite yielding significant p values, the linear regressions of temperature vs. feeding frequency and temperature vs. parental absence both had extremely low R -squared values. Thus, there was no true correlation seen in either regression. However, running one-way ANOVAs over large blocks of time (periods 2-8 and 9-15) with averaged values for temperature vs feeding frequency (Fig. 4) and parental absence (Fig. 5) revealed more interesting results. On cold mornings (time period 2-8 mean temperatures ranging from 9.1 °C to 13.1 °C), the mean feeding frequency is higher—though not significantly—than that of warm mornings (time period 2-8 mean temperatures ranging from 15.2 °C to 19.9 °C). This is contrary to what I predicted, as I expected more feedings to occur on warm mornings while temperatures are relatively mild and nestlings do not require as much incubation. However, on cold afternoons (19.4 °C to 23.5 °C), there was a significantly higher feeding frequency ($p = 0.03$) than on warm afternoons (23.6 °C to 45.0 °C). This supports part of my hypothesis, wherein parent MWCS must spend more time shading their nestlings than they do foraging when the afternoon sun and temperatures are harsh. In the comparison of temperature to parental absence, warmer mornings have noticeably but not significantly higher proportions of parental absence than colder mornings. This also supports part of my hypothesis, as I predicted that warmer morning temperatures will allow parents to spend longer stretches of time off of the nest foraging rather than incubating the young. In afternoons, however, the cold and warm days have nearly equivalent proportions of time spent off the nest. These results are interesting because the trends within feeding frequency and proportion of parental absence do not align; in some cases, they contradict each other. From this study, the causes of these differences remain unknown. A possibility for future investigation is determining what percentage of time that parents spend off the nest is devoted to foraging for their nestlings versus foraging for themselves, exhibiting territorial behavior, or performing another activity.

Temperature was the factor of primary interest in this study. However, there are a variety of other factors that may also be influential on feeding frequency and overall nest visitation, such as parent personality. A study on Carolina Chickadees (*Poecile carolinensis*) found consistent attentiveness within pairs of birds but variable attentiveness among individuals and between different pairs. This indicates that individual personality may play an important role in parental behavior (Eldredge et al. 2015). MWCS crown stripe width has been established as a reliable badge to indicate dominance among individuals, and thus may be a potential avenue of investigation – or, at the very least, a variable to account for in the future (Laubach et al. 2013). An additional factor to consider is that proximity to road may increase directly with parental attendance, since a study on MWCS found that nestling development was altered and parental attendance was higher in nests

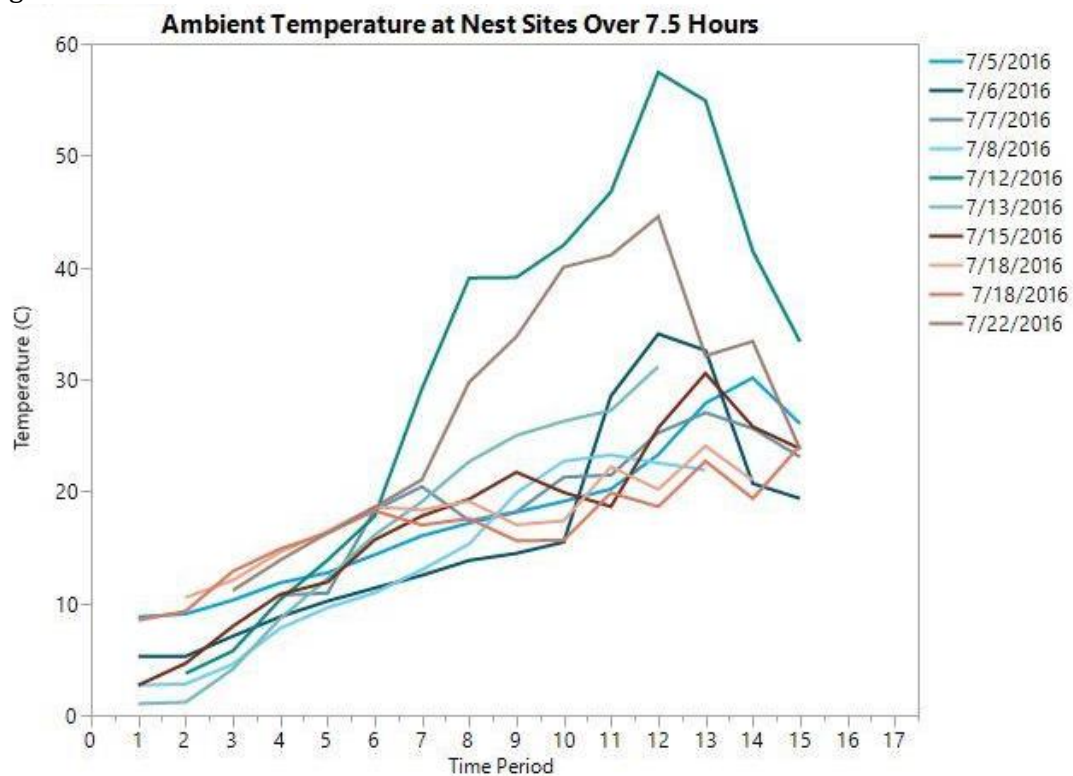
closer to a road (Crino et al. 2011). Due to a highly restricted sample size, I was unable to control for proximity to road in this study: my nests ranged from 5m to 114.09m away from the roadside. Finally, the frequency of feeding may decrease as the number of nestlings fed within one interval increases (Reed 2016). In future extensions of this project, I intend to consider how many nestlings are fed during one feeding interval, and whether or not this is correlated to temperature. Perhaps at colder temperatures, parents attempt to feed as many nestlings as possible in one interval so that more time can be devoted to incubation.

This project serves as a pilot study for what will hopefully be expanded upon in the future. I had restrictions on sample size due to a variety of factors—in order to collect as much data as possible, every MWCS nest that had been located was filmed. One restriction was that some nests were either filmed starting late due to logistical issues or depredation resulted in footage that ended too early. A potential bias in this study is that the nests we found may not be representative of the overall MWCS nests in our field sites. Because we use a rope drag to locate nests, there are some limitations to the potential nest sites we can search. In situations where the willows are taller than the people searching, the ability to see a female MWCS flush is inhibited. Furthermore, willow thickets with other types of vegetation interspersed, such as tall spruce trees, cannot be searched as thoroughly because we must avoid these obstacles to prevent the rope drag from tangling. A factor we could control for was elevation: all of the nests in this data set are within a similar range of elevation, from 2921m to 3169m. This minimized climatic variation that occurs over drastic changes in elevation. Thus, the sources of temperature variation should arise from differences in day-to-day weather, as intended by the study. To effectively expand this project, it is crucial that at least 15 more nests are correctly filmed for analysis. Nest camera-centered studies have highly variable sample sizes, ranging from 17 to 65 (Bolton et al. 2007; Danaë et al. 2008). From this year, I have four nests that were filmed without any issues from at least 07:30:00 til 14:30:00. With 15 additional nests, my total sample size would reach 19. This will be on the low end of acceptable sample sizes, and should permit more insightful statistical analysis. Should this project continue in future seasons and a larger sample size is gathered, I would maintain my original hypotheses and predictions.

There have been few studies investigating the role of temperature in determining parental nest attentiveness for nestlings rather than eggs. However, the nestling stage is one of the most demanding times of the breeding season for parent birds. Especially in MWCS, with the pressures of high elevation and nestlings with demanding energetic needs, nest thermoregulation and feeding accounts for most of the parents' activity during the day (Morton 2002). Gaining a clearer understanding of what the relationships are between temperature and nest attendance behavior in MWCS will thus provide insight into the behaviors and energy allocation of altricial passerine birds at high elevation for an important part of the breeding season.

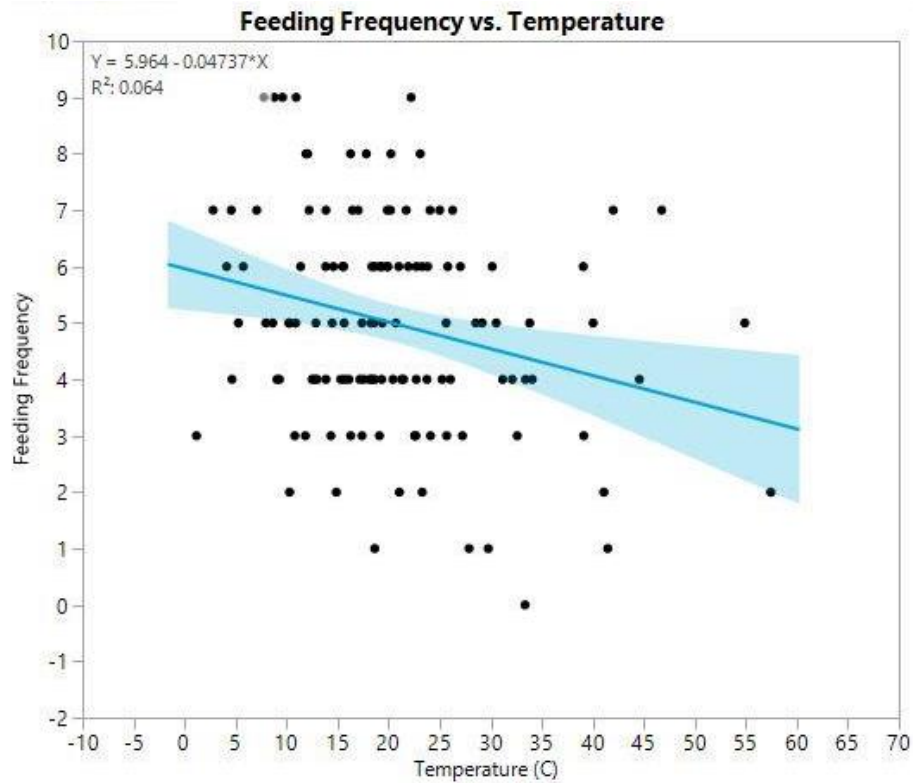
Figures

Fig. 1



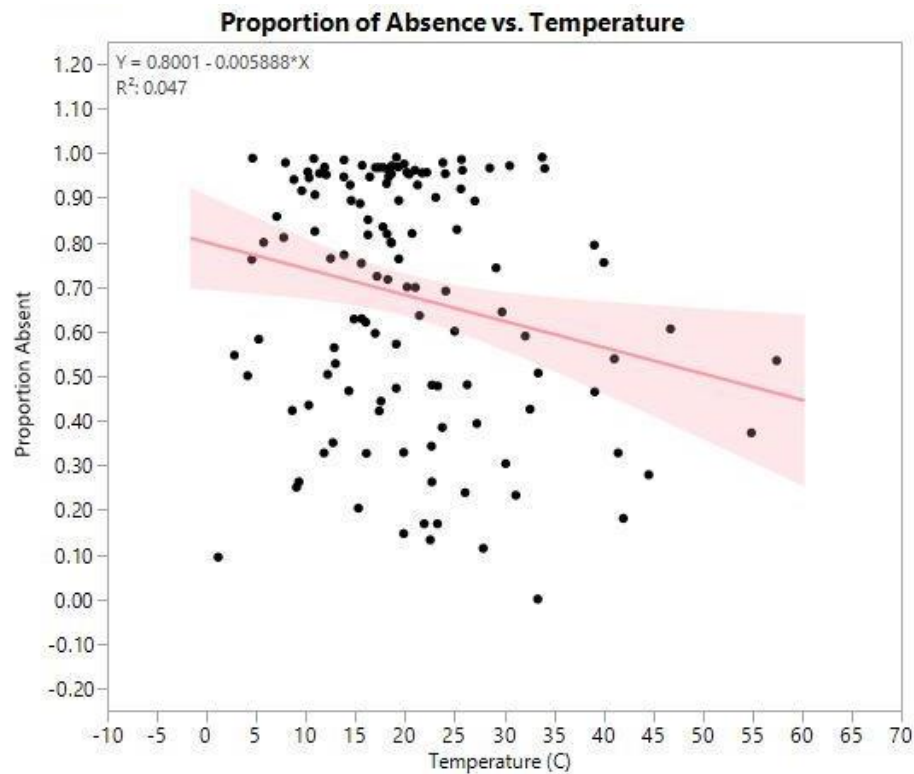
Graph of ambient temperature recorded during filming at each nest. Displays differences in daily temperature trends at study sites. Time periods are 30 minute intervals, with 1 being 07:00-07:30 and 15 being 14:00-14:30.

Fig. 2



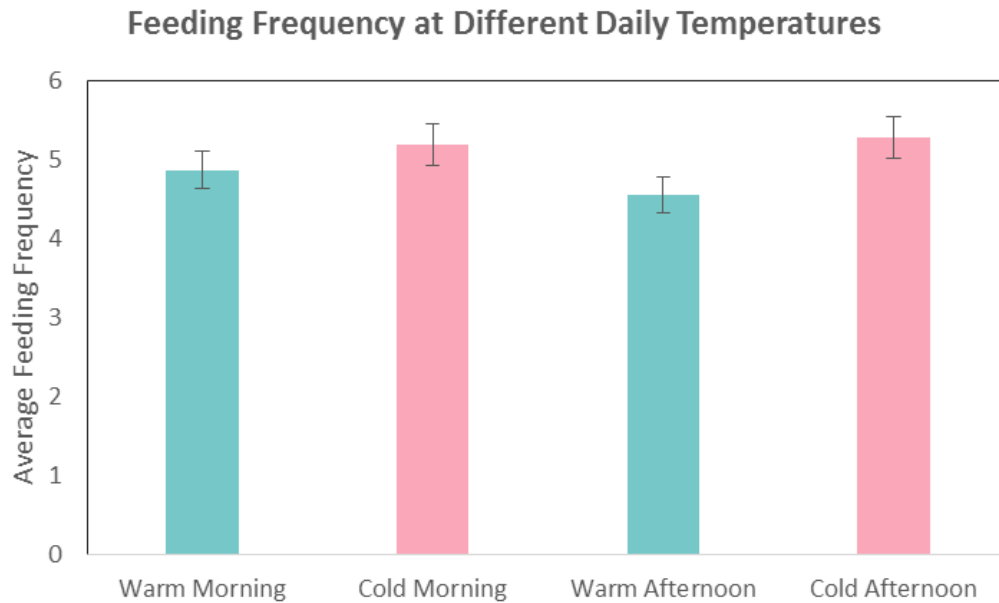
Graph of calculated feeding frequency per 30 minute time period against averaged temperature per 30 minute time period. Linear regression revealed weak negative correlation with $p = 0.0042$.

Fig. 3



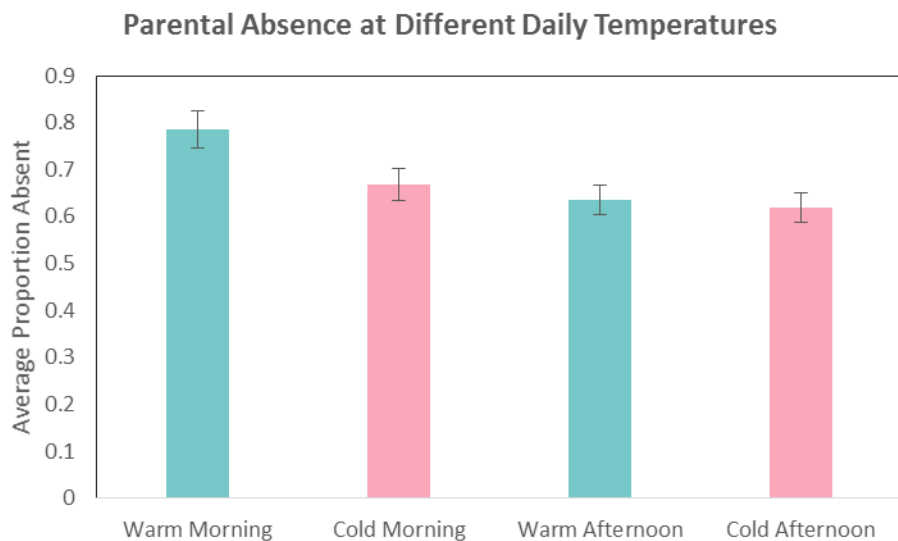
Graph of calculated proportion of parental absence per 30 minute time period against averaged temperature per 30 minute time period. Linear regression revealed weak negative correlation with $p = 0.0141$.

Fig. 4



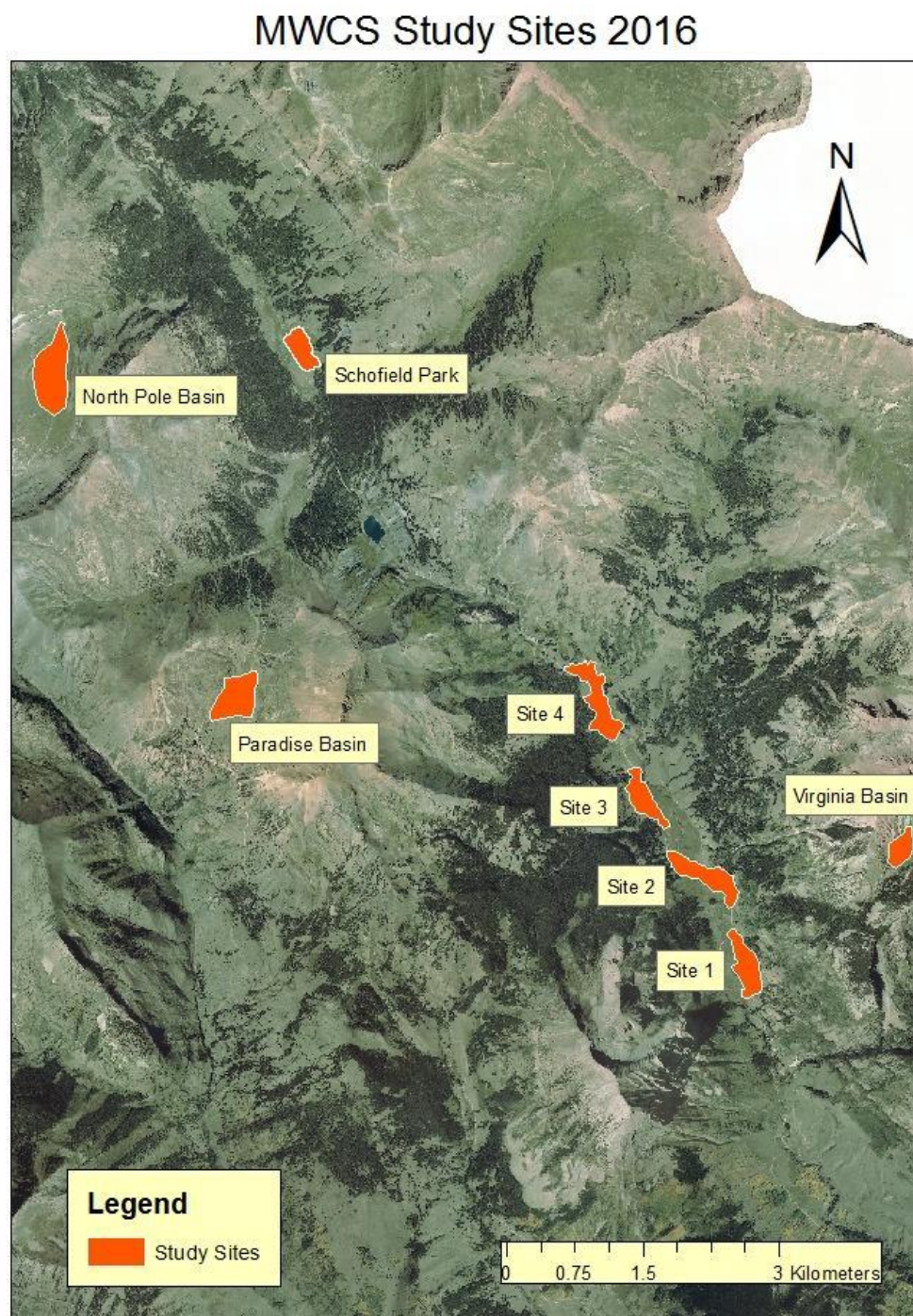
Graph of mean feeding frequency against mean temperature for morning (merged time periods 2-8) and afternoon (merged time periods 9-15). One-way ANOVA for mornings revealed $F_{1,9}$ ratio of 1.66, p value of 0.23, and effect size of 0.17. One-way ANOVA for afternoons revealed $F_{1,9}$ -ratio of 6.53, p value of 0.03, and effect size of 0.45.

Fig. 5



Graph of mean proportion of parental absence against mean temperature for morning (merged time periods 2-8) and afternoon (merged time periods 9-15). One-way ANOVA for mornings revealed $F_{1,9}$ -ratio of 0.59, p value of 0.46, and effect size of 0.07. One-way ANOVA for afternoons revealed $F_{1,9}$ -ratio of 1.45, p value of 0.26, and effect size of 0.15.

Fig. 6



Map of study sites surrounding the Rocky Mountain Biological Laboratory. Low elevation sites start at 2924m and include Sites 1, 2, 3, and 4. Medium elevation site at Schofield Park is at 3167m, and high elevation sites reaching 3465m include Virginia Basin, Paradise Basin, and North Pole Basin.

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