

The Effects of Nest-Site Selection and Microclimate on Nest Survival in
Sparrows of High Elevation

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Independent Research and Course 2016

Abstract

Nest-site selection is important in the determination of nest success in several bird species (Holway 1991, Wells and Fuhlendorf 2005). Birds that nest in high elevation breeding sites are under greater environmental stress, making it even more crucial for individuals to choose nest microclimates that buffer the nest and offspring from extreme weather events and provide stable conditions for the young (Bears et al. 2009). The Microclimate Selection Hypothesis predicts that females should choose nesting sites that best protect them and their offspring from severe or unpredictable weather events, such as extreme temperatures or high wind (With and Webb 1993, Wells and Fuhlendorf 2005). The relationship between nest-site characteristics, nest microclimate, and nest survival was examined in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) and the Lincoln's Sparrows (*Melospiza lincolnii*) in three subalpine meadow sites in Gothic, CO. There were no significant differences between the nest-site characteristics of nests with a more stable microclimate and nests with a less stable microclimate, though the two groups did have significantly different microclimates. Overhead nest concealment and distance to the nearest road had a positive effect on daily nest survival but none of the nest characteristics had a significant positive or negative effect on the model.

Introduction

Nest-site selection is an important factor that has been found to determine reproductive success in several bird species (Holway 1991, Wells and Fuhlendorf 2005). Given that limited lifetime breeding opportunities exist, the importance of nest microhabitat for offspring development has induced maternal selection for optimal nest sites (Lloyd and Martin 2004). To be successful, reproductive individuals must balance the trade offs of both biotic and abiotic factors to maximize the likelihood of nest survival (Holway 1991). For many bird species, it is crucial for the nest site to have favorable microclimate conditions to maintain optimal temperatures for the eggs during incubation and to accommodate the metabolic demands of the growing nestlings after hatching (Lloyd and Martin 2004). To maximize the probability of success, nests must also be placed in a microhabitat located in close proximity to accessible and stable resources to allow the parents to nourish themselves and to satiate their offspring's metabolic requirements (Holway 1991). Finally, because predation is the leading cause of nest failure in the majority of bird species, the nest site must balance both concealment from predators and the ability to view their surroundings to best minimize predation of eggs and nestlings (Morton et al. 1993, Gotmark et al. 1995).

Although nest predation is widely considered to be the strongest selecting factor for nest-site selection, studies have shown that nest microhabitat selection may also be in response to the fitness costs associated with variations in microclimate between nesting locations (Lloyd and Martin 2004). The Microclimate Selection Hypothesis predicts that females should choose nesting sites that best protect them and their offspring from severe or unpredictable weather events, such as extreme temperatures or high wind (With and Webb 1993, Wells and Fuhlendorf 2005). It has been suggested that nest-site characteristics, such as thick vegetation, could act as a wind screen and provide insulation

to prevent heat gain during the day and heat loss over night, helping to maintain nest temperature stability even when the parent is unable to incubate (Holway 1991).

Nest-site selection is likely even more important at high elevations, which commonly experience shorter growing seasons, more extreme weather, lower plant productivity, delays in vegetation emergence, and greater snow cover throughout the breeding season (Bears et al. 2009). According to the Microclimate Selection Hypothesis, species that are nesting at high elevation should select sites that best ameliorate the unpredictable conditions that are characteristic of alpine and subalpine environments to increase the likelihood of nest survival. The Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*; hereafter MWCS) and the Lincoln's Sparrow (*Melospiza lincolni*; hereafter LISP) are migratory passerines that breed in alpine and subalpine meadows within the mountainous regions of the western United States at elevations of 2,500m to 3,500m (Morton 2002, Stephens and Anderson 2003). Due to the harsh environmental conditions at high elevation, selecting nest-site locations that provide adequate shelter from predators and provide a buffer from inclement weather is of particular importance to the success and nest survival of these species.

The aim of this study is to test the Microclimate Selection Hypothesis by analyzing how nest-site characteristics influence microclimate and ultimately, nest survival, for two high elevation sparrows (MWCS and LISP). Nest-site characteristics, nest survival, and microclimate were quantified for MWCS and LISP nests over the breeding season. Based on current understanding of the ecology of high-elevation birds, I hypothesize that (1) nests located in sites with thick vegetation and high overhead concealment will have a more stable microclimate and that (2) nests situated in sites conducive to a more stable microclimate will have higher daily nest survival.

Methods

Study site

Data was collected from June 15th to July 29th 2016 at three sites located to the north of the Rocky Mountain Biological Laboratory in Gothic, CO, USA (38°95'N, 106°98'W, 2,910-3,000m). Nests were located and monitored at three montane meadows: two sites were within the East River Valley (2,921-3,004m) of the Gunnison National Forest and one site in Schofield Park (3,169m) in the White River National Forest (Fig. 1). Plant communities at these sites were predominantly willows (*Salix* spp.) and *Veratrum* spp, with many wildflowers interspersed within large meadows surrounded by mostly Engelmann's spruce (*Picea engelmannii*).

Nest searching and monitoring

An intensive nest searching effort commenced between June 15th, 2016 and July 14th, 2016, using a combination of behavioral observations and rope dragging. Rope dragging involved a 12-meter rope with 10 groups of three aluminum cans (12 oz) attached to the rope with zip-ties (Conover et al. 2011). The rope-drag was pulled across the willow canopy by two researchers to induce a flush by the attending parent. Researchers maintained constant visual focus down the rope drag to ensure the precise flushing location was observed. Upon observing a flushing parent, the location was investigated thoroughly by both researchers to quickly locate the nest. No more than 15 minutes were

spent investigating each flush to minimize negative impacts on nest outcome. Nests were marked with GPS coordinates and orange flagging. Flagging was placed three paces north and south from the nest and below the canopy to avoid attracting predators to the area. Nests were monitored every two to four days with observers being careful not to trample nest-site vegetation, leave dead end trails, or leave scent trails to minimize the probability of abandonment by the parents or inducing predation (Martin 1993). Data was collected on nest contents, age of eggs and/or nestlings, parental presence and behavior and nest outcome. Egg development was monitored by candling at least two eggs throughout incubation (Lokemoen and Koford 1996). We identified parents whenever possible by observing color bands. Nest monitoring continued until the nest was no longer active, at which point we declared the nest successful or unsuccessful based on nest age, parent behavior (chipping), and other clues at the nest site (feces, disturbance, egg shells, etc.) (Conover et al. 2011). Nests were deemed successful if one or more nestlings fledged and failed nests were classified as either abandoned or depredated.

Nest-site characteristics and microclimate

Vegetation surveys were performed between 26 and 32 days after clutch initiation to standardize vegetative growth based on time for each nest, regardless of duration of nest activity. We recorded nest height, vegetation height, overhead concealment, vegetation density and substrate type, and the distance of the nest from the nearest road. We determined overhead concealment by placing a nest-sized gridded circle on the nest and counting the number of squares that were visible when the nest was observed from directly overhead. The number of visible squares was then divided by the total number of squares to estimate nest concealment percentage. To determine vegetation density, an observer recorded the lowest height at which the nest area was visible on a 120-cm modified-Robel pole from a 4-m distance and 1-m height at all four cardinal directions (Robel et al. 1970, Renken and Dinsmore 1987). Four meters is a common distance at which predators will opportunistically predate a nest (Robel et al. 1970).

Nest microclimate was determined using Thermochron® iButton data loggers, which were preset to collect temperature readings every two minutes throughout the incubation period. Data loggers were placed beneath the nest lining and approximately 15-cm from the nest in a location that best represented the nest-site to monitor ambient temperature in the surrounding area.

Nest composition

Once inactive, nests were collected and dried in a 60° C drying oven for 24 hours before being weighed. Drying time was determined experimentally, as soaked nests took approximately 24 hours to dry completely. Total weight of the nest was first determined by weighing the entire nest, including both the lining and outer frame. After the nest had been weighed, the lining and outer frame of the nest were weighed separately as indicators of nest insulation (Kern 1984).

Data analysis

Data analysis was performed using JMP® statistical software and Microsoft Excel®. MWCS daily nest survival rates (DSR) and models were determined using Program MARK

(Dinsmore and Dinsmore 2007). DSR was not calculated for LISP due to inadequate sample size. The decreasing rate of change (ROC) of the ambient nest temperature was calculated every time the incubating parent left the nest during the incubation stage for each nest between 0700 and 0800. Non-incubation bouts were defined as periods of time when the nest temperature gradually decreased over several minutes. Mean adjacent temperatures were calculated over the same time period for comparison. The ROC and mean temperatures were averaged for our final analysis. Relative temperature differences were calculated by subtracting the adjacent temperature from the nest temperature. All viable nests were sorted into high ($\text{ROC} \geq -.025$) and low ($\text{ROC} \leq -.025$) groups. Mean nest-site characteristics of the two groups were then compared using two-sample t-tests. Linear regressions were analyzed using analysis of variance.

Results

We monitored and performed vegetation surveys on 26 MWCS and LISP nests over the course of the breeding season. Of these 26 nests, ten were used for microclimate analysis and eighteen MWCS nests were analyzed in Program MARK.

Thirteen of the 26 (50%) nests monitored over the course of the breeding season successfully fledged one or more nestlings. Of the 13 failed nests, 12 (92%) failed due to predation and one (8%) failed from parental abandonment. Four of the 26 nests were found while in the laying stage (15%), 20 nests were found in the incubation stage (77%), and two nests were found in the nestling stage (8%). Eighteen of the nests (of which six were used in microclimate analyses) were MWCS, while the remaining nests were LISP.

The high and low ROC groups differed significantly in their ROC ($p < 0.05$), but none of the other nest-site characteristics varied significantly between groups (Table 1). Nests that exhibited a low mean rate of change, on average, placed their nests higher from the ground than nests with a high mean rate of change, though this difference was not statistically significant (Table 1). The relative difference between the adjacent and nest temperatures was 57% greater in nests with a high mean rate of change than in nests with a low rate of change, but due to the small sample size, the difference is not significant (Table 1).

We found that nests had, on average, a 95.6% chance of surviving for every day of the breeding season, which equated to a 32.4% chance of survival per nesting cycle for each of the 18 MWCS nests that were analyzed in Program MARK. Nest concealment percentage positively affected DSR, but none of the nest-site characteristics had a significant effect in the model (Table 2).

Though not statistically significant, mean adjacent temperature was positively correlated with mean average rate of change (Fig. 2, $R^2 = 0.29$, $p = 0.10$). Nest concealment percentage had a weak positive relationship with mean average rate of change, though this relationship has little value as a predictive model (Fig 3. $R^2 = 0.06$, $p = 0.47$). Mean vegetation density exhibited a weak negative effect on mean rate of change (Fig. 4. $R^2 = 0.08$, $p = 0.40$). Mean relative difference and mean average rate of change were not significantly affected by nest weight, lining weight, outer frame weight, distance to road, or nest height. There was no significant difference between the nest lining weights of the two groups.

Discussion

Contrary to what we predicted in this pilot study, nests that had greater vegetative cover did not seem to be associated with a more stable climate. In addition, nests with nest-site characteristics that were predicted to be conducive to stable nest microclimate did not significantly alter daily nest survival, which does not support the Microclimate Selection Hypothesis. However, there were noticeable differences between nest microhabitats and nests with different levels of microclimate stability. Because very little is known about the validity of the Microclimate Selection Hypothesis in birds that breed at high elevations, these results offer insights into the nest-site preferences of high elevation birds and open up more questions regarding the relationship between nest microclimate and nest microhabitat that should be explored in future work.

Though we observed differences in microclimate between nests, there is no substantial evidence that these differences in microclimate are having a significant effect on nest survival. Similarly, there does appear to be a difference in nest-site characteristics between nests with a high and low mean rate of temperature change, but due to our insufficient sample size, these differences were not statistically significant.

Interestingly, a high temperature rate of change when the female leaves the nest was associated with taller vegetation over the nest and higher mean vegetation density surrounding the nest. This was unexpected, as vegetation and other objects around the nest, such as shrubs or rocks, can act as a barrier to protect the nest from sun, wind, and rain exposure (Davis 2005). One possible explanation is that high vegetative cover around the nest may prevent the nest from warming from the sun in the early morning, causing the nest temperature to become unstable when left unattended. Nests with a high temperature rate of change were also associated with a higher relative difference between the nest temperature and adjacent temperature. It is possible that because these nests are maintaining a temperature well above that of the immediate surrounding microhabitat, the nest is unable to conserve enough heat to maintain such a high relative difference when the incubating parent leaves the nest.

High nest concealment and taller nest height were both positively associated with a low mean rate of change. In the early morning when the parents are working to keep the nest warm enough to maintain the optimal incubation temperature, having a nest that is located close to the ground may be a disadvantage. Though nests located farther from the ground have greater wind exposure on average, nests located on or near the ground experience colder temperatures for longer and therefore may require greater insulation to maintain nest temperature stability (Kern 1984).

None of our model effects were able to significantly explain variation in nest survival, but there was a positive association between nest concealment and nest survival. To be able to fully explore the relationship between nest-site characteristics and nest survival, a nest sample size minimum of 28 nests would be needed. As this study was a pilot study, we would need to incorporate nesting data from at least one more breeding season to be able to fully understand if there is a significant association between nest microhabitat and the probability of fledging young. In addition, nest survival calculations can be highly variable due to the strong possibility of failure due to random chance, such as an opportunistic predator, making it difficult to fully understand the relationship between nest-site characteristics and daily nest survival.

Due to our small sample size, our data was too variable to make any reliable predictions about mean rate of change using mean adjacent temperature, nest concealment, or mean vegetation density. If this study is continued, I would focus my efforts on ensuring that iButton data loggers are placed on nests as early as possible in the incubation period. Once the nest enters the nestling stage, it is difficult to get reliable measures of nest microclimate because the nestlings gain the ability to thermoregulate between day five and seven after hatching (Morton 2002). Due to a malfunction with many of our data loggers that caused inconsistencies in temperature readings, a large portion of our data could not be used. Though examining the mean rate of change from 7 A.M. to 8 A.M. is informative, I would be interested in examining the rate of change in the early and mid-afternoon to better understand the tradeoffs of different nest-site characteristics throughout the day.

After running power analyses on the differences in nest-site characteristics between nests with low and high temperature rates of change, I have concluded that I would need a sample size of at least 40 nests to be able to confidently detect a significant association between nest-site characteristics and microclimate at our current effect size. Some characteristics, such as nest concealment percentage and mean vegetation density, may require an even larger sample size due to the large variation surrounding their means.

One major cause of potential error with this study is the fact that we incorporated LISP data into our models. LISP and MWCS are both ground nesting sparrows with similar life histories, clutch sizes, and body sizes, making them highly comparable (Morton 2002, Stephens and Anderson 2003). However, LISP and MWCS inherently have differences in their nest-site characteristics, including nest size, which may have contributed to the large amount of variation in our nest site data. To maximize our sample size for analysis, we decided to incorporate LISP data into our data set despite the small potential differences in nesting strategies. In future studies, I will focus more exclusively on the MWCS, or monitor enough nests to be able to separate MWCS and LISP without having an insufficient sample size.

Further work needs to be done to more confidently understand how nest-site characteristics are affecting the microclimate of the nest and whether these affects on microclimate can have a significant impact on nest survival. In the future, I would standardize the day that the data loggers are placed on the nest, and begin nest searching earlier in the season to maximize the amount of nests found in the laying and incubation stage. It would also be interesting to investigate how nest-site characteristics affect the amount of wind that the nest is exposed to by placing a high-powered fan at a set distance from the nest and recording wind speed. This experiment could give us important insights into the tradeoffs of parental decisions regarding nest sites.

Figures and tables:

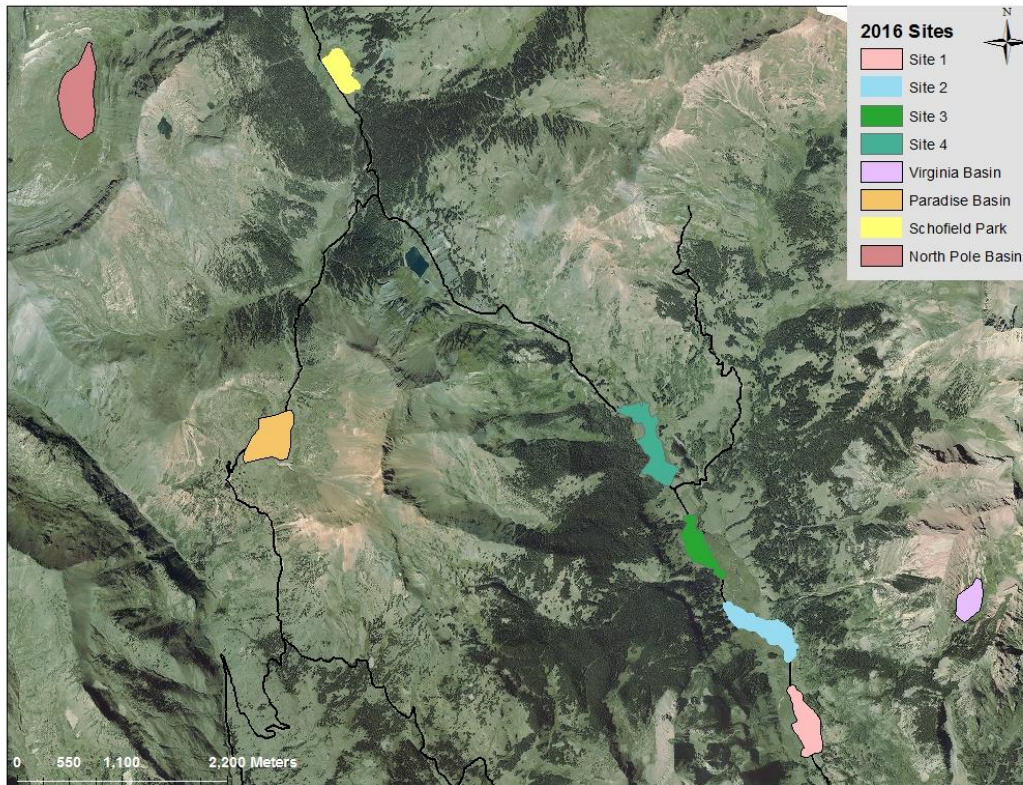


Figure 1. Topographical map of MWCS and LISP nest site locations. Nests were monitored at Site 2, Site 4, and Schofield Park.

Table 1. Nest-site differences between low and high temperature rate of changes from 0700 to 0800¹.

Nest-site characteristic	Low Mean +/- SD	High Mean +/- SD	P-value	T-value
Mean Adjacent Temp	7.0 +/- 2.7	6.2 +/- 2.4	0.668	0.446
Mean Rate of Change	-0.17 +/- 0.07	-0.50 +/- 0.25	0.026	2.712
Mean Relative Diff ²	8.5 +/- 1.6	13.4 +/- 5.2	0.080	1.887
Veg. Height	64.8 +/- 16.9	75.2 +/- 20.7	0.411	0.867
Distance to Road	29 +/- 39.6	47 +/- 37.6	0.482	0.736
Nest Height	9 +/- 9.7	0.2 +/- 0.4	0.077	2.022
NC% ³	47.5 +/- 39.3	35 +/- 37.5	0.621	0.513
Mean Veg. Density	71.5 +/- 30.6	77.7 +/- 27.4	0.743	0.339

¹ N= 5 nests for each group. DF= 8.

²Mean Relative Diff = Mean Relative Difference

³NC% = Nest Concealment Percentage

Table 2. Model results from 18 MWCS nests modeled using Program MARK. N=242 days.

Model	AICc	Beta	Standard Error	Upper 95% CI	Lower 95% CI
S+T	68.02	-0.334	0.327	-0.976	0.307
S+TT	68.33	-0.418	0.259	-0.926	0.089
S+NC%	68.46	0.009	0.009	-0.009	0.027
S+RoadDist	68.97	0.005	0.008	-0.011	0.023

¹T= linear seasonal trend; TT = quadratic seasonal trend; NC% = nest concealment percentage; RoadDist= distance to the nearest road.

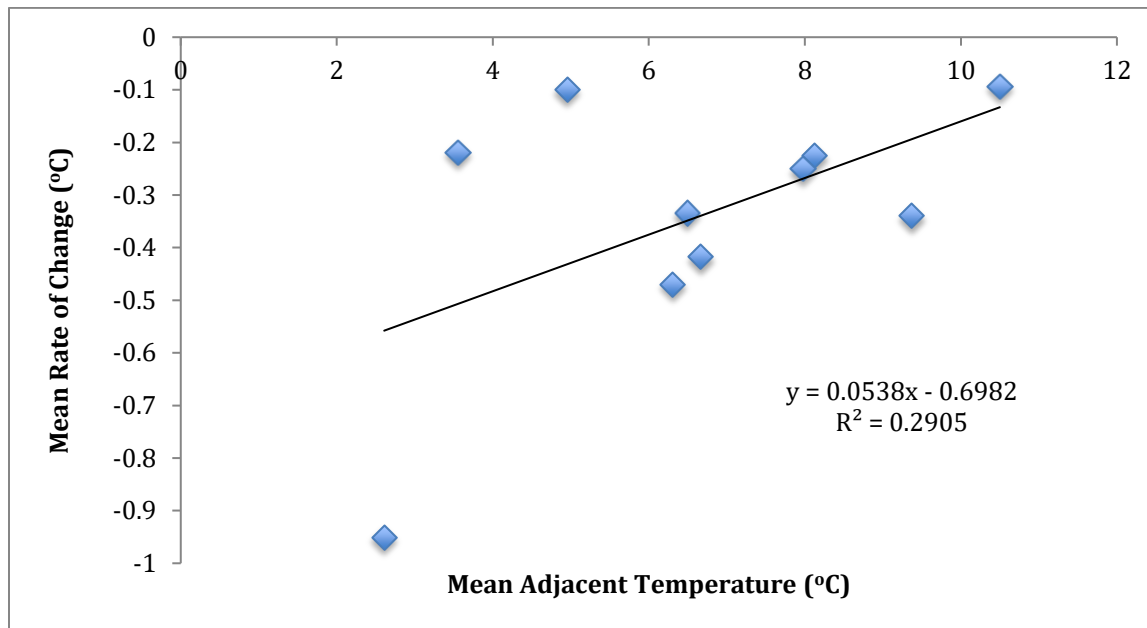


Figure 2. Mean rate of change (°C) from 0700 to 0800 as a function of mean adjacent temperature (°C) in 10 MWCS and LISP nests ($R^2 = 0.29$, ANOVA $p = 0.10$).

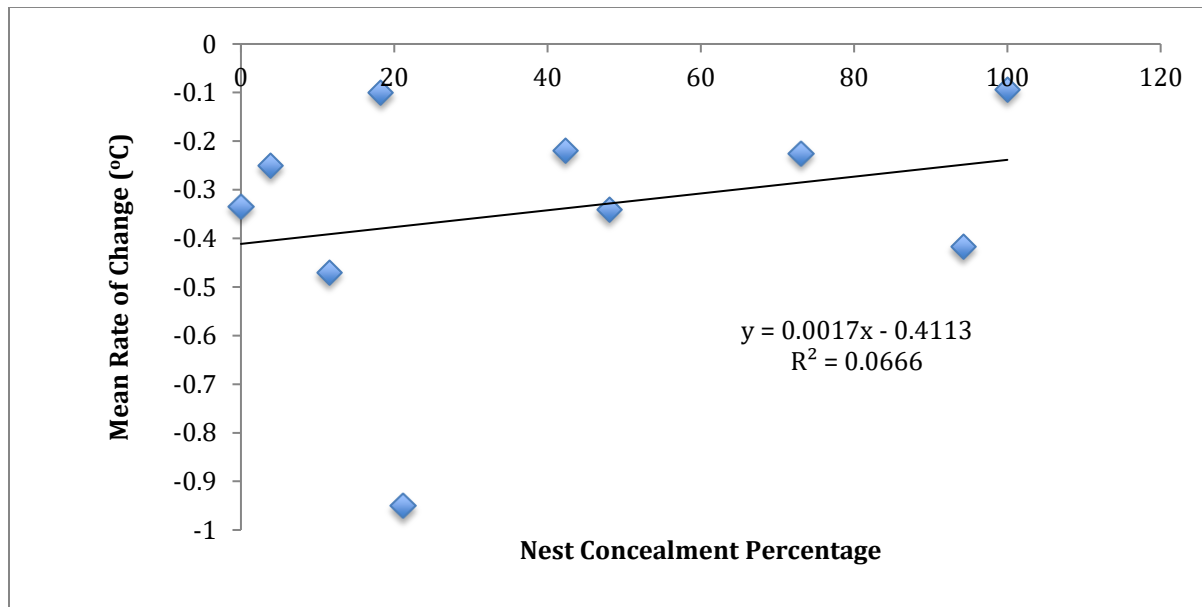


Figure 3. Mean rate of change (°C) from 0700 to 0800 . as a function of nest concealment percentage in 10 MWCS and LISP nests ($R^2 = 0.06$, ANOVA $p = 0.47$).

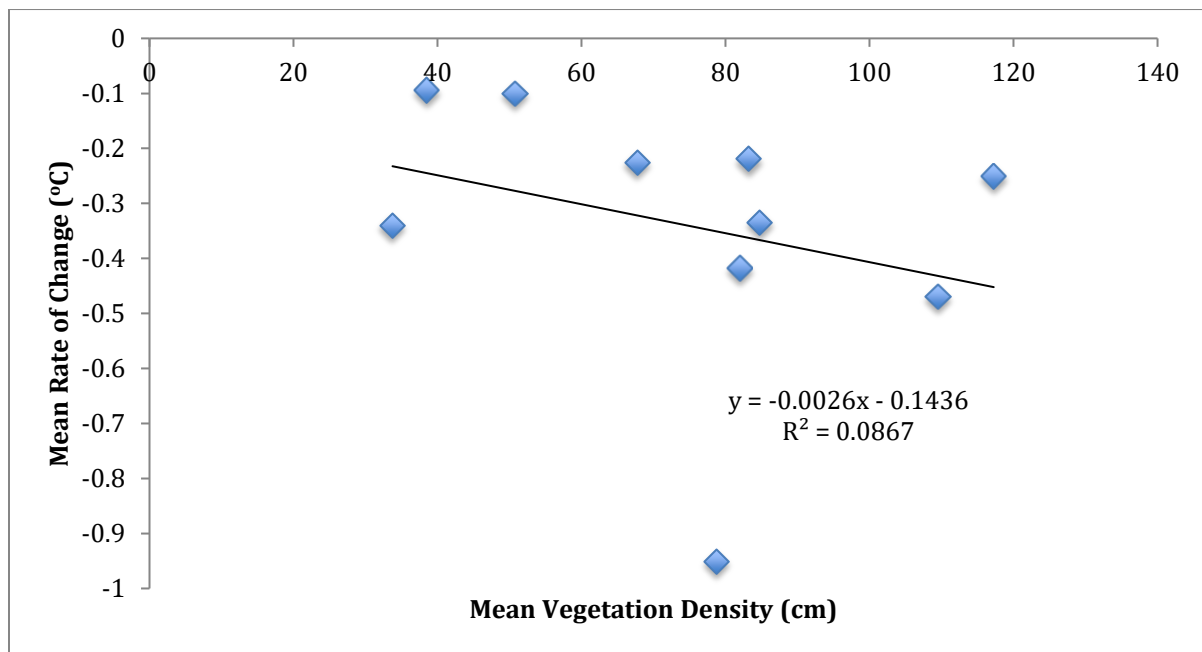


Figure 4. Mean rate of change (°C) from 0700 to 0800 as a function of mean vegetation density in 10 MWCS and LISP nests ($R^2 = 0.08$, ANOVA $p = 0.40$).

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