

Can Variation of Insect Populations Affect Mountain White-crowned Sparrow Daily Nest Survival?

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Abstract

Mountain white-crowned sparrows' (*Zonotrichia leucophrys oriantha*; hereafter MWCS) diet fluctuates across seasons given their changing nutrient requirements across life stages and environment. Insect population densities may influence the daily nest survival of MWCS who depend upon these organisms as food because the transition from egg to adult occurs in less than one year. Insect population fluctuation is influenced by temperature (°C) and precipitation (cm), which were also examined in this nest survival study. Our objective was to determine nest success relative to insect prey availability with corresponding abiotic shifts. Nest data was collected in the upper East River Valley, Colorado, over a period of seven years (2005, 2007, 2008, and 2014-2017). We calculated daily nest survival using a time-sensitive, hierarchical modeling procedure in program MARK to determine the effects of insect population density (Diptera and Lepidoptera), weather, nest stage (incubation or nestling), clutch size, and seasonality (linear and quadratic). We found a slight, but significant negative correlation between nest survival and Diptera abundance and significant positive correlation between nest survival and Lepidoptera abundance. This study helps us to understand the resource requirements of MWCS throughout the nesting season so that we may predict future patterns in population fluctuation based on prey population density as impacted by temperature and precipitation.

Introduction

Mountainous environments are impacted by climate change as a consequence of the diversity of sub-ecosystems created by elevational gradients (Fort 2015). Each sub-ecosystem endures unique weather patterns and subsequently, support unique communities which are adapted to these abiotic conditions (Rahbek 1995, Fort 2015). Climate change has altered the abiotic effects on these subecosystems and hence, resulted in seasonal shifts (Loarie et al. 2009) that increase seasonal variation in temperature and precipitation. Intensified fluctuation of abiotic components may produce negative consequences for montane organisms, such as reduced fitness and reproductive success (Morton 2002). Hence, it is increasingly important to understand how these shifts alter abiotic and biotic interactions regarding species' survival and reproduction (Boggs and Inouye 2012).

Environmental change is happening too quickly for adaptation to occur in many birds, therefore songbirds' reproductive cycles may not synchronize appropriately with altered abiotic and biotic conditions (Crick 2004). Mountain breeding birds' reproductive strategies are particularly vulnerable to rapid abiotic shifts because they are already limited by a short breeding season, food scarcity, harsh weather conditions, and late snowmelt (Cockrem 1995, Weiser et al. 2017), all of which have been impacted by climate change (Carey et al. 1982, Crick 2004). A wide elevational breeding range makes mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*; hereafter MWCS) an ideal study species for nest survival. Harsh weather (i.e., prolonged hot or cold temperatures or high precipitation) may indirectly increase egg and nestling mortality through reduced parental contribution of food and thermoregulation (Morton 2002, Martin et al. 2017). Earlier snowmelt, warmer temperatures, and higher precipitation have been shown to significantly reduce egg and nestling survival in species such as savannah sparrows (*Passerculus sandwichensis*), horned larks (*Eremophila alpestris*) (Martin et al. 2017),

and MWCS (Morton 2002, E. Putnam, unpublished data). Abiotic shifts can also reduce foraging and courtship activities which may negatively impact reproductive success (Crick 2004). Climate change can alter reproductive timing, thus disrupting the existing temporal relationship between avian reproduction and insect emergence (Visser et al. 2006).

Insect populations and the timing of their emergence is dependent upon environmental factors that are impacted by climate change (Boggs and Inouye 2012). Insect populations are specifically influenced by temperature thresholds, as most require warm temperatures for a predetermined to promote enzyme activity and facilitate successful transition between life stages (i.e., egg, larvae, pupae, and adult; Damos and Savopoulou-Soultan 2011). However, temperature extremes can inhibit these enzymes, thus limiting crucial physiological responses, such as chitin production. Therefore, temperature is the primary limiting factor for insect populations in some climates (Damos and Savopoulou-Soultan 2011). Furthermore, abiotic factors also drive vegetative growth, which is important for insect food and incubation substrates (Nieuwenhove et al. 2016). Ultimately, areas with altered climates can induce insect distributional shifts and/or population declines, which may translate into a lack of food for their predators, such as birds (Visser et al. 2006).

In many bird species, prey availability triggers breeding behavior and promotes nest success (Morton 2002 Nooker et al. 2005). The presence of these food resources may lead to earlier clutch laying, shorter incubation, and higher nestling fitness (Nooker et al. 2005). Whereas songbirds (order: Passeriformes) feed on insects during all life stages, certain stages are targeted depending on the consumer's nutritional requirements (Visser et al. 2006). For example, insect larvae are more important during the nestling stage (Dunn and Winkler 2010). Avian reproduction has evolved to temporally coincide with peak insect emergence (Visser et al. 2006), primarily to maximize the availability of food for adequate egg production and proper offspring development (Both et al. 2006). Asynchronization between insect phenology and avian reproduction has led to as much as 90% nestling survival decline in some species (Both et al. 2006). Density-dependent survival of insectivores (i.e., MWCS nestlings) and clutch size are positively correlated with insect population density (Boggs and Inouye 2012). Sparrows rely on insects in the orders Diptera and Lepidoptera as protein-dense food for their young (Best 1977). When seasonal insect die-offs occur, MWCS' diets may change to include a higher proportion of plant materials (Morton 2002). This diet does not provide enough protein to fully nourish nestlings, therefore it is important that maximal insect density co-occurs with bird reproduction (Visser et al. 2006, Dunn and Winkler 2010). A lack of food resources likely causes the average negative linear trend in avian reproduction across the breeding season (Gruebler and Naef-Daenzer 2010) as it correlates with normal insect life cycles (Visser et al. 2006).

The primary objective of this study is to determine if annual insect population densities can influence the daily nest survival (DNS) probability of a breeding songbird at high elevation. I hypothesized that annual insect population densities would be positively correlated with DNS in MWCS because of the high nutritional demands of breeding females and insectivorous, protein-dependent nestlings in a resource-stressed system. Our ability to connect the abiotic impacts of climate change with the subsequent biotic consequences (e.g., songbird reproduction) is increasingly important to predict future population trajectories and assist guiding management actions aimed at population sustainability. It is important for wildlife managers to understand

how and why reproduction is altered, as reproductive success is a crucial metric to predict songbird population sustainability (Martin and Geupel 1993, Morton 2002).

Methods

Study Site

This study was conducted north of Rocky Mountain Biological Laboratory, in the upper East River Valley of the Gunnison National Forest, Colorado, USA (38.9592° N, 106.9898° W) (Fig. 4) in summers (May-September) of 2005, 2007, 2008, 2014-2017. The elevation at these sites was between 2800-3000m. Vegetative cover was mainly comprised of willows (*Salix spp.*), Engelmann spruce (*Picea engelmannii*), and cinquefoil (*Potentilla spp.*), with interspersed herbaceous species, such as corn lily (*Veratrum spp.*) and mountain bluebell (*Mertensia spp.*). Weather during these time periods was highly variable with overnight temperatures often below freezing and daytime temperatures up to 27°C. Precipitation is typically minimal in May and June, with monsoon rains in July.

Insect Abundance

Weekly abundance (number of individuals) data for Diptera were collected on the southern side of the Gothic townsite using a malaise trap (D. Inouye, unpublished data). The malaise trap was set for 48 hours (same days of week and time of day) per sampling period, starting when overnight temperatures were above freezing and continuing through September (D. Inouye, unpublished data). Lepidoptera (*Euphydryas gillettii*) abundance data was collected within single plots in south Gothic and in the upper East River Valley using standard mark release recapture techniques, where individuals were distinguished by marking their hind wings with a marker (Boggs and Inouye 2012).

Nest Searching and Monitoring

Nests were located actively by dragging a rope with aluminum cans attached through areas considered suitable for nesting (willow and cinquefoil cover) to flush out females (Winter et al. 2003). Nests were also found passively by observing parental behaviors and movements in our study sites. We visually searched the area and marked nest locations with flagging tape 4m to the north and south of the nest. We also recorded the location using a GPS so that we could return to monitor offspring development. Potential for nest disturbance was reduced through avoiding presence during nest construction, spending less than five minutes at a nest per visit, observing from a distance when possible, and not creating dead-end paths to nests (Martin and Geupel 1993).

Nests were monitored every two to four days (to ensure consistent and accurate nest fate determination), in which we recorded stage, number and age of eggs or nestlings, time, parental presence, and nest fate (fail or success). Egg stage was estimated using candling against the sun (Lokemoen and Koford 1996) and nestling development by comparing to images (S. Troy, unpublished data). DNS was defined as the number of days that eggs or nestlings are observed in the nest (Martin and Geupel 1993). A nest was considered successful if at least one nestling fledged. We also recorded depredation evidence (i.e., tracks, torn nest lining, parents' chipping).

Video footage of nests was also taken and analyzed. Screenshots of MWCS bringing food items to their nestlings were taken from these videos and the items were identified to confirm which insect order was most often utilized.

Nest Survival

We used time sensitive hierarchical modeling with a logit link function in program MARK to analyze DNS (Dinsmore 2002). Model covariates included insect population density by order (Diptera and Lepidoptera), stage (incubation or nestling), clutch size, seasonality (linear and quadratic), temperature, and precipitation. The relationship between temperature, precipitation, and DNS was tested to account for confounding factors. Models were run on individual covariates, as well as on the additive effects of combined covariates (Shaffer and Thompson 2007). Our hierarchical approach included steps 1) stage and seasonality 2) clutch size, temperature, and precipitation and 3) Lepidoptera and Diptera abundance. A second set of analyses were run following the same sequence but with the incubation stage excluded as a covariate to focus on impacts during the nestling stage. We used an adjusted Akaike Information Criterion (AICc) to optimize parsimony in the model selection process (Burnham and Anderson 2002). The top two ($\Delta AICc < 2.0$) models from the prior model-selection step were used in subsequent steps as reference models. Model coefficients were considered statistically significant if they did not overlap zero in their 95% confidence interval.

Clutch sizes were imputed for one nest in 2005, one in 2014, and for all nests in 2008 by calculating the mean of all nests in the year and using that value. The mean value for clutch size in 2005 was 3.6, in 2008: 4.0, and 2014: 3.2. When nest dates were not recorded in our archived data, we extrapolated based on egg or nestling age. MWCS incubate their eggs for 12-13 days on average and then nestlings remain in the nest for approximately nine days before fledging (Morton 2002). Fledging occurs during a two-month period between mid-June and mid-August (Morton et al. 2004).

Minimum daily temperature ($^{\circ}\text{C}$) and total daily precipitation (cm) data were provided by Rocky Mountain Biological Laboratory (N $38^{\circ} 57' 47''$, W $106^{\circ} 59' 36''$) from the years 2005, 2007, 2008, and 2014-2017.

Results

A total of 150 nests (896 nest days) were used in my original analyses and 112 (343 nest days) were used in my analyses that excluded stage as a covariate. More nests were found but insufficient data was collected so they were not used. Clutch sizes ranged from 1-5 eggs or nestlings. Additionally, a few dates were excluded from the malaise trap insect data because of errors in data collection. Minimum daily temperatures ranged from -4.0°C - 11.0°C and total daily temperature ranged from 0.0cm-1346.2cm. Mean Lepidoptera abundance was 3114 with a standard deviation of 3632.44. Mean Diptera abundance was 2042 with a standard deviation of 800.40 across all years of the study.

A significant positive correlation was shown between Lepidoptera abundance and DNS in both life stages (Table 3). In contrast, a slight but significant negative correlation was

discovered between Diptera abundance and DNS in each life stage (Table 3). Clutch size was positively correlated with DNS (Table 3). However, our results suggest that there is more survival in the nestling stage than in the incubation stage (Fig. 1-3). We determined that stage did not have an effect on whether insect abundance influenced DNS, although it was more significant in the nestling stage (Table 3). Our seasonality model showed a negative linear relationship throughout the nest season (Fig. 1-3). In each of the analyses, the top models were ones that did not include weather effects but did include insect abundance (Table 1). Neither minimum daily temperature nor total precipitation had a significant influence on DNS (Table 2), although they were slightly positively correlated.

Discussion

The significant positive correlation between Lepidoptera and DNS in the both stages suggests that these are important food sources for MWCS nestlings, as well as parents. This, along with the non-significant correlation between weather effects and DNS support our original hypothesis that insects may provide enough energy for nestlings to mitigate the energy spent thermoregulating in fluctuating weather conditions. The order Lepidoptera appeared to comprise the largest proportion of the MWCS diet, while other insects provided additional supplementation, possibly because of the nutritional profile of these prey relative to other available food items (Best 1977). This was concluded both through modeling and from our nest camera footage (personal observation). If insect population density is the most significant influence on nest survival of MWCS, then we may predict that in habitats and time periods with relatively high insect availability, DNS will be high. However, the negative correlation between Diptera population density and DNS suggests that there may be other confounding relationships occurring. One possible explanation is that biting Dipterans may lower the fitness of adults through introduction of parasites and diseases (Morton 2002). These may reduce the number of eggs produced by a female or cause mortality of young indirectly through reduced parental contribution (Morton 2002). Alternate possibilities may be that the Dipterans measured in this study were not representative of those utilized by MWCS or that insufficient data on this order was used to adequately test our hypothesis.

The insignificant slightly positive correlation between temperature, precipitation, and DNS suggests that insect abundance has a more pronounced effect on nest survival than weather. This corresponds with a trend in other Passerines whose body condition, and therefore ability to lay larger clutches and provide parental care, is heavily influenced by food availability (Nooker et al. 2005). However, body condition has less of an impact on time of laying than the rate of food intake during egg formation (Nooker et al. 2005) and insect prey abundance is largely dependent on weather conditions (Damos, P., and M. Savopoulou-Soultan 2011). Nonetheless, lack of reproductive plasticity may make breeding birds more vulnerable to nest failure if their breeding cycle is determined by factors independent of food availability, temperature, and precipitation, such as photoperiod (Cockrem 1995, Dunn and Winkler 2010).

Nest success in MWCS typically follows a quadratic trend from the beginning of the breeding season to the end (Morton et al. 2004). Our model of seasonality was not consistent with this trend. We found a negative linear correlation in DNS across the season in populations

of MWCS within the years of this study, which is consistent with Nooker et al. 2005 and Gruebler and Naef-Daenzer 2010. This may be due to a variety of factors including: predator search-image learning, food scarcity, lower temperatures, increased precipitation, and reduced availability of preferable nest habitat (Morton 2002). Furthermore, the positive correlations between nestling stage and survival and clutch size and survival may be due to higher parental contribution. When parents have invested more in their offspring, such that they have produced more eggs or have successfully incubated their young into the nestling stage, they are more likely to continue contributing to that nest rather than abandoning (Morton et al. 2004). Another possible explanation is that the parents of a nest with a larger clutch or with live nestlings may have higher reproductive fitness. Thus, these parents would likely be able to capture more insect prey and provide more food for their offspring (Visser et al. 2006).

Research on the influence of insect population variation on MWCS nest survival has not been conducted previously at Rocky Mountain Biological Laboratory. Due to a time constraint and limited amount of data, we could not conduct as thorough statistical analyses as we had aimed. We had a relatively small sample size for the conclusions we tried to make so we had to assume no year effect and exclude year as a covariate. Nest data (clutch size or nestling age) had to be imputed for a few nests to avoid removing samples from our analyses. Even so, some nests did not have sufficient data for the analyses in MARK and had to be removed. Furthermore, to save whole years of data, we had to remove Hymenoptera, the upper East River Valley population of Lepidoptera, and the Other category of insects from our dataset because we did not have data on these from 2005, 2007, or 2008. Another limitation was that there was no insect data collected in the upper Valley, where our MWCS nest sites were located. Although we were informed that insect populations and phenology were comparable between the upper and lower Valley sites (J. Ogilvie and C. Boggs, personal observations), it is possible that enough variation occurred to influence DNS. Additionally, we cannot confirm that MWCS utilize the same species of insects as were used as covariates in our modeling. Lack of literature on MWCS specific dietary preferences led us to make assumptions about the correlation between daily nest survival and the insect species that have already been studied at Rocky Mountain Biological Laboratory. Conducting new research led to trial and error in our methods and there is much to be built upon in future studies.

To add to the value of this study, one may want to confirm insect species diversity and abundance in MWCS nesting habitat via sweep netting vegetation or malaise trapping in the upper East River Valley. More camera footage from separate nests should also be analyzed to determine whether habitat parameters influence insect abundance or utilization of different insect orders by MWCS. Furthermore, additional years of complete data should be added to the analyses to evaluate the possible influence of year as a covariate and increase the viability of the results.

The compounding impacts of climate change, such as changes in the phenology of insects from increased fluctuation in abiotic conditions, may lead to more instances of nest failure in migratory birds (Both et al. 2006). Seasonal abiotic shifts will likely cause dramatic declines in bird populations, as well as alter their range and distributions (Crick 2004). Birds that historically

breed at low elevation or in southerly habitats are moving upward and into previously unsuitable habitat (Crick 2004), thus impacting the entire ecosystem because birds fill niches as both predator and prey. When a new predator is introduced, its prey organisms (e.g., insects) may experience significant population decline. Subsequently, overall reproductive success in songbirds would be negatively impacted. Wildlife researchers should consider further examining the effects of asynchrony between mountain birds' breeding and food availability, such as clutch initiation date shift (Dunn and Winkler 2010) and reduced number, size, and survival of nestlings (Visser et al. 2006).

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Table 1. Hierarchical modeling steps in final selection process to determine the best model results for mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) daily nest survival analyses with and without stage (incubation or nestling) as a covariate.

Model ^a	AIC ^b	wi ^c	K ^d	Deviance	Model ^a	AIC ^b	wi ^c	K ^d	Deviance
{S(stage+T)}	0.00	0.67	3.00	336.00	{S(T)}	0.00	0.82	2.00	160.80
{S(stage+TT)}	3.07	0.14	3.00	339.08	{S(TT)}	3.20	0.17	2.00	164.00
{S(T)}	10.94	0.00	2.00	348.95	{S(.)}	7.75	0.02	1.00	170.55
{S(stage+T+clutch)}	0.00	0.51	4.00	320.91	{S(T+clutch)}	0.00	0.45	3.00	156.71
{S(stage+T+clutch+precip)}	1.69	0.22	5.00	320.60	{S(T+temp+clutch)}	1.89	0.17	4.00	156.59
{S(stage+T+clutch+diptera+lepidoptera)}	0.00	0.36	6.00	314.63	{S(T+clutch+lepidoptera+diptera)}	0.00	0.43	5.00	149.41

^a Models are ranked by ascending AICc T=linear seasonality, TT=quadratic seasonality, stage=life stage, clutch=number of eggs or nestlings, lepidoptera=total number of Lepidoptera, diptera=total number of Diptera

^b Shows the difference of AICc (Akaike's information criteria corrected for small sample size) between candidate models. AIC of the best model with stage included=326.67, stage excluded=159.47

^c AIC model wt.

^d Number of parameters

Table 2. Final model selection results from mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) nest survival analyses in relation to insect abundance, with both stages (nestling and incubation) included and with incubation excluded in Gothic, Colorado, USA, 2005, 2007, 2008, and 2014-2017.

Model ^a	AICc ^b	wi ^c	K ^d	Deviance
{S(stage+T+clutch+diptera+lepidoptera)}	0.00	0.36	6	314.63
{S(stage+T+clutch+precip+lepidoptera+diptera)}	1.77	0.15	7	314.38
{S(stage+T+clutch)}	2.26	0.12	4	320.91
{S(stage+T+clutch+lepidoptera)}	2.58	0.10	5	319.23
{S(stage+T+clutch+diptera)}	2.98	0.08	5	319.62
{S(stage+T+clutch+precip)}	3.95	0.05	5	320.60
{S(stage+T+clutch+precip+lepidoptera)}	4.25	0.04	6	318.88
{S(stage+T+clutch+temp)}	4.26	0.04	5	320.91
{S(stage+T+clutch+precip+diptera)}	4.74	0.03	6	319.36
{S(stage+T+clutch+temp+precip)}	5.95	0.02	6	320.58
{S(stage+T)}	15.34	0.00	3	336.00
{S(stage+TT)}	18.42	0.00	3	339.08
{S(T)}	26.28	0.00	2	348.95
{S(TT)}	27.99	0.00	2	350.65
{S(stage)}	35.93	0.00	2	358.59
{S(.)}	37.82	0.00	1	362.49
{S(T+clutch+lepidoptera+diptera)}	0.00	0.43	5	149.41
{S(T+temp+clutch+diptera+lepidoptera)}	1.74	0.18	6	149.12
{S(T+clutch)}	3.27	0.08	3	156.71
{S(T+clutch+lepidoptera)}	3.47	0.08	4	154.90
{S(T+clutch+diptera)}	3.67	0.07	4	155.10
{S(T+temp+clutch)}	5.16	0.03	4	156.59
{S(T+temp+clutch+diptera)}	5.32	0.03	5	154.73
{S(T)}	5.35	0.03	2	160.80
{S(T+temp+clutch+lepidoptera)}	5.43	0.03	5	154.84
{S(T+temp)}	6.97	0.01	3	160.41
{S(T+precip)}	7.23	0.01	3	160.67
{S(TT)}	8.54	0.01	2	164.00
{S(T+precip+temp)}	8.91	0.01	4	160.34
{S(TT+temp)}	10.33	0.00	3	163.78
{S(TT+precip)}	10.53	0.00	3	163.98
{S(TT+temp+precip)}	12.30	0.00	4	163.73
{S(.)}	13.09	0.00	1	170.55

^a Models are ranked by ascending AICc T=linear seasonality, TT=quadratic seasonality, stage=life stage, clutch=number of eggs or nestlings, lepidoptera=total number of Lepidoptera, diptera=total number of Diptera

^b Shows the difference of AICc (Akaike's information criteria corrected for small sample size) between candidate models. AIC of the best model with stage included=326.67, stage excluded=159.47

^c AIC model wt.

^d Number of parameters

Table 3. LOGIT Link Function Parameters of top model in program MARK analysis with stage (incubation and nestling) and without stage (only nestling) at 95% confidence.

Parameter	Beta	Standard Error	Lower	Upper
1:Intercept	5.28000	0.93	3.46	7.09
2:Stage	-1.29000	0.33	-1.94	-0.64
3:T	-0.60000	0.16	-0.91	-0.29
4:Clutch	0.51000	0.16	0.19	0.82
5:Diptera	-0.00047	0.21	-0.00089	-0.00049
6:Lepidoptera	0.00013	0.59	0.00011	0.00024

1:Intercept	5.84000	1.25	3.39	8.29
2:T	-0.79000	0.27	-1.31	-0.26
3:Clutch	0.33000	0.21	-0.09	0.75
4:Lepidoptera	0.00021	0.96	0.00025	0.0004
5:Diptera	-0.00080	0.33	-0.0001	-0.0002

T=linear seasonality, Stage=life stage, Clutch=number of eggs or nestlings, Lepidoptera=total number of Lepidoptera, Diptera=total number of Diptera. Relationship considered statistically significant if 95% confidence interval did not overlap zero.

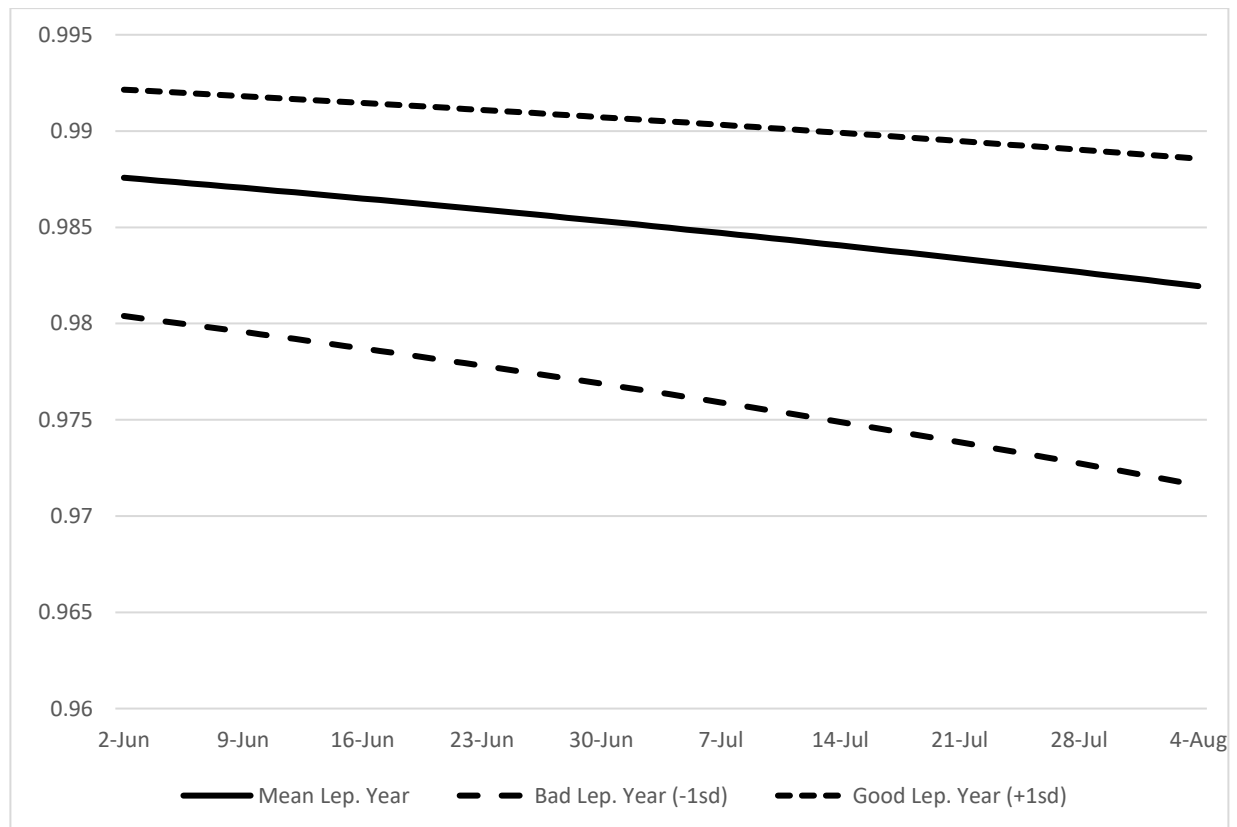


Figure 1. Daily nest survival in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*), including incubation and nestling stages, across the summer breeding season (in 2005, 2007, 2008, and 2014-2017) as influenced by low, mean and high Lepidoptera abundance years.

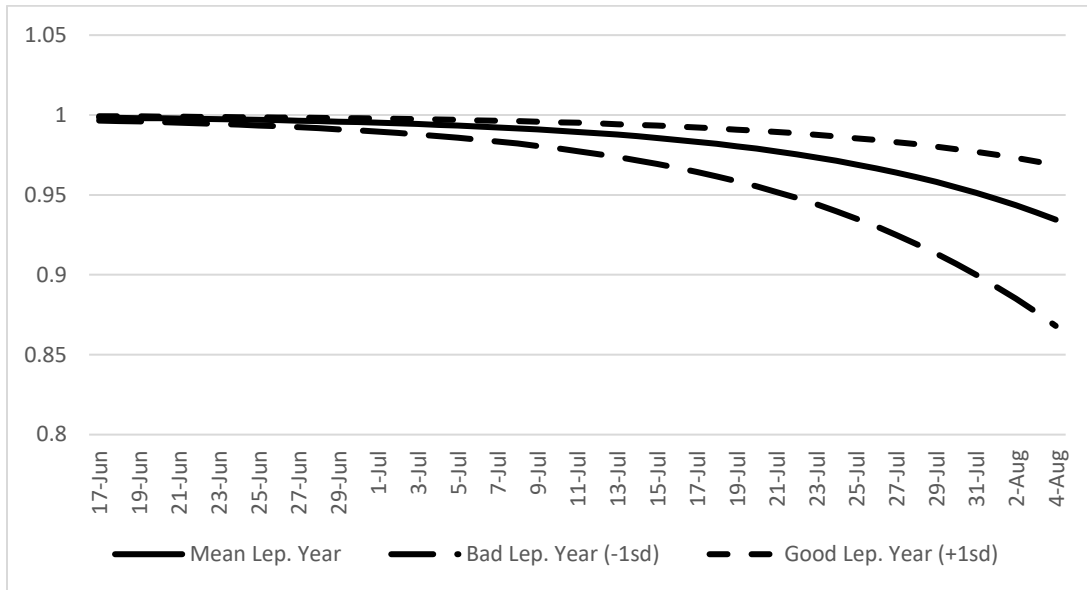


Figure 2. Daily survival of mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) nestlings across the breeding season (in 2005, 2007, 2008, and 2014-2017) relative to low, mean, and high Lepidoptera abundance years.

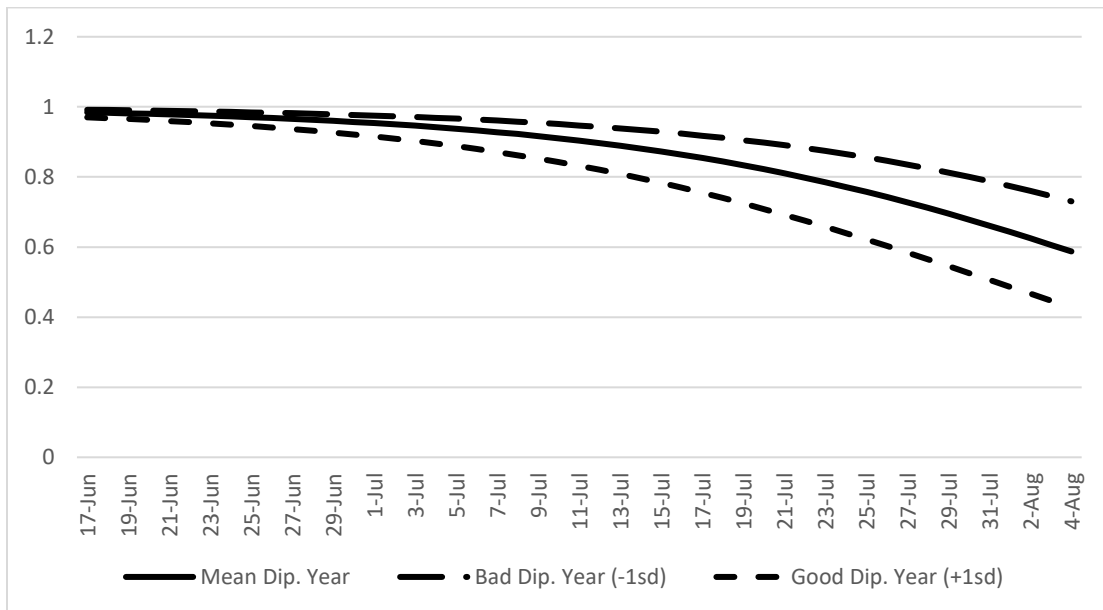


Figure 3. Daily survival of mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) nestlings across the breeding season (in 2005, 2007, 2008, and 2014-2017) relative to low, mean, and high Diptera abundance years.

Mountain White-Crowned Sparrow Research Sites 2018

By Audrey Emerson

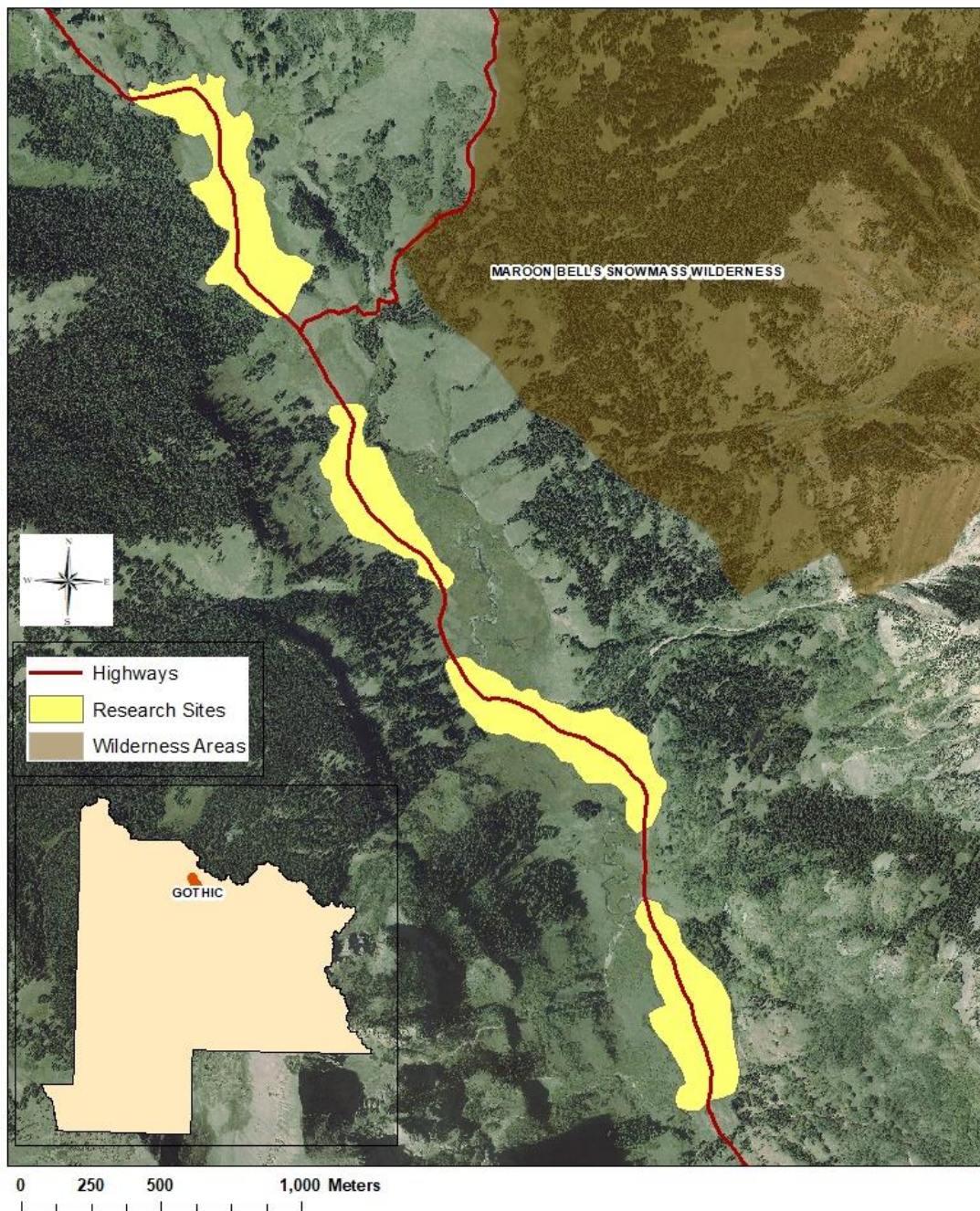


Figure 4. Mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) research sites in the upper East River Valley along Gothic Road, near the Maroon Bells Snowmass Wilderness Area in Gothic, Colorado, U.S.A.