

## Research Prospectus

**Title:** Why do the effects of temperature on nestling growth and survival vary across land uses?

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## Introduction

The interactive effects of climate change and habitat conversion to agriculture constitute the primary threat to terrestrial wildlife (Travis 2003). Efforts to increase biodiversity in agricultural landscapes, such as planting polycultures, may allow more species to thrive in human-dominated landscapes (Kremen and Merenlender 2018). However, as climate change progresses, human-dominated landscapes may expose birds to new temperature extremes because converting forested land to agriculture removes trees that insulate the understory from ambient temperature (Suggitt et al. 2011, De Frenne et al. 2019). In bird species with altricial young, nestlings are ectothermic, so both low and high temperatures divert energy from growth to thermoregulation (Dunn 1979). The lethal effects of cold are well-documented (Shipley et al. 2020). But in the future, climate change will drive temperature increases globally and exacerbate the intensity of short-term temperature spikes. Especially in hot ecosystems, climate change-driven temperature spikes often induce nest failure and drive population collapse (Socolar et al. 2017). For example, in the Putah Creek ecosystem near Davis, CA, warm temperatures during nesting are associated with lower nestling growth (and survival in some species) (Riggio et al. in prep). Furthermore, our preliminary results from an analysis of Cornell University's NestWatch database (N= 152,863 nesting attempts across 58 species) show that, across North America, temperature spikes lower nesting success in agriculture and urban environments. However, nesting success remains stable in grassland and increases in forested areas following temperature spikes.

For this project, we will investigate the two main mechanisms that could underlie the effects of heat waves: direct thermoregulation challenge for nestlings and food availability. Nestlings can survive heat waves by using more energy to thermoregulate, but this may increase stress, decrease growth, and lead to lower survival (Wingfield et al. 2017). Furthermore, heat waves may reduce food provisioning to nestlings, either by forcing adults to spend more energy thermoregulating or by reducing prey availability. For example, warming temperatures are driving lepidopteran declines across the U.S. (a key resource for young birds; Forister et al. 2021). Here, I propose to investigate the relative contributions of thermoregulation challenge and food provisioning to nestling growth under temperature spikes across four land cover types: natural open canopy (grassland), natural closed canopy (riparian forest), agricultural open canopy (row crop), and agricultural closed canopy (orchard).

## Questions

*Question 1.* How do ambient temperature and land cover affect nest box internal temperature?

*Hypothesis 1.* In habitats that have closed canopies (i.e. closed riparian and orchard sites) we expect nest boxes to show fewer and less severe temperature spikes over the nesting season. Forest canopies insulate the area below the canopy from both high and low macroclimatic temperatures, so we expect that more closed canopies will offer a higher buffering capacity (De Frenne et al. 2019).

*Question 2.* How do ambient temperature and land cover affect food provisioning of nestlings?

*Hypothesis 2.* Temperature spikes will be more frequent and more severe in open lands (i.e., grassland and row crop (i.e., open lands)), decreasing provisioning rates. Additionally, parents may decrease foraging time to meet thermoregulatory demands or lower insect availability in agriculture may increase search effort.

*Question 3.* How do temperature spikes affect nestling stress physiology across land-use types?

*Hypothesis 3.* Temperature spikes will increase nestling stress (i.e., cortisol and heat stress protein levels) most in open-canopied environments because the lack of thermal buffering may leave nestlings more vulnerable to hyperthermia, which can elevate cortisol in nestlings (Wingfield et al. 2017).

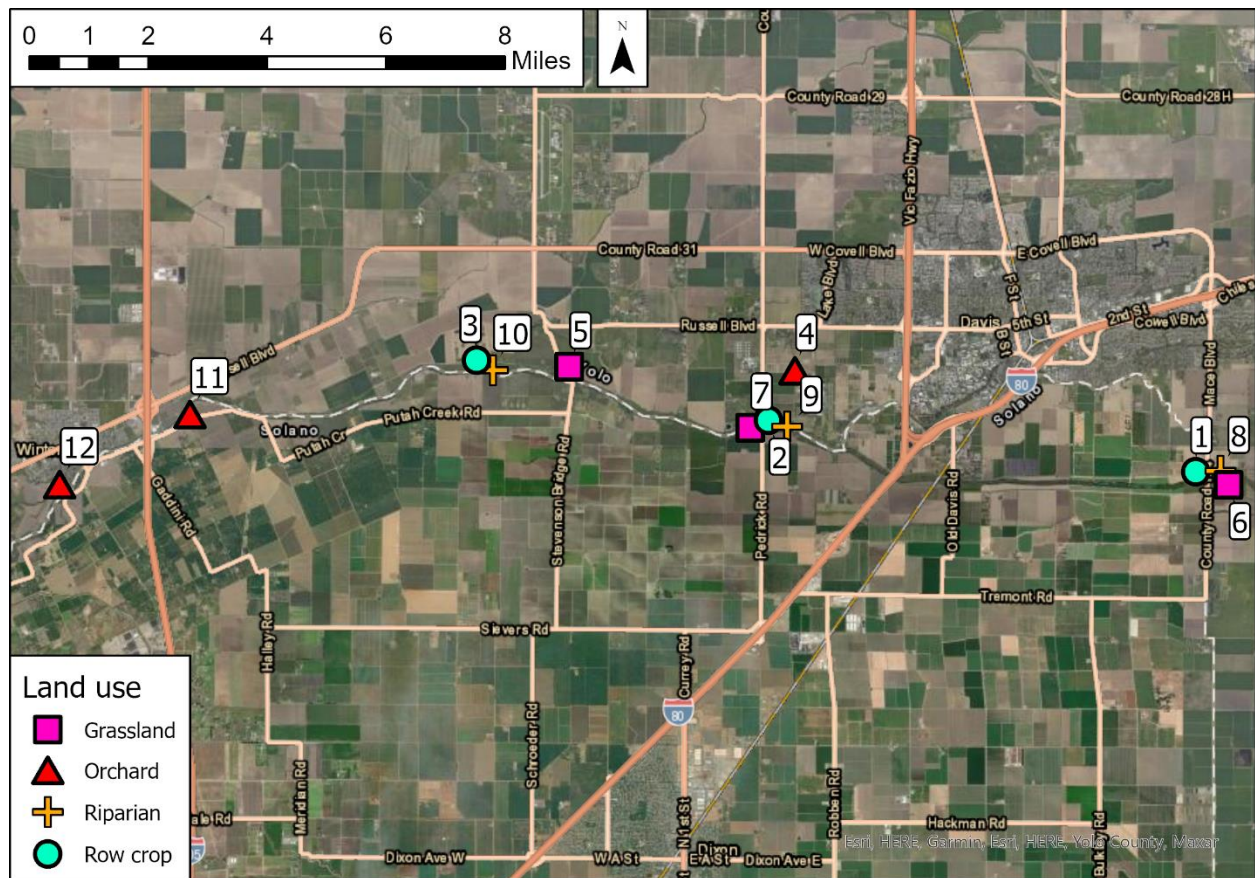
*Question 4.* What are the cascading consequences of physiological heat effects (Q3) and food-mediated effects (Q2) for nestling growth and survival?

*Hypothesis 4.* In open land covers (i.e., grassland and row crops), the direct physiological effects of heat on nestlings will eclipse effects of food provisioning. Hyperthermia will drive cellular damage, forcing nestlings to expend more energy on maintenance, lowering their growth (Wingfield et al. 2017). However, because hyperthermia may also cause adults to decrease provisioning during temperature spikes, food-mediated effects may also be important, causing lower nestling growth and survival. Finally, compared to open natural habitats with similar levels of shade, low resource (i.e., insect) availability in agriculture will exacerbate food-mediated effects on nestlings.

## **Methods**

To address these questions, I propose to monitor Tree Swallow and Western Bluebird nest boxes in four land cover treatments: row crops, orchards, grasslands, and high canopy cover riparian forests. Our focus is on the two most common nest box species: Tree Swallow and Western Bluebird, both of which nest in nest boxes in all four studied land covers. Birds in this area experience severe temperatures while nesting, with temperatures regularly soaring over 40 degrees Celsius. The system is therefore ideal to study whether closed canopies buffer nesting birds from temperature spikes.

The MWFB maintains 165 boxes across 8 sites along Putah Creek. Most boxes are in riparian forest habitat, but two sites, with 10 boxes each, are in orchards. In 2021, we supplemented this main network with two existing grassland sites (~30 boxes each) located on City of Davis and Putah Creek Riparian Reserve (PCRR) land, both of which have been monitored for multiple years by members of the Patricelli lab at UC Davis. We also obtained permission from PCRR, UC Davis Foundation Plant Services, Russell Ranch, and the UCD-H.M. Clause Innovation Center to supplement the Nestbox Highway with five sites of ten boxes each: three sites in row crops, one in orchard, and one in grassland. We grouped the sites when possible, seeking to set up three meta-sites with one site each of the four land covers, for 12 sites in total, to ensure land-use types were not spatially clustered. All sites except the two MWFB orchard sites (marked with 11 and 12 in Figure 4) were grouped within 2 km of each other near the Putah Creek South Fork Reserve (38.517575, -121.694762), Putah Creek Riparian Reserve (38.526902, -121.804745), and Russell Ranch (38.542834, -121.869838; Fig. 3).



*Figure 1. Locations of sites. Each site encompasses at least 10 nest boxes, with some as many as 30.*

In April–August 2021, we visited all boxes weekly and recorded the contents of each box (nest status, contents, species, etc). From the occupied boxes, we selected ~20 active nests per habitat type for monitoring ( $N = 80$  boxes; 20 boxes/habitat  $\times$  4 habitats; at end of season, 71 boxes monitored). We used a fisheye lens to take a standardized picture of the canopy cover at each box and placed temperature loggers inside and outside each nest to record temperature every 5 min from egg-laying to fledging. We also placed one relative humidity sensor per site. To track nestling growth and survival, we visited active nests each week, hand-captured nestlings, and collected morphometric growth data (nestling weight, wing chord, tarsus length, and bill length). We tracked each individual nestling’s growth by painting its nails with colored nail polish. One to two weeks prior to fledging, we affixed a small metal leg band to the nestling’s leg.

From these intensively monitored nests, we selected two to three per site to quantify food provisioning rates (at end of season,  $N = 19$  nest attempts monitored for food provisioning: 5 in orchard, 6 in row crops, 3 in forest, and 5 in grassland). To do so, we affixed a Raspberry Pi-based motion-activated camera (Phillips et al., in press) to the side or top of the box that saved videos 30 seconds before and after each motion activation. We will quantify hourly provisioning rate by using an image recognition algorithm to identify adult arrivals.

In 2022, we plan to add one additional site cluster of all four land cover types at Full Belly Farm in the Capay Valley (location TBD). We will use the same study design but monitor twice as many nests for food provisioning rates (i.e., 40 boxes, 10/land cover type). In addition, to quantify nestling stress physiology, we will collect a small blood sample from each nestling in

intensively monitored nests ( $N = 240$ , 3 nestlings/nest \* 20 boxes/land cover \* 4 land covers). In addition, we will capture females during the incubation period using flap-traps and collect a small blood sample to account for maternal effects on hormone levels. To do so, we will puncture the medial metatarsal vein (for nestlings) or the basilic vein (for adults) with a sterile needle and collect blood into a sterile hematocrit tube (approximately 50 microliters and/or <1% of the individual's body mass). We will collect the blood within 30 seconds of handling each nestling to ensure that handling has a minimal effect on blood hormone levels. Samples will be kept on ice (max. 4h) and then centrifuged to separate plasma from red blood cells. Plasma will be aspirated, frozen (-20 °C), and corticosterone concentrations will be quantified via an immunosorbent assay (ELISA, DetectX Corticosterone Enzyme Immunoassay Kit, Arbor Assays). Samples (5uL) will be treated with a steroid dissociation reagent, diluted 1:40, and then placed in a microtiter plate coated with CORT antibody. Then, a corticosterone-peroxidase conjugate will be added to the wells. The binding reaction is initiated by adding a polyclonal antibody to corticosterone. After an hour of incubation, the plate will be washed, and substrate added. After a 30 min incubation, the reaction will be read at 450 nm. All samples will be run in duplicate and one 9 points standard curve will be run on each assay.

I will apply generalized multilevel path models to differentiate among multiple mechanisms by which temperature and habitat types may affect avian fitness. These models can be constructed to accommodate various error distributions of continuous, count, and binary responses (*e.g.*, food provisioning rates, nesting growth, survival; Shipley 2009, Lefcheck 2015). They can also account for spatiotemporal autocorrelation via modified error structures or random effects. For question 1, I will model internal nest box temperature as a function of ambient temperature (as measured by the UC Davis weather station), land cover type, and canopy cover. For question 2, I will model hourly food provisioning rates as a function of hourly temperature maximum (as measured by external box sensors), land cover type, and canopy cover, and include random effects for species and nest box number to account for other sources of variation among parents. For question 3, I will model blood cortisol levels and heat shock proteins as a function of weekly mean maximum internal temperature, land cover, and maternal cortisol, and include random effects for individual and nest box (to account for pseudoreplication) and for species. For question 4, I will use the path models to assess how nestling growth (daily mean mass gain over the nestling period) and survival to fledging (a binomial variable) change as a function of mean hourly provisioning rates, blood cortisol, temperature spikes, and land-use types, including random effects for nest box and species (to account for other likely sources of variation).

## **Significance**

This project seeks to unravel the mechanisms through which climate change may affect the ability of birds to survive in human-dominated habitats. Understanding the relative contributions of thermoregulation challenge and reduced food provisioning to decreased reproductive success under temperature spikes in agriculture and other land covers will provide concrete avenues through which working landscapes could be modified to better accommodate birds. If the direct effects of heat are more important than food-mediated effects, providing microclimate refugia (*e.g.* shade trees) in agriculture may buffer temperature spikes to some extent, or nest boxes could be modified to reduce their internal temperature (*e.g.* by painting them with white or reflective paint). If food-mediated effects predominate, then maintaining patches of non-crop habitats in working landscapes to support food resources and provide thermal refuges for parents may be more effective (Nimmo et al. 2016). Regardless of potential conservation implications, the findings of this study will advance our knowledge of the ecology of working landscapes by clarifying the mechanistic underpinnings of the fitness consequences of the interaction between land cover and climate change.