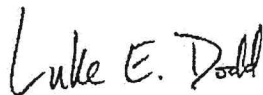


BAT BOXES AS MITIGATION TOOLS: FACTORS IMPACTING
MICROCLIMATE AND MYOTIS SODALIS ROOST SELECTION


BY

REED D CRAWFORD

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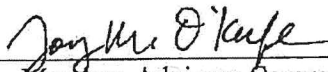


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MICROCLIMATE AND MYOTIS SODALIS ROOST SELECTION

BY

REED D CRAWFORD

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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ABSTRACT

Environmental degradation has led to declines in available natural roosting habitat for bats. To mitigate this loss, practitioners often deploy artificial roosts (e.g., bat boxes). There are no established species-specific practices for deployment strategy and roost design selection, but occupancy rates are known to vary across species and roost microclimates can be harmful to bats. Providing bats with thermally beneficial roosts during summer could enhance overwinter survival of WNS-affected species. To further our understanding of roost preference and microclimate, we deployed 40 rocket box roosts of 5 designs at field sites in Indiana and Kentucky. Roosts were deployed in clusters of 5 at 4 distinct solar exposures within each site. From April-September of 2019, we collected hourly roost microclimate data via Thermochron iButtons (12 sensors/box) and monitored occupancy of resident Indiana bats (*Myotis sodalis*) via spotlight checks and emergence counts 2–4 times per week. Following an information theoretic modeling approach, we used hurdle models to assess the effects of design, solar treatment, and weather on occupancy and abundance. We used linear models and beta regression to test the effects of design, solar treatment, weather, and bat abundance on roost microclimate. Indiana bats showed no preference for roost design, but preferred roosting in easterly and westerly sun roost clusters, which provide solar exposure and access to cover upon emergence. Bats were more likely to be present and more abundant under warm, calm weather conditions. Vent removal and reference designs logged the most unsuitably hot recordings across solar treatments, while unsuitably cold recordings were similar across designs and solar treatments. At low ambient temperatures ($< 20^{\circ}\text{C}$), large groups of bats (≥ 30) had a substantial positive impact on within-roost temperature availability (hourly

$T_{\text{MAX}}-T_{\text{MIN}}$) and variability (daily $T_{\text{MAX}}-T_{\text{MIN}}$) as compared to unoccupied roosts. Group size had varying effect strengths based on interactions with roost design. Further, during the summer months (June-August), 3 designs (external water jacket, chimney, and white tile roof) had microclimates more suitable for bats as compared to a reference design. Though during the cool spring months, landscape position and design had little effect on roost suitability, though further investigation is warranted. To promote warm roosting conditions and access to cover upon emergence, we recommend deploying boxes on solar-exposed tree-lined edges. Researchers should further consider the potential impact that bats may have on a prospective artificial roost before deployment, as social thermoregulation could alter box microclimates, thereby affecting bats' energetic budgets. Additional roost monitoring is warranted as bats may or may not develop a preference for roost designs in subsequent years. Further development and testing of roost designs that can buffer against unsuitably hot and cold temperatures is likely critical to improve conservation outcomes for bats.

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CHAPTER 1 : INDIANA BATS SELECT ARTIFICIAL ROOSTS BASED ON SOLAR EXPOSURE AND WEATHER

INTRODUCTION

Roost selection is critical for the survival and successful reproduction of many bat species. Specifically, selection of a quality roost can result in increased energetic savings (Solick and Barclay 2006), protection from extreme weather (Bondarenko et al. 2014), refugia from predators (Kunz 1982), and communal spaces for information transfer and pup rearing (Wilkinson 1992; Lewis 1995). On many landscapes, bats have lost suitable roosting habitat due to anthropogenic land modification, resulting in the loss of large snag and hollow bearing trees which various bat species use for roosts (Lacki 2018). These limited roosting resources are not readily replaced, as large hollow/cavity bearing trees can take decades to form (Vesk et al. 2008). In instances where natural roost trees are sparse, resource managers often deploy artificial roosts (i.e., bat boxes) to supplement natural roosting habitat (Flaquer et al. 2006; Adams et al. 2015; Hoeh et al. 2018). While artificial roosts are commonly deployed by resource managers, occupancy varies widely among studies and there are many unknowns remain regarding species-appropriate design, number of roosts to deploy, placement on the landscape, and the microclimate being provided (Mering and Chambers 2014).

Artificial roost placement on the landscape is a critical factor influencing roost selection of bats, as landscape position affects solar exposure and microclimate (Mering and Chambers 2012; Rueegger 2019), thus altering the suitability of a roost. For

example, Brittingham and Williams (2000) found maternity colonies of little brown bats (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) more likely to use artificial roosts placed in locations receiving ≥ 7 hours of direct solar exposure, potentially exploiting the thermoregulatory benefits of a warm roost. Further, in Indiana, Whitaker et al. (2006) noted the lack of solar-exposed artificial roosts at their site may have resulted in limited uptake of roosts by Indiana bats. Solar exposure influences the microclimate provided by the roost and, during lactation, females will often select warm, solar-exposed roosts to promote the growth and development of pups and decrease the energetic costs of maintaining normothermia (Racey and Swift 1981; Kunz 1987; Lausen and Barclay 2003a). However, for non-reproductive and post-lactating bats with no burden of pups, finding cool roosts that facilitate deeper torpor may be more important for conserving energy (Hamilton and Barclay 1994; Dzal and Brigham 2013). Based on the varying physiological and thermoregulatory constraints faced by bats, providing a variety of roosting conditions during the summer maternity season is likely important to accommodate the variety of thermoregulatory strategies used by bats.

Artificial roost placement on the landscape is also likely to influence predation risk. Many Myotid bats are slow-flying and clutter adapted with corresponding morphology — low wing loading and low aspect ratio wing (Norberg and Rayner 1987). Bats with these morphological traits often rely heavily on cluttered forests for foraging (Aldridge and Rautenbach 1987) and protection from predation (Russo et al. 2007). While roosts in open habitats may be warmer, they may also be riskier choices for slow flying bats, due to the potential for detection by diurnal/crepuscular raptors

(Lima and O’Keefe 2013; Arndt et al. 2018). Thus, predation risk may alter the behavior of reproductively active bats during the maternity season as they may face a trade-off between selecting a warm solar exposed roost or a roost that minimizes predation risk. Roosting near tree lines provides bats with forest cover upon emergence (Lima and O’Keefe 2013; Arndt et al. 2018) and facilitates a warm microclimate for pup rearing, as forest edge roosts are not within the shaded forest interior and, depending on aspect, can receive solar exposure for portions of the day. Roosting in the forest interior and switching roosts often could facilitate predator avoidance, similar to the strategy used by male Indiana bats (*Myotis sodalis*) (Bergeson et al. 2018), but these conditions would not be conducive to the development of pups. Deploying a variety of roost clusters may allow bats to select optimal roosting conditions which maximize solar exposure and minimize predation risk.

Roost detectability and fidelity are likely influenced by the number of roosts available on the landscape (Lewis 1995; Rueegger 2016). For example, in Arizona, Mering and Chambers (2012) found that bats occupy artificial roost clusters more frequently than artificial roosts deployed singly, suggesting that clusters may provide better concealment and could support larger colonies of bats. Furthermore, high roost availability could promote lower roost fidelity and smaller colony sizes (Brigham 1991; O’Keefe and Loeb 2017). Deploying clusters of roosts could provide a variety of microclimates within one discrete roosting locality (Mering and Chambers 2012; Rueegger 2016), which may be important as many bat species switch roosts frequently to find optimal microclimates based on reproductive condition (Lausen and Barclay 2003b). Further, it is thought that maternity colonies of Indiana bats likely need large

numbers roosts, both primary and alternate, to support their physiological needs (Callahan et al. 1997; Silvis et al. 2014; Bergeson et al. 2018). Resource managers should consider deploying artificial roosts in clusters to enhance roost discovery, promote predator avoidance, and supply a variety of microclimates to suit a multitude of thermoregulatory needs.

Artificial roosts are often used to provide roosting habitat for the Indiana bat, a federally endangered species found throughout the Midwest and parts of the northeastern and southeastern United States (USFWS 2007). This species may live at least 10 years, and has a low reproductive output of just one pup per year, which is typically born in June or early July (Kurta and Rice 2002; USFWS 2007). The loss of suitable summer roosting habitat for Indiana bats is a topic of concern for the protection and persistence of this species (Sparks et al. 2005; Whitaker et al. 2006; USFWS 2007). While much research has focused on Indiana bats' selection of natural roosts (e.g., Callahan et al. 1997; Britzke et al. 2003; O'Keefe and Loeb 2017; Bergeson et al. 2018), few studies have focused on artificial roost selection and preference (Whitaker et al. 2006; Adams et al. 2015; Hoeh et al. 2018). Of the two studies that examined multiple roost designs (Whitaker et al. 2006; Hoeh et al. 2018), neither examined the effect of differential solar exposure on roost selection, and due to differences in volume and entrance area of the designs tested, it is unknown if microclimate was the only factor influencing roost preference. Occupancy rates within these studies varied widely, which could be caused by several factors like roost design, landscape position, solar-exposure, and climate.

Selecting an artificial roost design for deployment is critical to effective management, as roosts that can buffer against thermal extremes could confer substantial energetic savings to bats. Most artificial roost designs are deployed without thorough investigation of the microclimate provided. Of the few studies that have investigated artificial roost microclimate, most have found that some artificial roost designs offer microclimates that are harmful to bats (Brittingham and Williams 2000; Bideguren et al. 2018; Hoeh et al. 2018). Temperatures $> 40^{\circ}\text{C}$ can induce heat stress and prolonged exposure at these temperatures can result in physiological damage and mortality (Licht and Leitner 1967). Further, Hoeh et al. (2018) found that, of the 3 artificial roost designs tested, none buffered cold temperatures. Roosting conditions that are too cool can reduce the growth rate of pups (Kunz 1987), reduce milk production in females (Wilde et al. 1999), and delay parturition (Racey and Swift 1981).

Artificial roosts allow for controlled experiments that involve the fine-scale manipulation of design, placement, and availability; manipulating these factors can give a detailed look at the landscape and thermoregulatory preferences of bats (Mering and Chambers 2012; Hoeh et al. 2018). In contrast, the outcomes of studies that examine bat preferences for natural roosts are often driven by natural roost availability and type (Brigham 1991; O’Keefe and Loeb 2017), chance events (e.g., beetle kill and lightning strike; Rabe et al. 1998), and management history (Bergeson et al. 2018) and patterns observed may reflect responses to such events as opposed to bat preference. In the present study, our goal was to assess the artificial roost selection of Indiana bats with regard to 5 rocket box style roost designs specifically altered to manipulate microclimate and to evaluate the impact of roost placement and weather on the presence

and abundance of Indiana bats at our artificial roosts. We aimed to understand Indiana bats' preferences for artificial roost microclimate and landscape placement during the maternity season so that we can provide more specific information on effective deployment strategies, thus enhancing ongoing conservation efforts for this imperiled bat.

STUDY SITES

Historically, the Indiana bat ranged throughout most of the east-central United States, with the core of their range in the Midwest (USFWS 2007) and with many major hibernacula throughout Indiana and Kentucky (USFWS 2007). The two field sites for this study have known maternity colonies of Indiana bats and are in the central part of the species' range.

The first site is the Indianapolis Airport mitigation site in central Indiana (39°38'59"N, 86°20'57"W; hereafter, the Indiana site; Figure 1-1: A) and the second site is located at Veterans Memorial Wildlife Management Area in north-eastern Kentucky (38°19'20"N, 84°32'57"W; hereafter, the Kentucky site; Figure 1-1: B). The Indiana field site is located within the Eastern Corn Belt Plains ecoregion and is characterized by an abundance of soybean, corn, and wheat fields with small mixed forest fragments (U.S. Environmental Protection Agency 1997). The Indiana bat maternity colony at this site has used artificial structures as roosts since ~2003–2019 (Ritzi et al. 2005; Whitaker et al. 2006; Hoeh et al. 2018). In the mid-1990s, Whitaker et al. (2006) observed the deployment of over 3,000 artificial roosts, of varying designs, at the Indiana site and documented minimal roost occupancy. Recently, Hoeh et al. (2018) deployed 6 clusters of 3 roost types (rocket box, bark-mimic, and bat box style) at the Indiana site, of which

Indiana bats preferred the rocket box style based on occupancy; these roost clusters have been in place since ~2015.

The Kentucky field site is located within the Interior Plateau ecoregion and is characterized by mostly forested rolling hills containing predominantly white oak (*Quercus* spp.), hickory (*Carya* spp.), and eastern red cedar (*Juniperus virginiana*) (Woods et al. 2002). At this site, the Indiana bat maternity colony was previously documented using BrandenBark™ artificial roost structures that were installed around Summer 2016 (pers. comm. KDFWR). These structures are composed of a polyurethane sheet of synthetic bark wrapped around and affixed to the top of a 7.6 meter tall telephone pole (Gumbert et al. 2013). During the spring of 2019, 17 of the 18 original Brandenbark™ roosts were removed and replaced by 18 newer versions, as the posts for the old roosts were badly decayed and posed a safety hazard. A total of 3 roost clusters are spread across the site, 2 of the clusters containing 6 BrandenBark™ artificial roosts and 1 cluster containing 7 roosts (6 new and 1 old, 19 total at site) (pers. comm. KDFWR).

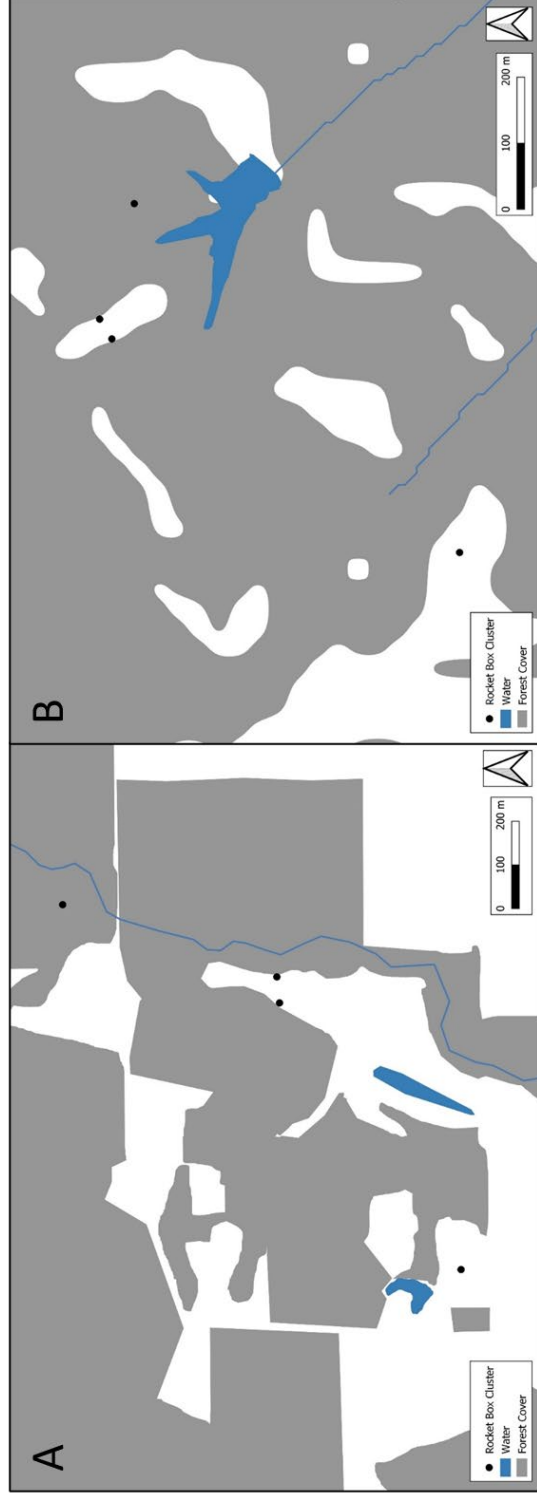


Figure 1-1: Relative positions of rocket box clusters at the A) Indiana field site and B) Kentucky field site.

METHODS

Rocket Box Deployment~

We deployed 20 rocket boxes at Indiana and Kentucky field sites ($n = 40$ total), with all boxes in place by 1 April 2019. At each field site, rocket boxes were deployed in 4 clusters, with 5 boxes (1 per design) present within each cluster ($n = 8$ total clusters between both field sites). Box designs developed include: reference (REF), vent removal (VR), chimney (CH), white tile roof (WTR), and external water jacket (EXTJ). Each box was marked with a unique tree tag with the last digit on the tag identifying its design. Rocket box clusters ran along a north-south axis, and boxes within each cluster were spaced 2m apart (Figure 1-2). We randomly determined the order of rocket box designs within each cluster. We set boxes in ~1.3m deep holes so that the top of each rocket box was ~6.1m above ground. Boxes were set in 45.4kg of fast-setting concrete and the above-ground base of each box post was braced with 4 angled 2"x4"x4' (4.4cm x 8.9cm x 1.2m) boards.

We deployed boxes in clusters to facilitate roost discovery, roost switching, and provide bats a variety of available microclimates within one locality (Lewis 1995; Ruegger 2016) (Figure 1-2). Of the 4 clusters within each field site, one “open” cluster was located away from tree lines so that boxes received solar exposure throughout the day. A “forest” cluster was in a closed canopy condition in which boxes would receive little to no direct solar exposure. An “easterly sun” cluster was ~5m from an east-facing tree line such that boxes primarily received morning solar exposure. A “westerly sun” cluster was ~5m from a west-facing tree line such that boxes primarily received

afternoon solar exposure. This deployment strategy exposed box designs to varied solar conditions, thus potentially altering the performance of each design in a situation.



Figure 1-2: Open treatment rocket box cluster featuring post braces, guano traps, and weather station. From left to right: EXTJ, VR, WTR, REF, CH.

Weather Data Collection~

To monitor cluster-specific weather conditions, we collected hourly weather data at each cluster via Ambient Weather WS-1201 weather stations powered by a 12v-18amh battery and locked in weatherproof Pelican (Model 1500) cases (4 stations per site, $n = 8$ total). Each weather station was mounted on a 3.2m tall fence top rail post and was concreted into the ground so that each weather station was 3m above ground. Each station was placed 2m from the south side of each rocket box cluster so that the stations would not be shaded by the boxes.

Weather stations recorded temperature ($^{\circ}\text{F}$, accuracy $\pm 2^{\circ}\text{F}$, converted to $^{\circ}\text{C}$ after download), solar radiation (lux, $\pm 15\%$, converted to w/m^2), rainfall (inches, \pm accuracy

0.01 inches, converted to mm), and wind speed (mph, accuracy ± 2.2 mph, converted to m/s). While weather stations recorded data hourly, data were not able to be collected on the hour. Rather, stations recorded on a 60-min time interval starting when power was connected to the station. Thus, this interval changed each time the power supply for a weather station's data receiver was changed (roughly every 2–3 days). Subsequently, we binned data on an hourly basis.

Roost Checks~

To survey all 40 rocket box roosts, of 8 different roost clusters, for the daily presence/absence (P/A) and abundance of Indiana bats, we performed spotlight checks 2–4 times per week at both the Indiana and Kentucky field sites. The number of surveys per week varied based on weather and conflicts with hunting seasons. Spotlight checks began on 6 April 2019 and ended on 15 September 2019 at the Kentucky field site and began on 28 March 2019 and ended on 10 October 2019 at the Indiana field site. Spotlight checks involved shining a ~1000 lumen spotlight (Stanley Fatmax Model #SL10LEDS) up into each roost and visually determining P/A of bats (Whitaker et al. 2006; De La Cruz et al. 2018; Hoeh et al. 2018). When two observers were present, each individually checked the roost and conferred on their assessments. For roosts where bats were present, bats were visually counted to estimate abundance and to aid in determining where to conduct emergence counts. We classified bats to genus visually via spotlight checks and took non-flash photos when conditions were favorable (e.g., Figure 1-3). To minimize stress to bats, spotlight checks typically lasted < 20 seconds. We made a concerted effort to not check roost clusters in the same order in consecutive

visits to field sites, this reduced the effect of time of day and solar position on our ability to detect bats in a roost.

We conducted emergence counts 2–4 times per week, weather dependent, at roosts we considered likely to contain the most bats based on spotlight checks and guano accumulation. Emergence counts help to reduce the error in abundance estimates based on data collected from spotlight checks, given that bat counts from spotlight surveys are less accurate for larger colony sizes. Observers arrived at roosts ~30 min before sunset and stayed at least 10 min after the last bat emerged or 30 min after sunset if no bats emerged (Arndt et al. 2018; Hoeh et al. 2018; Oyler-McCance et al. 2018). Observers recorded the roost ID number, time of first emergence, time of last emergence, and total number of bats emerged for each roost watched. Each observer typically watched ~3 roosts within a cluster during emergence counts, varying based on weather and visibility. The total number of roosts counted per night varied with personnel availability.



Figure 1-3: Indiana bats (top, outer chamber) roosting with a big brown bat (bottom, inner chamber) in westerly sun EXTJ box (905).

Guano Collection and DNA Analysis~

Guano traps were installed below all 20 rocket boxes at the Indiana field site and below 17 of the 20 boxes at the Kentucky field site (i.e., traps were absent from all EXTJ roosts save the open cluster). Guano traps hung 1m above ground, were made of $\frac{3}{4}$ " PVC and window screen, and covered a $\sim 1\text{m}^2$ area below each roost (Robinson et al. 2019). At the Kentucky site, we collected guano every 2–3 days, depending on weather and personnel. We counted pellets on site, stored them in a zip-lock bag labeled with date and total pellets collected, and stored them at -80°C until the samples were shipped for DNA analysis. Outsourced genetic analyses are still pending.

Analysis~

For our response variable “Total Bats” we compiled both spotlight check and emergence count abundance data, when available, to create a daily presence/absence and abundance record for each roost on each survey day. Though we acknowledge that a limitation of spotlight checks to measure abundance is that this method likely underestimates abundance, we mitigated for this by performing emergence counts at roosts that we thought would contain the most bats. Thus, we strove to use the most accurate estimates of abundance to minimize underestimation. We used hurdle models, which are appropriate for zero-inflated data, to assess factors affecting P/A and abundance of Indiana bat rocket box roost use. The hurdle model approach allowed us to separately model the factors affecting the P/A of bats at all rocket boxes and then, for occupied rocket boxes only, we could then assess factors affecting abundance.

We defined several prerequisites for vetting our dataset prior to modeling. First, because our rocket boxes were newly deployed at both field sites, bats were naïve to

their presence on the landscape and, thus, we judged the subsequent discovery of these roosts by bats would take time, similar to observations in a previous study (Mering and Chambers 2012). To address “discovery time”, we used occupancy data starting from when Indiana bats were first detected in the new roosts (i.e., 15 May 2019 for the Indiana site; 3 May 2019 for the Kentucky site). From these dates on, roosts were considered discovered by bats at each site. Next we assessed use; 6 of 8 clusters were used and we removed the unused open solar treatment clusters from the analysis to improve model stability. Finally, we insured there was available weather data corresponding to each survey day. We dropped bat usage data for clusters on days when the weather station had a power failure. The EXTJ box in the easterly sun cluster at the Indiana site was damaged on 25 June 2019, so we dropped this box from our analysis after this date.

We used R (version 3.6.2; R Core Team 2019) to conduct all analyses. We used the R package glmmTMB to build and run our hurdle models (Brooks et al. 2017). We assessed the normality of our abundance response variable “Total Bats” using a Shapiro-Wilk Normality Test ($p < 0.05$; indicating non-normality; Shapiro and Wilk 1965). We tested for multicollinearity among predictor variables with a variance inflation factor (VIF) test and considered $VIF \geq 5$ as an indicator of multicollinearity; all VIF scores were < 5 . To address the non-normality of our abundance data, we compared AIC_C (Akaike’s Information Criterion corrected for small sample sizes) scores for 3 different error distributions: `truncated_poisson`, `truncated_nbinom1`, and `truncated_nbinom2`; we selected `truncated_nbinom2` because this model had the lowest

AIC_c score (Burnham and Anderson 2002; Brooks et al. 2017). Subsequently, we used zero-truncated negative binomial hurdle models, following an information theoretic approach (Burnham and Anderson 2002) to test a set of 19 a priori candidate models including 2 global models and a null (Table 1-1). We based all candidate models on ecologically relevant hypotheses describing Indiana bat artificial roost selection. We attempted to use all parameters in a consistent and balanced manner.

Table 1-1: Candidate set of 19 a priori hurdle models. All models include a nested random effect of roost ID nested within field site.

Model	K	Included predictors
Null	7	-
m2	15	Design
m3	11	Reproductive Period
m4	11	Solar Treatment
m5	9	Average Previous Day Temperature
m6	19	Design + Reproductive Period
m7	19	Design + Solar Treatment
m8	17	Design + Average Daily Temperature
m9	13	Solar Treatment + Average Daily Temperature
m10	17	Design + Average Daily Wind Speed
m11	15	Solar Treatment + Reproductive Period
m12	13	Reproductive Period + Average Previous Day Temperature
m13	23	Design + Reproductive Period + Solar Treatment
m14	21	Design + Reproductive Period + Average Previous Day Temperature
m15	22	Design + Reproductive Period + Average Morning Solar Radiation + Average Evening Solar Radiation
m16	21	Solar Treatment + Average Morning Solar Radiation + Average Evening Solar Radiation + Average Daily Temperature + Average Previous Day Temperature + Average Daily Wind Speed
m17	17	Average Morning Solar Radiation + Average Evening Solar Radiation + Average Daily Temperature + Average Previous Day Temperature + Average Daily Wind Speed
Solar Treatment Global	25	Solar Treatment + Reproductive Period + Average Morning Solar Radiation + Average Evening Solar Radiation + Average Daily Temperature + Average Previous Day Temperature + Average Daily Wind Speed
Design Global	29	Design + Reproductive Period + Average Morning Solar Radiation + Average Evening Solar Radiation + Average Daily Temperature + Average Previous Day Temperature + Average Daily Wind Speed

We ranked candidate models via AIC_C (Akaike's Information Criterion corrected for small sample size) even though $n/K > 40$ ($1790/29 = 61.7$). Burnham and Anderson (2002) note that as sample size increases the bias correction term in AIC_C

becomes negligible, thus, converging with AIC. We derived inferences from models within $\Delta AIC_C \leq 2$ of the top model and considered model averaging of a 90% confidence set if the top ranked model did not have substantial support (i.e., $w_i < 0.90$; Burnham and Anderson 2002). We calculated the 85% confidence intervals for all parameters from the top model, and defined parameters as informative if their 85% confidence intervals did not overlap 0. This practice has been noted to be more AIC compatible, because AIC model selection favors the inclusion of additional parameters in models if the 85% confidence intervals of these parameters does not overlap 0 (Arnold 2010). We qualitatively visualized all informative parameters to determine their relative effect on Indiana bat P/A and abundance. We calculated odds ratios for P/A parameters to better quantify relationships between parameters. We scaled odds ratios for continuous P/A parameters, when appropriate, to values that are ecologically relevant (Hosmer and Lemeshow 2000). All means are reported as $x \pm SE$ unless otherwise stated.

We used a variety of predictor variables and candidate models to model the daily P/A and abundance of Indiana bats in rocket boxes. Predictor variables included box design (REF, VR, CH, WTR, EXTJ; Design), cluster solar treatment (East, Forest, Open, West; Solar Treatment), reproductive period (Pregnancy [P], Lactation [L], Post-Lactation [PL]; Repro Period), mean daily morning solar radiation (w/m^2 ; AvgAMSolRad), mean daily evening solar radiation (w/m^2 ; AvgPMSolRad;), mean daily temperature ($^{\circ}C$; AvgDailyTemp), mean previous day temperature ($^{\circ}C$; AvgPrevDayTemp), and mean daily wind speed (m/s; AvgDailyWindSpd). A nested random effect of roost ID nested within field site was included as a random effect in

every model to account for differences in bat abundance and habitat quality between the Indiana and Kentucky sites, which might have influenced roost usage and uptake, and to account for subtle differences between roosts of the same design that could detract from overall performance.

Roost design was included as a predictor variable to account for the possible differences in microclimate offered by different box designs. Temperature can directly influence the energetic expenditure of bats (Racey and Swift 1981; Kunz 1987; Sedgeley 2001). Selecting roosts with an optimal microclimate could result in substantial energetic savings during summer, and potentially increase fitness and overwinter survival (Wilcox and Willis 2016; Cheng et al. 2018).

We included solar treatment as a predictor variable in the analysis, as solar exposure has a direct impact on the microclimate experienced by a roost (Brittingham and Williams 2000; Mering and Chambers 2012), is an important facet of bat maternity roosts (Callahan et al. 1997; Brittingham and Williams 2000; Bergeson et al. 2018), and might have a strong effect on roost selection. Further, in our study, solar treatment could reflect predation risk, as the open cluster was farther from tree cover when compared to the easterly sun, westerly sun, and forest clusters. Bats may face a trade-off when selecting roosts with optimal solar exposure that are far away from tree cover as the potential risk of being depredated by raptors may be greater (Lima and O'Keefe 2013).

Reproductive period was selected as a predictor variable as energetic constraints and physiological needs of individual bats vary based on reproductive condition (Hamilton and Barclay 1994; Lausen and Barclay 2003a; Arndt et al. 2018), and this

might be reflected in temporal preferences for roost type or position. We classified bat P/A and abundance data into one of 3 Indiana bat reproductive periods, modifying the start and end dates of each reproductive period as necessary based upon information from 2019 Indiana bat mist net captures at both sites (F. Tillman at ISU and M. Rogers at KDFWR, pers. comm). Dates for the start and end of each reproductive period were thus defined as follows: P: 3 May to 10 June, L: 11 June to 13 July, PL: 14 July to 10 October.

We tested the effects of mean morning and mean evening daily solar exposure for each cluster to account for the effects of differential solar radiation on roost microclimate. Certain roost designs may heat faster than others, and areas of low solar radiation may offer refugia from extreme high temperatures, while areas of high solar radiation may provide warmer microclimates. Further, measures of solar radiation will allow for fine-grain analysis of P/A and abundance on overcast days when solar radiation may be limited, as this trend would not be elucidated with the sole use of the solar treatment parameter. Mean daily morning solar radiation was the mean amount of solar radiation experienced at a roost cluster over a 6-hour period beginning during the sunrise hour. Weather stations did not record on the hour; to avoid large amounts of variability in the initial solar radiation reading, all calculations started during the hour of sunrise. We calculated mean daily evening solar radiation as the mean amount solar radiation experienced by a cluster over a 7-hour time window ending during the hour in which sunset occurred.

We tested the effects of mean daily temperature and mean previous day temperature because ambient temperature affects roost microclimate (Hoeh et al. 2018).

Temperature can affect roost temperature availability and variability which could cause bats to shift roost preferences (Hoeh et al. 2018). We calculated mean daily temperature and mean previous day temperature as the average value of each respective measure over a 24-hour window (0000 to 2300 hours).

Lastly, we included mean daily wind speed as a predictor variable because convective cooling and wind throw are likely to be key factors for roost selection. Convective cooling from high wind speeds will likely reduce temperatures within a roost and potentially decrease roost temperature availability (Tillman 2019). Wind throw is also likely important to roost selection, as a typical snag roost is ephemeral and more susceptible to falling (Timpone et al. 2010; Bergeson et al. 2018). Also, wind speed predicts the timing of Indiana bats' spring/fall migration and arrival to their maternity site; bat presence and abundance is often low during periods of high wind (Pettit and O'Keefe 2017). We calculated mean daily wind speed as the mean daily wind speed over a 24-hour window (0000 to 2359 hours).

This research was approved by Eastern Kentucky University IACUC protocol number 01-2019.

RESULTS

Weather~

At the Indiana site, from 11 April (date of weather station installation for IN) to 10 October 2019, ambient air temperature (T_a) across roost clusters ranged from -1.2 – 34.7°C (mean = 19.7°C). Hourly wind speeds ranged from 0 – 10.4 m/s (mean = 0.51 m/s) across roost clusters, though gusts likely exceeded the recorded hourly wind speed. Total rainfall accumulation for the study period at the Indiana site amounted to 677.7

mm. Solar radiation ranged from 0–1116 w/m² (mean = 154.03 w/m²) across roost clusters. Differences in tree line density and forest composition likely influenced all microsite weather parameters.

At the Kentucky site, from 5 April (date of weather station installation for KY) to 15 September 2019, T_a across roost clusters ranged from 2.5–36.4°C (mean = 20.8°C; See Appendix A). Hourly wind speeds ranged from 0–9.9 m/s (mean = 0.46 m/s) across roost clusters. Total rainfall accumulation for the study period was 803.7 mm. Solar radiation ranged from 0–1138 w/m² (mean = 168.93) across roost clusters. Differences in tree line density and forest composition likely influenced all microsite weather parameters.

Survey Effort~

In 2019, we accumulated 85 survey days at the Kentucky site, with 1700 individual spotlight checks and 255 emergence counts (mean of 3 counts/day). There were 91 survey days at the Indiana site, with 1591 individual spotlight checks and 501 emergence counts (mean of 6 counts/day).

Roost Occupancy Overview~

We observed substantial variation in roost usage between field sites. While supporting similar sized colonies of Indiana bats, the colony at the Kentucky site was spread out across existing structures, leading to fewer bats in our new roosts. In total, we observed Indiana bats for 1,575 total bat days (1 bat day = 1 bat present in a roost on a given day) at the Kentucky field site, with bats using 15 of 20 rocket boxes, save those in the open cluster, with 5 rocket boxes reaching primary roost status (i.e., colony size ≥ 30 bats as per Callahan et al. 1997). A total of 8,804 bat days were logged at the Indiana

site, with Indiana bats using 14 of 20 rocket boxes, with no Indiana bats detected at the open cluster, and with 9 rocket boxes reaching primary roost status. The maximum emergence count for a rocket box at the Kentucky site was 59 (mean count = 7.5 ± 0.7 bats) and at the Indiana site the maximum emergence count was 174 bats (mean count = 33.6 ± 2.7 bats).

We discerned no patterns regarding bat preferences for a specific rocket box design (Figure 1-4). The REF design received comparatively little use at the Kentucky site, while the EXTJ design received little use at the Indiana site. At both field sites, VR designs seemed to have consistent use, and Indiana bats tended to colonize the easterly sun and forest roost clusters earlier in the year, then transition to the westerly sun clusters later in the maternity season (Figure 1-5). Peak usage of the forest and easterly sun clusters occurred during the same biweekly interval at both field sites.

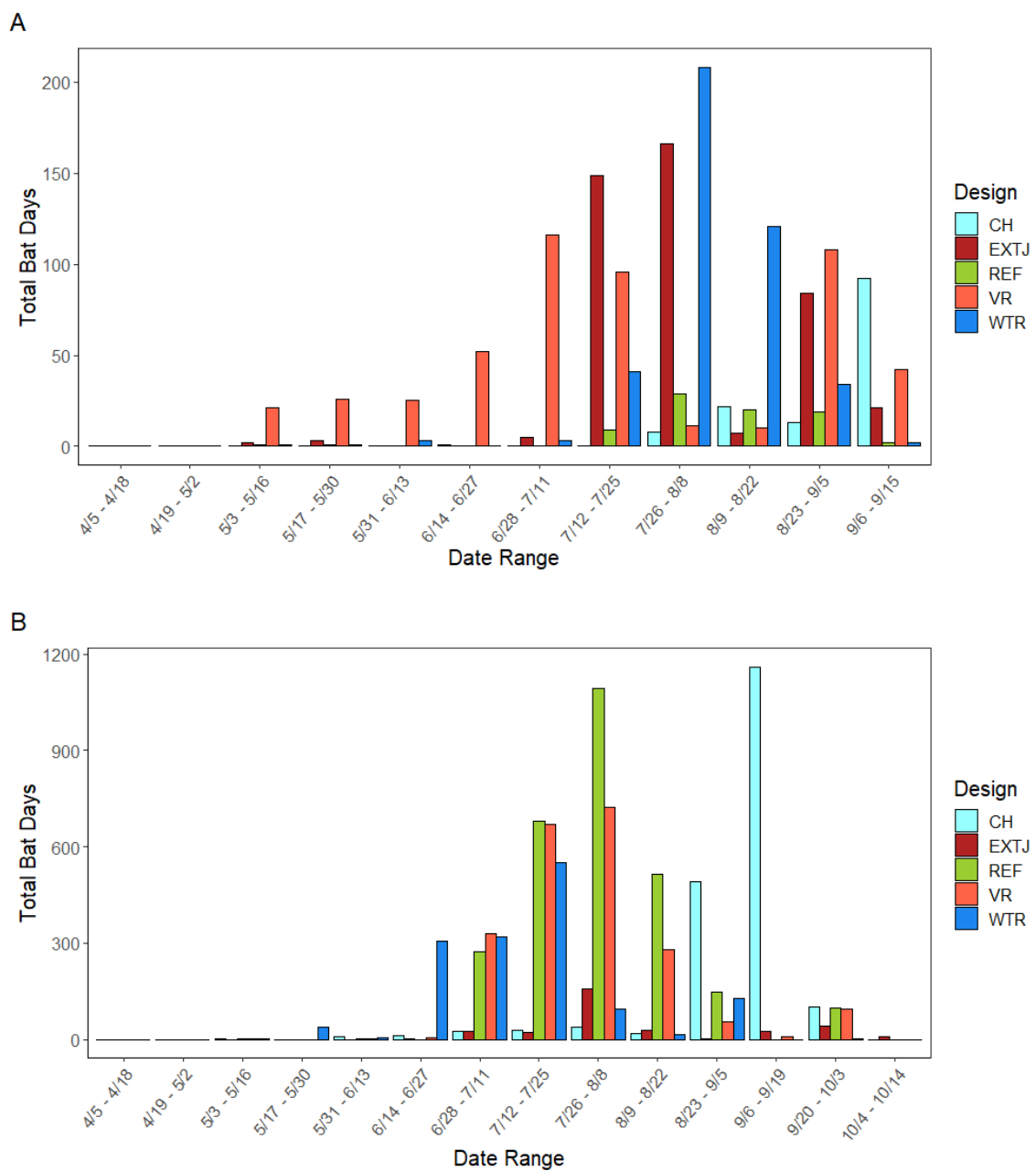


Figure 1-4: A) Bi-weekly total bat days per roost design for the Kentucky field site. B) Bi-weekly total bat days per roost design for the Indiana field site.

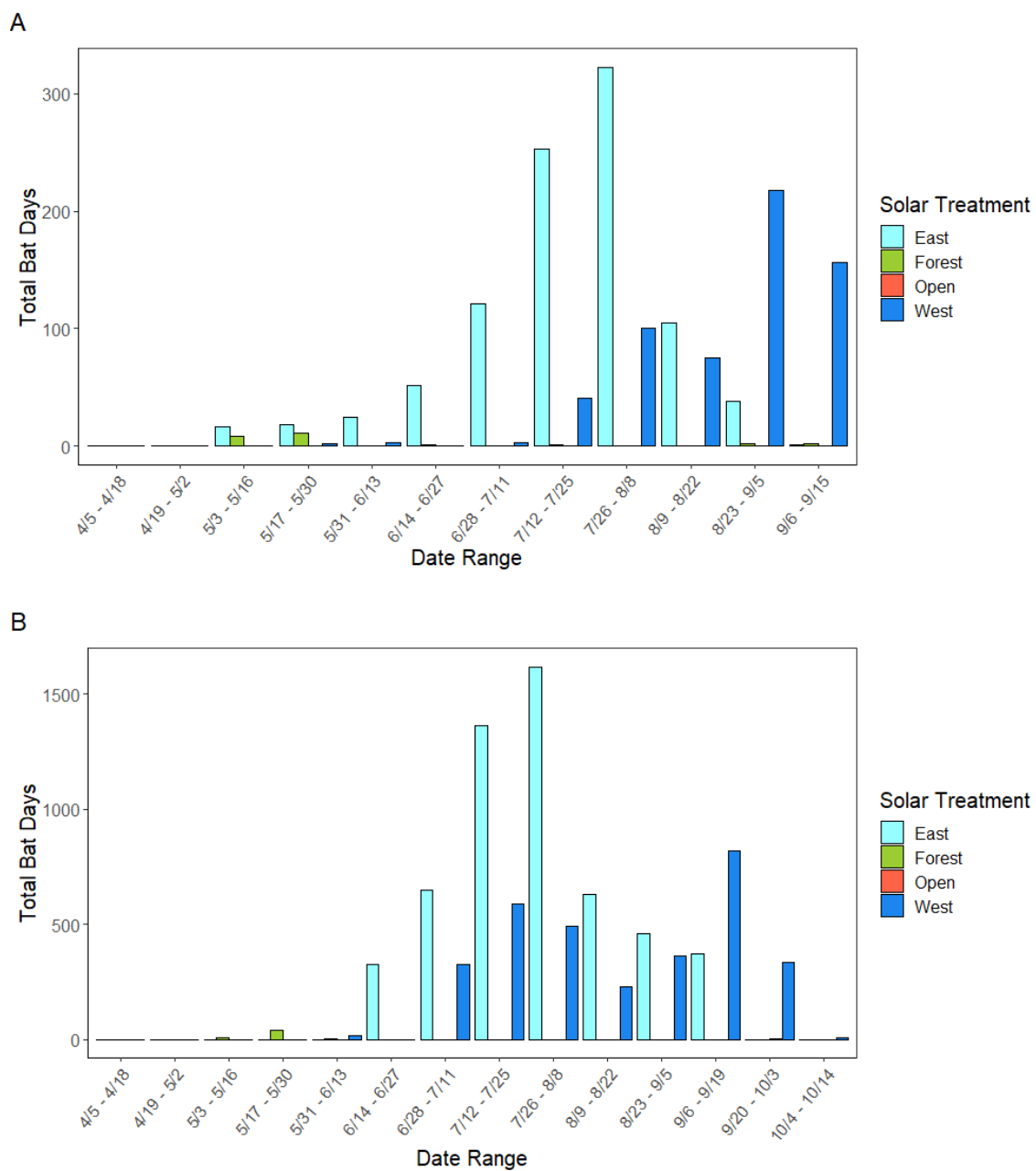


Figure 1-5: A) Bi-weekly total bat days per solar treatment for the Kentucky field site. B) Bi-weekly total bat days per solar treatment for the Indiana field site.

Presence/Absence and Abundance~

We removed open clusters from the analysis for both field sites as we never detected Indiana bats at either open cluster. We do note that 3 bat days were logged at the Indiana open cluster by bats we were unable to identify with confidence. The easterly sun EXTJ roost at the Indiana site was damaged on 6 June 2019 and no observations from this roost were used after this date. After removing observations from unused/avoided open solar treatment clusters, damaged roosts, observations pre-roost discovery, and weather station power failure days, there were 1790 individual observations of P/A and abundance for use in the hurdle model analysis.

Based on AIC_C model selection, the Solar Treatment Global model was the most plausible model with > 99.9% of all model weights (Table 1-2). No other models were within 2 AIC_C units of the top model. The next highest-ranking model was the Design Global model. This model carried < 0.001% of all model weights and was 13.9 AIC_C units below the top model. This result highlights the critical role of the solar treatment parameter in the best-fitting model as the Design Global model substitutes roost design for solar treatment. There was no support for the other candidate models. Within the top model, we identified 7 informative parameters in the P/A portion of the hurdle model (Table 1-3) and 6 informative parameters from the abundance portion (Table 1-4).

Table 1-2: AIC_C ranks of the 19 candidate hurdle models used to describe P/A and abundance.

Model Name	ΔAIC_C	K	w_i
Solar Treatment Global	0.0	25	1.0000
Design Global	13.9	29	<0.001
m13	44.9	23	<0.001
m11	46.4	15	<0.001
m16	50.2	21	<0.001
m12	69.3	13	<0.001
m14	76.3	21	<0.001
m17	76.5	17	<0.001
m3	76.9	11	<0.001
m15	79.1	22	<0.001
m6	84.1	19	<0.001
m9	102.4	13	<0.001
m4	134.1	11	<0.001
m7	135.1	19	<0.001
m10	155.0	17	<0.001
m5	168.3	9	<0.001
m8	169.1	17	<0.001
Null	191.2	7	<0.001
m2	201.2	15	<0.001

Table 1-3: Parameter estimates and 85% confidence intervals for the P/A portion of the top model. Note that a positive parameter estimate, in this case, indicates an increased probability of an absence (informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
Intercept	3.324	2.325	4.323
`Solar Treatment` Forest	1.798	1.111	2.485
`Solar Treatment` West	0.259	-0.252	0.770
`Solar Treatment` West(Forest RefLvl)	-1.539	-2.234	-0.844
`Repro Period` P	0.000	-0.356	0.356
`Repro Period` PL	-0.530	-0.776	-0.283
`Repro Period` PL(P RefLvl)	-0.530	-0.829	-0.230
AvgAMSolRad	-0.001	-0.002	0.001
AvgPMSolRad	-0.002	-0.003	-0.001
AvgDailyTemp	-0.071	-0.120	-0.021
AvgPrevDayTemp	-0.011	-0.059	0.037
AvgDailyWindSpd	1.650	1.174	2.126

Table 1-4: Parameter estimates and 85% confidence Intervals for the abundance portion of the top model (informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
Intercept	2.764	1.020	4.507
`Solar Treatment` Forest	-1.878	-2.984	-0.773
`Solar Treatment` West	-0.469	-1.157	0.220
`Solar Treatment` West(Forest RefLvl)	1.410	0.290	2.533
`Repro Period` P	-2.155	-2.801	-1.510
`Repro Period` PL	0.952	0.596	1.307
`Repro Period` PL(P RefLvl)	3.107	2.462	3.752
AvgAMSolRad	0.001	-0.001	0.003
AvgPMSolRad	0.000	-0.001	0.001
AvgDailyTemp	-0.081	-0.141	-0.020
AvgPrevDayTemp	0.025	-0.038	0.088
AvgDailyWindSpd	0.344	-0.309	0.997

Table 1-5: Odds ratios (OR), scaled where appropriate, and 95% confidence intervals for P/A parameters.

Parameter	OR	Scaled OR	Unit Change	95% Confidence Interval	
				Scaled Upper	Scaled Lower
`Solar Treatment` Forest	6.039	-	-	15.393	2.369
`Solar Treatment` West	1.296	-	-	2.599	0.646
`Solar Treatment` West(Forest RefLvl)	0.215	-	-	0.553	0.083
`Repro Period` P	1.000	-	-	1.623	0.616
`Repro Period` PL	0.589	-	-	0.823	0.421
`Repro Period` PL(P RefLvl)	0.391	-	-	0.886	0.391
AvgAMSolRad	0.999	0.962	50	1.060	0.864
AvgPMSolRad	0.998	0.905	50	0.959	0.851
AvgDailyTemp	0.932	0.703	5	1.039	0.366
AvgPrevDayTemp	0.989	0.946	5	1.272	0.620
AvgDailyWindSpd	5.209	5.209	1	9.960	2.724

Based on odds ratios for informative P/A parameters, Indiana bats were 6.04 times more likely to be absent at forest clusters when compared to easterly sun clusters, and 1.30 times more likely to be absent in westerly sun clusters when compared to the

easterly sun cluster (Table 1-5; Figure 1-6: A). Bats were 78% more likely to be present in the westerly sun cluster compared to the forest. Indiana bats were 41% more likely to be absent during lactation when compared to post-lactation, and bats were equally likely to be absent during pregnancy when compared to lactation (Table 1-5; Figure 1-6: B). Indiana bats were 61% more likely to be present during post-lactation when compared to pregnancy. Indiana bats were 30% less likely to be absent in rocket boxes for every 5°C increase in mean daily temperature (Figure 1-7: A). Indiana bats were 9% less likely to be absent for every 50w/m² increase in mean daily solar radiation (Figure 1-7: B). Finally, bats were 5.21 times more likely to be absent for every 1 m/s increase in mean daily wind speed (Figure 1-7: C).

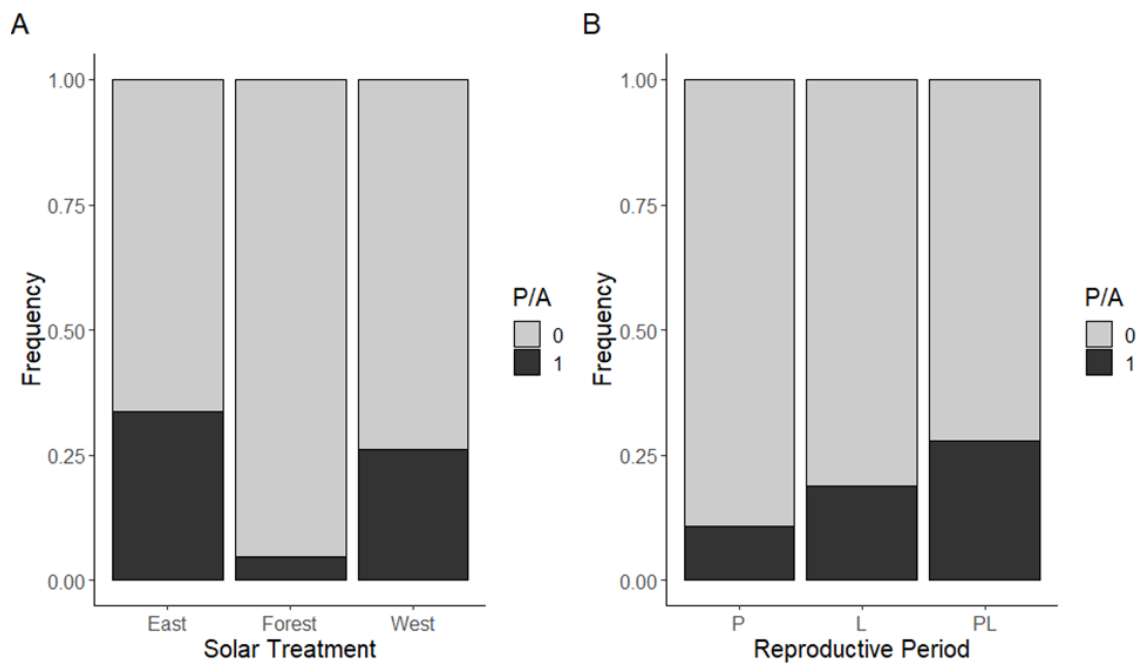


Figure 1-6: Relative frequency of presences (1) to absences (0), grouped by A) solar treatment and B) reproductive period.

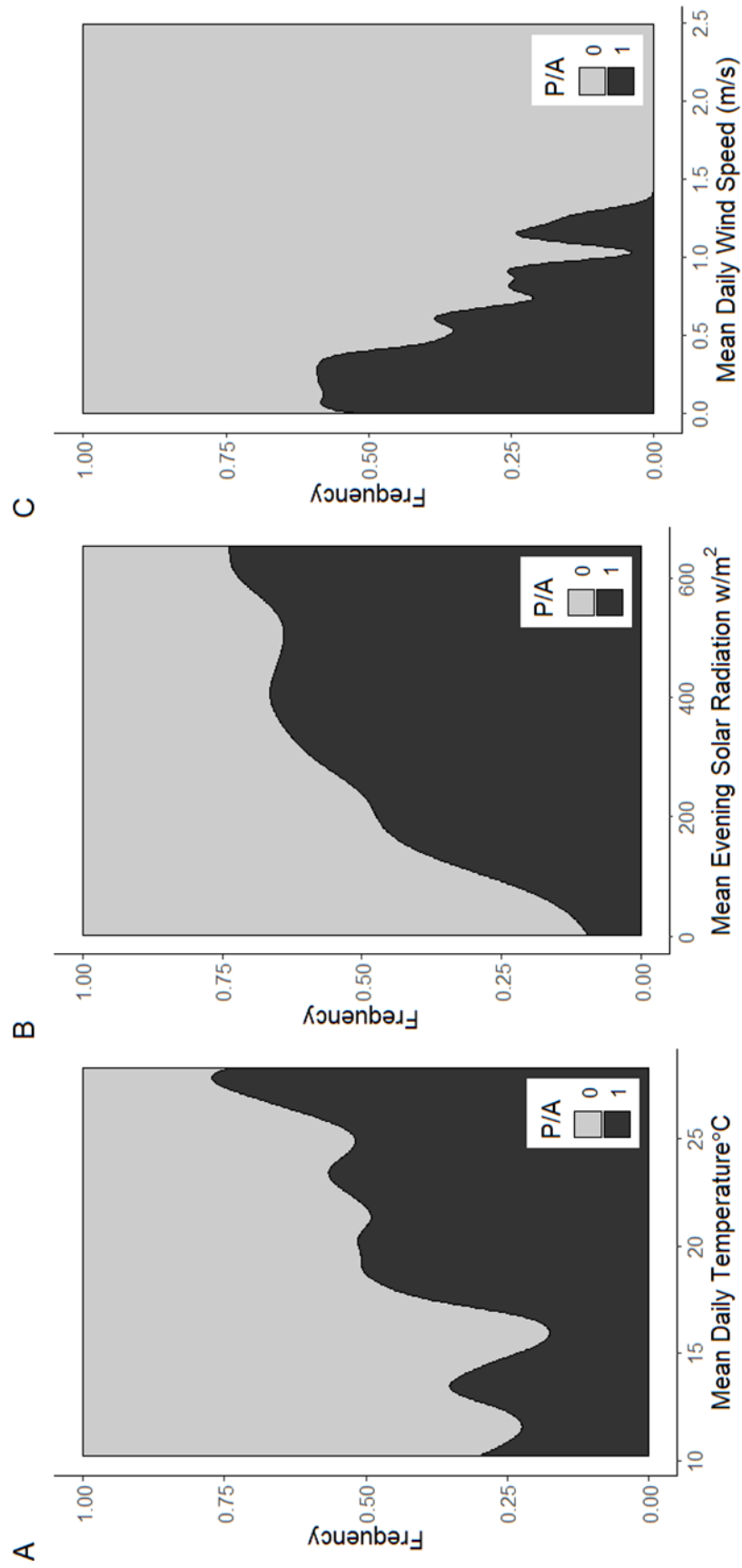


Figure 1-7: Smoothed kernel density graph showing the frequency of presences (1) and absences (0) of Indiana bats in rocket boxes in relation to A) mean daily temperature B) mean evening solar radiation C) mean daily wind speed.

Solar treatment, reproductive period, and mean daily temperature were informative parameters for the abundance portion of the hurdle model (Table 1-4). Mean colony size was conspicuously larger for easterly and westerly solar exposed roosts when compared to the forest cluster roosts (Table 1-6; Figure 1-8: A, C). Indiana bat colony sizes were larger during lactation and post-lactation versus pregnancy (Table 1-6; Figure 1-8: B, D). Furthermore, Indiana bat colony sizes were larger during periods of warmer mean daily temperatures (Figure 1-9).

Table 1-6: Mean and standard error of emergence counts by roost cluster and reproductive condition for the Indiana and Kentucky field sites.

	Field site					
	Indiana		Kentucky		Combined	
	Mean	± SE	Mean	± SE	Mean	± SE
Roost Cluster						
Easterly sun	47.7	4.9	9.2	1.2	28.1	2.8
Westerly sun	28.5	5.0	7.3	0.9	17.4	2.6
Forest	2.0	0.4	1.1	0.1	1.3	0.1
Repro Condition						
Pregnancy	2.6	0.7	1.8	0.2	2.0	0.2
Lactation	26.6	5.4	7.4	1.7	19.2	3.5
Post-lactation	45.5	4.5	9.2	0.9	26.2	2.4

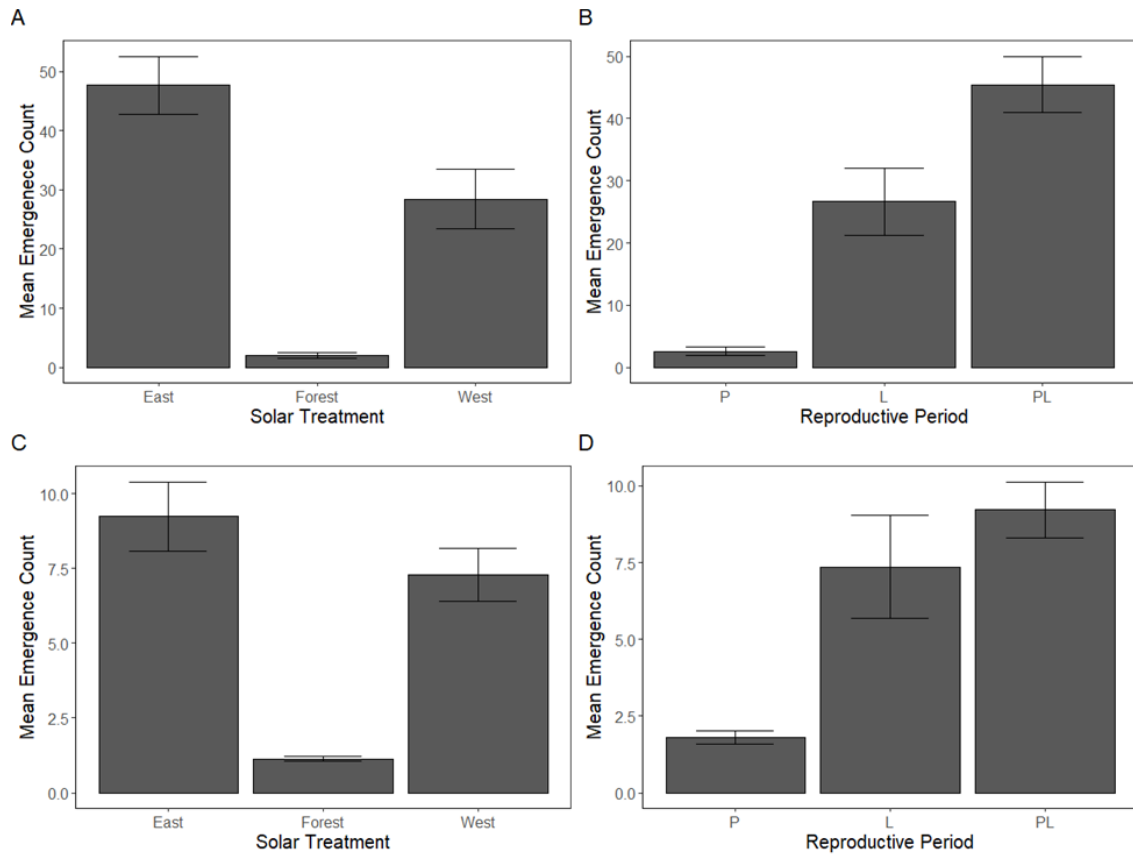


Figure 1-8: Mean emergence count at the Indiana field site by A) solar treatment and B) reproductive period. C) Mean emergence count at the Kentucky field site by C) solar treatment and D) reproductive period.

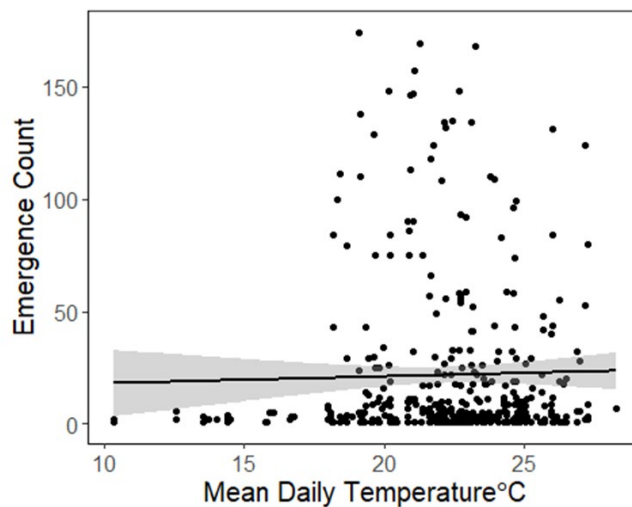


Figure 1-9: Scatter plot of the total emergence count per roost as a function of mean daily temperature with trend line and 95% confidence intervals. Trend line (black) and 95% confidence interval (gray).

DISCUSSION

Roost Uptake and Occupancy~

Our results indicate strong inter-site variation in artificial roost use by Indiana bats. While bats used a similar number of roosts across sites, the mean colony size, maximum emergence count, and total number of bat days logged at the two sites were dissimilar. The Indiana field site accumulated over 5 times the number of bat days and had a maximum emergence count that was 2.9 times larger compared to that of the Kentucky site. Considering these observations, there are several factors regarding site history that may have influenced roost uptake and use at each field site.

We judge the most plausible hypothesis for greater roost usage at the Indiana site is that Indiana bats have developed search images for rocket box roost structures as a result of previous exposure to this style of roost. Considering classic examples of prey detection being enhanced by the buildup of search images overtime (Zentall 2005), it seems plausible Indiana bats may be identifying potential roost structures in a similar manner. The Indiana field site has a long history of artificial bat roost deployment and research (Ritzi et al. 2005; Whitaker et al. 2006), and rocket boxes have been deployed at this site previously (Hoeh et al. 2018). In contrast, at the Kentucky site there were no rocket box style roosts deployed prior to this study. Roost familiarity may play an important role in roost uptake, as individual bats become familiar with the rocket box design, they may develop search images for them and thus be more likely to detect and subsequently use or avoid that structure in the future. Because rocket boxes were in place and used at the Indiana site for several years prior to our study, Indiana bats at this site may have be more willing to move into these structures in large numbers due to

possessing a search image and prior knowledge of this roost style. In contrast, Indiana bats at the Kentucky field site were likely more naive to the idea of rocket boxes as potential roosts.

Another likely explanation for dissimilar roost usage between sites could be the Indiana bats at the Indiana field site are more restricted to using artificial roosts as a result of increased urbanization and fragmentation of this landscape (Sparks et al. 2005; Whitaker et al. 2006; Bergeson et al. 2020). The Kentucky site likely possesses much larger tracts of contiguous forest with ample amounts of large dead snags which could potentially serve as natural roosts. Ample natural roosting habitat available at the Kentucky site may partly explain smaller colony size and lower fidelity to artificial roosts (Brigham 1991; Lewis 1995). For example, O’Keefe et al. (2017) found that in the southern Appalachians where roost availability was high, Indiana bats formed smaller colonies and switched roosts more often when compared to Indiana bat populations in the Midwest. Further, Brigham (1991) found big brown bats in British Columbia showed less fidelity to roosts than conspecifics in Ontario, suggesting limited roosting opportunities in Ontario led to higher roost fidelity. Thus, it is likely that decreased availability of natural roosting habitat at the Indiana field site may have led to larger numbers of bats using individual roosts.

Solar Treatment~

The importance of high solar exposure for Indiana bat maternity roosts is well-documented (Humphrey et al. 1977; Callahan et al. 1997; Kurta and Rice 2002; Britzke et al. 2003; O’Keefe and Loeb 2017). Our results further confirm that solar exposure is important to roost habitat selection, as our top model indicated that Indiana bats roosted

in rocket boxes receiving easterly and westerly solar exposure more often than they used shaded forest cluster roosts. Our results suggest potential tradeoffs and thresholds regarding solar exposure, as Indiana bats avoided using rocket boxes in the open solar treatment clusters, which were a considerable distance away from any tree line. A likely hypothesis explaining our result could be that Indiana bats perceive a high predation risk when flying in the open (Lima and O’Keefe 2013; Arndt et al. 2018), as this species is typically considered slow-flying and clutter-adapted, possessing both relatively low wing loading and low aspect ratio morphology. Roosting near tree lines may provide these bats with cover and fast access to sheltered areas safe from predation by diurnal and nocturnal raptors (Lima and O’Keefe 2013; Arndt et al. 2018). However, the fact that bats selectively roosted in clusters with eastern or western exposures over the forest cluster demonstrates the relative importance of high solar exposure for maternity roosting Indiana bats. If predator avoidance was the sole focus, bats would be more likely to roost in forest boxes that offered immediate cover upon emergence. Further, we would expect roost selection more similar to that of male Indiana bats, which typically roost alone or in small groups and select roosts with characteristics facilitating predator avoidance, such as high snag density and taller roost trees (Bergeson et al. 2018).

Reproductive Condition~

Reproductive condition was an important determinant of Indiana bat presence and abundance at our artificial roosts. We note greater abundance and increased frequency of presence with each successive reproductive stage, from pregnancy to post-lactation. We note that abundance and likelihood of presence is inflated during post-

lactation (and, to a certain extent, during lactation) due to pups gradually becoming volant and thereby increasing emergence count numbers, as well as by exploring and potentially using more roost structures (Whitaker and Sparks 2008; Oyler-McCance et al. 2018). Another explanation for this observed result is that Indiana bats at both field sites were likely naïve to the presence of the new rocket box structures on the landscape and thus there may be a period of time over which bats discovered roosts and then relayed this information to other bats before large colonies formed (Flaquer et al. 2006; Mering and Chambers 2012; Rueegger 2016). For instance, Mering and Chambers (2012) deployed 104 artificial roosts of 2 basic types in Arizona and found mean colonization time to be just over 400 days after installation. Additionally, Flaquer et al. (2006) found the abundance of soprano pipistrelles (*Pipistrellus pygmaeus*) in artificial roosts in wetland paddies increased with each subsequent year. We may have observed a similar effect on a much shorter time scale over the course of one maternity season, during which bats accumulated knowledge and subsequently began to aggregate in our rocket box roosts.

Wind~

Higher mean daily wind speeds led to a decrease in the likelihood of the presence of Indiana bats in our artificial roosts. This could be, in part, due to the seasonal timing of higher wind speeds at the study sites coinciding with the spring migration of bats to our sites and the fall migration away from the sites (see Appendix A). For example, Pettit and O’Keefe (2017) found high seasonal winds coincided with the arrival and departure of Indiana bats at their respective study sites. Due to this seasonal movement, Indiana bats were less abundant during these transition periods as

opposed to the generally calmer summer months (Pettit and O’Keefe 2017). Another plausible hypothesis is that during periods of high winds (e.g., during storms), Indiana bats shifted to more sheltered or forested roost structures, as typical maternity roosts are generally solar-exposed, ephemeral snags (Timpone et al. 2010; Hammond et al. 2016), which may be more susceptible to falling and thus may pose a safety risk to bats during periods of high wind.

Mean Daily Temperature~

Ambient temperature is well documented as a factor known to impact artificial roost microclimate, metabolic energy expenditure of bats, as well as a factor influencing the growth and development of pups (Racey and Swift 1981; Kunz 1987; Hoeh et al. 2018). Our results suggest a weak trend in which the presence and abundance of bats increased with increasing mean daily temperature. One hypothesis explaining this result could be that the warmest days during our study occurred during the middle of the maternity season (See Appendix A) when bats are most abundant, and that Indiana bats are likely to be migrating and less abundant on cooler days during the spring and fall (Pettit and O’Keefe 2017). Another explanation could be that Indiana bats accumulated knowledge of roost locations over time and, thus, the discovery period led to a gradual accumulation of bats in roosts over time. In turn, this may have contributed to the weak trend with temperature as average temperatures increased as the summer progressed. In this scenario, time is the determinant of abundance and just happens to coincide with increasing periods of temperature.

Evening Solar Radiation~

Our results show evening solar radiation as an important predictor of Indiana bat presence, with bats more likely to be present in rocket boxes with increasing evening solar radiation. The level of solar radiation received is likely linked to the solar treatment of the roost cluster, with easterly sun and westerly sun roost clusters receiving higher evening solar radiation than the forest roost clusters. Our result is supported by the literature; high solar exposure is well-documented as an important characteristic of Indiana bat maternity colonies (Callahan et al. 1997; Britzke et al. 2003; O’Keefe and Loeb 2017). Our observed preference for high evening solar exposure is likely a result of Indiana bats selecting warmer roost microclimates as the growth and development of pups is favored under warmer conditions (Kunz 1987; Zahn 1999).

Non-preference of Roost Design~

We found little evidence of bats selecting any particular rocket box design, which could be due to several factors. First, because these roost were newly-deployed at both field sites, bats lacked prior knowledge about what type of microclimate each roost design might provide and likely did not have time to “sample” each roost to assess its microclimate during different periods and weather conditions (Kerth et al. 2001). Selection and preference are likely the result of associative learning impacting behavior (e.g., Swift et al. 2002), which may influence future actions. As our results only encompass a single maternity season, there likely has not been enough time for testing of all roosts to occur. Another possibility is that bat principally select roosts at dawn when roosts have likely reached their coolest temperatures and, as shown in several studies, artificial roost temperatures can be very similar during the overnight even when

daytime temperatures can be drastically different (Kerth et al. 2001; Bartonicka and Rehak 2007). If bats lack prior knowledge about roost microclimate, they likely would not be able to discern differences between roosts and thus would not prefer one to another with at first testing each roost (Kerth et al. 2001). Another plausible scenario is our roost designs may not be providing microclimates that are different enough to influence roost preference. Rocket boxes have been documented to support large internal temperature gradients (i.e., 7°C; Hoeh et al. 2018), making it possible that all of our rocket box designs may have provided large enough temperature gradients so that bats could find suitable temperatures within any roost. For example, a bat roosting in the cooler chimney design may roost near the top of the box if warmer temperatures were desired, while in the warmer vent removal box a bat could roost lower within the roost to find a cooler condition. If these two designs supported a large enough temperature gradient, it is possible that Indiana bats may find similar roosting temperatures within each box by changing their vertical positioning. Several studies have documented bat movements within roosts, presumably to locate desired temperatures (Humphrey et al. 1977; Hamilton and Barclay 1994; Lourenço and Palmeirim 2004); it is reasonable to assume the populations of Indiana bats under study at our field sites might behave similarly.

Transitions across Roost Clusters~

Differential solar radiation and the associated reproductive costs of thermoregulation may be a driving force behind the observed transition of Indiana bats from easterly to westerly sun clusters, which occurred during the same biweekly interval at both field sites (26 July – 8 August 2019). Indiana bat pups are born altricial

and are poor thermoregulators; using warm roosts favors the growth and development of pups, as less metabolic energy is devoted towards thermoregulation (Racey and Swift 1981; Kunz 1987; Hoying and Kunz 1998). It logically holds in our study system that Indiana bats selected easterly sun roosts during lactation, as these roosts are likely to warm faster in the morning as compared to forest and westerly sun clusters (Mering and Chambers 2012) and, thus, reduce energetic costs associated with maintaining normothermia (Hamilton and Barclay 1994). For example, Hamilton and Barclay (1994) found that female big brown bats rearing young preferred to roost on the easterly side of an attic roost and, thus, inferred passive rewarming in the morning was the main driver of selection for roost aspect. In our system, the mid-July/early-August transition to westerly sun roosts may have been the result of lactating bats transitioning to the post-lactation stage, at which point pups are weaned and presumably volant (Kurta and Rice 2002). The transition may thus be related to differing energetic constraints following pups becoming independent. Post-lactating Indiana bats might have transitioned to westerly sun roosts for the increased energetic savings gained through passive rewarming before emerging at night (Lacki et al. 2013), as bats need to arouse to near an active body temperature before taking flight (Hamilton and Barclay 1994; Willis and Brigham 2003).

Though observed usage of the forest cluster rocket boxes was low, we note peak usage of these roosts occurred during the same biweekly period at both field sites (17 May – 30 May 2019). This peak in usage occurred during pregnancy and may have occurred due to shaded roosts supporting cooler microclimates and, thus, facilitating deeper torpor and resulting in increased thermoregulatory savings from not maintaining

normothermia (Hamilton and Barclay 1994; Lausen and Barclay 2003b; Willis and Brigham 2003). This supposition is further supported by the findings of Lausen and Barclay (2003), who found that big brown bats in Canada were more likely to use torpor during pregnancy and post-lactation than during lactation. Further investigation of forest cluster roosts is needed to provide clearer support for this hypothesis.

Management Implications~

We stress that if artificial roosts are deemed necessary for management then resource managers should deploy multiple artificial roosts (of the same or differing designs) at a variety of solar exposures to suit the changing thermoregulatory and physiological needs of Indiana bats over the maternity season. Deploying artificial roosts in clusters and in varying solar treatments could facilitate roost discovery and provide bats with a variety of microclimatic options to choose from within a microsite (Lewis 1995; Rueegger 2016). In both of our field sites, Indiana bats used artificial roost clusters in easterly sun, westerly sun, and forest locations. We provide evidence that Indiana bats may avoid artificial roosts in open areas away from tree lines. Providing bats with high-quality artificial roosting habitat during the summer may enhance energetic savings and, thus, could potentially lead to increased overwinter survival as bats that accumulate larger fat stores pre-hibernation may be more likely to survive WNS infection (Cheng et al. 2018). Additionally, providing multiple roost designs and deployments may provide bats refugia from extreme temperatures, as overheating events in artificial roosts are likely to become more common as a result of a changing climate (Flaquer et al. 2014; Bideguren et al. 2018). It logically follows that

providing a variety of roosting conditions may enhance survival during extreme temperature events.

Future Directions~

We note several additional avenues of research for further investigation. Future work should assess whether our observation regarding transitions across roost cluster locations (i.e., from easterly to westerly sun) holds true over successive years and is thus predictable. If so, consistent observations would provide further evidence that Indiana bats switch roost clusters to gain thermoregulatory advantages that align with their current physiological state. Additionally, now that bats have had time to sample each roost in our study system, work focusing on roost selection is needed to determine if bats begin to show preference (or continue not to show preference) for roost design. We also note several other tree line deployments (e.g., south, south-east, south-west, northern orientations) could be tested alongside current deployments to further investigate the effects of differential solar exposure on roost selection. Additional research focusing on the longevity and viability of artificial roosts is needed to investigate the cost-benefit ratio of artificial roost deployment, as some designs may last longer and maintain thermal performance overtime more effectively than other designs. Alongside deployment of artificial roosts, researchers should also investigate reproductive success of bats at artificial roosts, as information on reproductive success and pup viability are largely unknown. Further, roost dominance and the community composition at artificial roost sites following deployment should be investigated as relative roost importance and interspecific competition may change occupancy and abundance rates over time (Mering and Chambers 2014; Rueegger 2016, 2017;

Rueegger et al. 2019). Lastly, further research is needed to assess the potential that artificial roosts could be altering the behavior of bats and subsequently serving as ecological traps wherein bats may experience subsequent declines in survival or fecundity (Bideguren et al. 2018). In such cases, artificial roosts may mimic the appearance of natural roosts and be placed in theoretically “prime” locations, but thermally and functionally may not act in the same manner as a natural roost. Thus, bats might be tricked into using these structures by visual and environmental cues they think are optimal (Battin 2004). Such scenarios should be investigated more thoroughly in the future to justify the use of artificial roosts as tools for management of at-risk bat species.

CHAPTER 2 : BAT BOX MICROCLIMATE IS IMPACTED BY DESIGN, PLACEMENT, WEATHER, AND OCCUPANCY

INTRODUCTION

Thermal environments of roosts, both natural and artificial, can vary greatly in regard to temperature stability, availability, and suitability (Lacki et al. 2013; Hoeh et al. 2018; Rueegger 2019). Temperature variability within environments, often inducing physiological stress, has led to the evolution of varied coping mechanisms and behaviors organisms use in an attempt to stay within the operative temperature limits of their bodies (Huey et al. 2003; Buckley and Huey 2016). In many cases, temperature extremes may delineate the suitability of a site based upon an organism's thermal tolerance thresholds and coping behaviors (Sunday et al. 2012); in many cases temperature extremes exceeding tolerance thresholds render sites unusable and potentially dangerous (Lourenço and Palmeirim 2004; Camacho et al. 2015). As such, access to roost structures and microhabitats within thermal tolerance thresholds may be critical to the survival and persistence of many species (Kunz 1982; Buckley and Huey 2016; Jarolimek and Vierling 2019).

For temperate region bats, finding roosts that suit their thermoregulatory and physiological needs is paramount to survival and rearing offspring successfully (Kunz 1982, 1987; Sedgeley 2001). Roost temperatures can occasionally exceed the thermal tolerance thresholds of bats, rendering these roosting areas unusable and dangerous (Bartonicka and Rehak 2007; Flaquer et al. 2014; Bideguren et al. 2018). Temperatures exceeding 40°C can induce heat stress and prolonged exposure to these high

temperatures within a roost can lead to mortality (Henshaw and Folk Jr 1966; Licht and Leitner 1967). For example, Flaquer et al. (2014) report an overheating event in an artificial roost leading to 22 soprano pipistrelles (*Pipistrellus pygmaeus*) falling from the roost upon emergence. Further, Lourenço and Palmeirim (2004) note that soprano pipistrelles sought warm roosting positions within an attic, but avoid areas exceeding 40°C, suggesting that the upper temperature limit for these bats is near this temperature. In contrast, cold roosts can prolong the gestation period of pregnant bats (Racey and Swift 1981), reduce milk production of lactating bats (Wilde et al. 1999), and slow the development of pups, which are born altricial and are poor thermoregulators expending excess energy to maintain normothermia (Kunz 1987; Hoying and Kunz 1998). Delayed development in cool roosting conditions could impact overwinter survival, as body fat accumulation can increase the probability of surviving white-nose syndrome (WNS) infection during winter (Cheng et al. 2018). At temperatures near or below 0°C, bats must arouse from torpor and expend excess energy generating heat to prevent freezing (Henshaw and Folk, Jr 1966; Davis and Reite 1967). Thus, having access to roosts that offer suitable microclimates may increase the likelihood survival.

Thermal environments of roosts directly influence bats' energetic expenditures (Kunz 1987; Hoying and Kunz 1998; Zahn 1999; Lausen and Barclay 2003; Wilcox and Willis 2016). In cool roosts, bats can enter torpor and experience increased energetic savings resulting from not maintaining normothermia (Hamilton and Barclay 1994; Lausen and Barclay 2003; Willis and Brigham 2003). Even so, the negative reproductive costs of low body temperature during lactation often limit female bats' use of torpor (Kunz 1987; Hamilton and Barclay 1994; Solick and Barclay 2006). For

example, Lausen and Barclay (2003) note that lactating big brown bats (*Eptesicus fuscus*) in Alberta, Canada select rock crevice roosts that are more thermally stable, retaining more heat through the course of the overnight than other available rock crevices; these conditions allow lactating bats to use deep torpor less frequently than pregnant and post-lactating individuals. Selecting roosts that retain heat could expedite juvenile development (Zahn 1999; Lausen and Barclay 2006). Further, as adult bats emerge for foraging and are no longer providing body heat, heat retention by roosts through the overnight could be critical for juvenile development and survival. Notably, lactating female Indiana bats (*Myotis sodalis*) can spend > 5 hours per night foraging, visiting pups intermittently to nurse (Murray and Kurta 2004), which could result in significant roost cooling. Additionally, Kerth et al. (2001) found that, of 2 roost designs tested, artificial roosts with significantly different peak temperatures during the day decline to near identical temperatures 1–3 hours after sunset as a result of poor heat retention. Based on the costs of variable roost microclimate, it is clear strong selective pressure is placed on bats to find roosts that suit their thermoregulatory and reproductive needs. Providing thermally beneficial roost alternatives could enhance outcomes when artificial roosts are used as effective conservation and management tools.

Microclimates of both natural and artificial roosts are influenced by a multitude of structural, environmental, and landscape components. Artificial roost construction material (Bideguren et al. 2018), color and reflectance (Doty et al. 2016; Griffiths et al. 2017), and volume (Sedgeley 2001) can influence microclimate suitability. For example, Lourenço and Palmeirim (2004) found that black boxes are on average 5°C

warmer than white boxes of the same design. Environmental factors like cloud cover (Hoeh et al. 2018), ambient temperature (Lacki et al. 2013), wind (Tillman 2019), humidity (Rueegger 2019), and solar exposure (Brittingham and Williams 2000) all alter microclimate. For example, on days with clear skies, the temperature gradient within rocket and bat box style roosts can be as high as 10°C (Hoeh et al. 2018). Larger-scale components like roost aspect (Mering and Chambers 2012), canopy closure (Jarolimek and Vierling 2019), and slope position (Lacki et al. 2013) all impact microclimate. Several studies suggest bats prefer roost aspects and slope positions that promote warm microclimates, like south and east aspects (Mering and Chambers 2012) and south facing slopes (Hammond et al. 2016). Detailed consideration of roost microclimate relating to structure, weather, and landscape position should be investigated as potential drivers of roost occupancy. Such investigations could inform effective artificial roost placement and identification of high-quality natural roost sites.

The physiological state of bats in roosts can significantly impact roost temperature. Physiological components influencing microclimate include colony size, which can influence temperature and humidity, and the metabolic state of the bats occupying the roost (Bartonicka and Rehak 2007; Willis and Brigham 2007). For example, the differential use of torpor and normothermia can influence roost microclimate, as bats can drop their body temperature to within a few degrees of ambient conditions, thus exerting minimal influence on roost temperature. Bats maintaining an active body temperature could impact roost microclimate substantially on days when ambient temperature is low (Hamilton and Barclay 1994; Dietz and Kalko 2005; Willis and Brigham 2007; Dzal and Brigham 2013). For instance, Willis

and Brigham (2007) found that the presence of bats in a roost could increase roost temperatures by as much as 7°C. Interactions among physiological factors likely have an impact on the microclimate provided by a roost and may determine its overall suitability. Developing a better understanding of how different combinations of physiological components influence roost microclimate is critical to improve future conservation efforts and artificial roost design.

Artificial roosts (e.g., bat boxes), which are often deployed as mitigation tools, have been under much scrutiny recently as a result of ongoing investigations into their efficacy, microclimate, and proper usage. Current studies show that many modern artificial roost types are inadequate at buffering against extreme temperatures (Bideguren et al. 2018; Hoeh et al. 2018; Rueegger 2019), and do not retain heat at night (Kerth et al. 2001; Lourenço and Palmeirim 2004). Finding roosts that support favorable microclimates could be critical for the summer survival of bats impacted by WNS (Wilcox and Willis 2016). Additionally, in Australia, Rueegger et al. (2019) found that bats rarely used artificial roosts deployed for mitigation on degraded landscapes and noted that current designs may not be effective substitutes for natural roosts for some bat species. Artificial roost design, microclimate, landscape position, and local climate likely interact to influence bat occupancy and abundance.

Due to the gaps in our knowledge and deficiencies noted regarding current artificial roost designs, microclimates, and landscape positions, continued rigorous investigation of these factors is needed to further justify and revise the use of artificial bat roosts as mitigation tools. For the present study, we aimed to profile the microclimates of 4 rocket box style artificial roosts specifically altered to manipulate

microclimate compared to a reference design, and to further investigate the effects of landscape position, weather, and bat occupancy and abundance on roost microclimate.

STUDY SITES

Historically, the Indiana bat ranged throughout most of the east-central United States, with the core of their range in the Midwest (USFWS 2007) and with many major hibernacula throughout Indiana and Kentucky (USFWS 2007). The two field sites for this study have known maternity colonies of Indiana bats and are in the central part of the species' range.

The first site is the Indianapolis Airport mitigation site in central Indiana (39°38'59"N, 86°20'57"W; hereafter, the Indiana site) and the second site is located at Veterans Memorial Wildlife Management Area in north-eastern Kentucky (38°19'20"N, 84°32'57"W; hereafter, the Kentucky site). The Indiana field site is located within the Eastern Corn Belt Plains ecoregion and is characterized by an abundance of soybean, corn, and wheat fields with small mixed forest fragments (U.S. Environmental Protection Agency 1997). The Indiana bat maternity colony at this site has used artificial structures as roosts since ~2003–2019 (Ritzi et al. 2005; Whitaker et al. 2006; Hoeh et al. 2018). In the mid-1990s, Whitaker et al. (2006) observed the deployment of over 3,000 artificial roosts, of varying designs, at the Indiana site and documented minimal roost occupancy. Recently, Hoeh et al. (2018) deployed 6 clusters of 3 roost types (rocket box, bark-mimic, and bat box style) at the Indiana site, of which Indiana bats preferred the rocket box style based on occupancy; these roost clusters have been in place since ~2015.

The Kentucky field site is located within the Interior Plateau ecoregion and is characterized by mostly forested rolling hills containing predominantly white oak (*Quercus* spp.), hickory (*Carya* spp.), and eastern red cedar (*Juniperus virginiana*) (Woods et al. 2002). At this site, the Indiana bat maternity colony was previously documented using BrandenBark™ artificial roost structures that were installed around Summer 2016 (pers. comm. KDFWR). These structures are composed of a polyurethane sheet of synthetic bark wrapped around and affixed to the top of a 7.6 meter tall telephone pole (Gumbert et al. 2013). During the spring of 2019, 17 of the 18 original Brandenbark™ roosts were removed and replaced by 18 newer versions, as the posts for the old roosts were badly decayed and posed a safety hazard. A total of 3 roost clusters are spread across the site, 2 of the clusters containing 6 BrandenBark™ artificial roosts and 1 cluster containing 7 roosts (6 new and 1 old, 19 total at site) (pers. comm. KDFWR).

METHODS

Box Construction~

We constructed 4 replicates of 5 designs (i.e., 20 rocket boxes total) at Eastern Kentucky University for deployment at the Kentucky field site. Concurrent efforts were directed by Francis Tillman at Indiana State University to produce the same complement of boxes for deployment at the Indiana field site. All designs were modifications of the reference rocket box design described by Tillman (2019) (Figure 2-1). Designs developed include: reference (REF), vent removal (VR), chimney (CH), white tile roof (WTR), and external water jacket (EXTJ) (Table 2-1). Each altered

design was intended to promote a microclimate different from the REF design, though each design provided equal entrance area, roosting surface area, and volume.

All rocket boxes were constructed from 1" thick (3/4" actual; 1.9cm) untreated pine (*Pinus* spp.) lumber. Untreated lumber is preferred as various lumber treatments can be harmful to bats (Racey and Swift 1986). We used 1" x 8" x 8' (1.9cm x 20.3cm x 2.43m) boards to cut inner shell pieces, and 1" x 10" x 6' (1.9cm x 25.4cm x 1.8m) boards to cut outer shells. Inner shell boards measured 42" (106.7cm) long and 5-3/4" (14.6cm) wide. When attached to the other inner shell pieces with an edge overlap for anchoring (Figure 2-1), total inner shell face width was 6.5" (16.5cm). We cut outer shell boards to 36" (91.4cm) long and 8-3/4" (22.2cm) wide, and with edge overlap from other outer shell boards, outer shell box faces measured 9.5" (24.1cm) wide. We used exterior grade plywood for both the inner and outer roofs, measuring 6.5" (16.5cm) and 9.5" (24.1cm), respectively (EXTJ outer roof 12-3/4"). Boxes were mounted around the top of one untreated 4" x 4" x 12' (8.9cm x 8.9cm x 3.7m) post.

For the EXTJ design, we added an additional 3/4" (1.9cm) chamber to the exterior of the box. We did this by sistering two 6" x 36" (15.2cm x 91.4cm) boards together with three 2" X 3/8" (5.1cm x 0.95cm) pine dowel rods spaced 6" (15.2cm) from the top, 18" (45.7cm) down, and 6" (15.2cm) from the bottom of the board; anchored with wood glue. This resulted in external chamber boards measuring 12" (30.5cm) wide, so that the boards encompassed the outer shell of the reference rocket box design. Thus, we filled the resultant external chamber with 12 water packets (3 packets per side) each measuring 11" x 11" (27.9cm x 27.9cm) (Figure 2-2). Packets were filled with 750ml of DI water and four foam supports which supported the edges.

Packets were constructed using heavy duty plastic and a commercial vacuum sealer for food storage. This additional chamber was sealed off with four 10.5" (26.7cm) wood spacers to prevent entry by vertebrates. Additionally, we used two 6" (15.2cm) spacers to separate water packets within the chamber.

We used 1-1/4" (3.2cm) exterior grade screws to attach spacers to the 4" x 4" (8.9cm x 8.9cm) posts and inner shells and used a 1-1/2" (3.8cm) hole-saw to cut a transfer hole 18" (45.7cm) from the top of the inner shell. This transfer hole gives bats the option to move between the inner and outer chambers without leaving the interior of the box. We used 1-5/8" (4.1cm) exterior grade screws to assemble the inner and outer shell pieces, and we used 2" (5.1cm) exterior grade screws to anchor the inner shells to their respective posts. The portion of the 4" x 4" (8.9cm x 8.9cm) post inside the roost, in addition to the inner shell boards, were scuffed using a 1-1/2" (3.8cm) hole-saw held at an acute angle (Figure 2-3). Scuffing provides bats with footholds for roosting and climbing inside boxes. We sealed all seams with clear paintable latex caulk to increase weather and rain resistance. We covered exteriors of all outer shells and outer roofs with 2 coats of a flat brown exterior grade paint. We reinforced the bottom corners of the outer shell with 2.5" (6.4cm) metal corner brackets. For all designs, excluding the WTR, a dark colored roofing shingle was cut to fit and attached with roofing tar. Completed rocket boxes were subsequently attached to an additional 4" x 4" x 12' (8.9cm x 8.9cm x 3.7m) treated base post using 2" x 4" x 4' (4.4cm x 8.9cm x 1.2m) boards on each side of the post seam fastened down with 3" (7.6cm) exterior grade screws. We used treated base posts to increase the longevity of the boxes on the landscape, as untreated base posts would deteriorate much faster once in the ground.

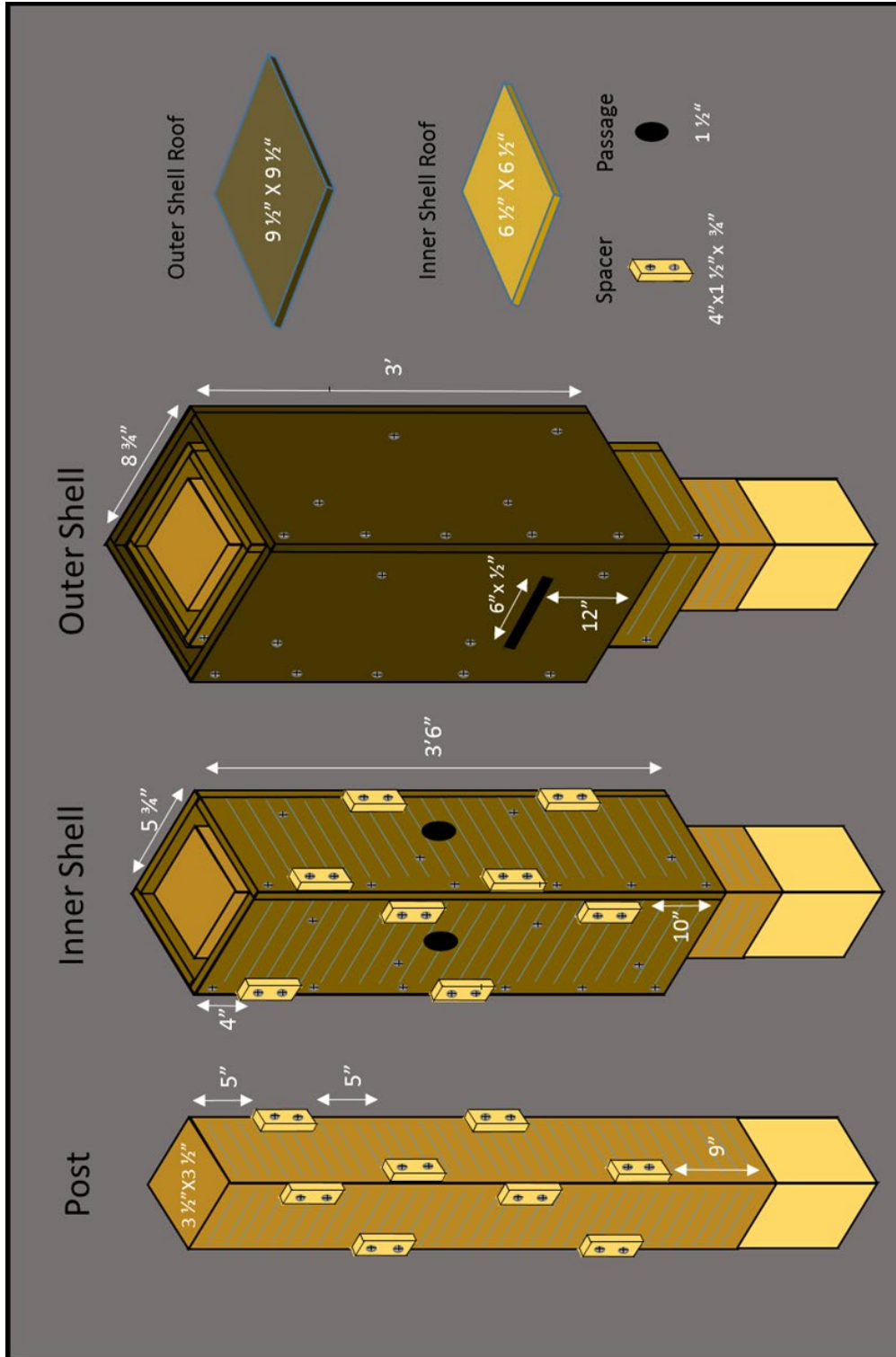


Figure 2-1: REF rocket box design as described by Tillman (2019) (rendering not to scale).

Table 2-1: Details for all variant rocket box designs. All designs are derived from the standard design described by Tillman (2019) and provide the same roosting surface area, volume, and entrance area.

Design	ID	Description	Hypothesized effect
Reference (REF)	1	The is a 2 chambered box with two 6" x 1/2" (15.2cm x 1.3cm) horizontal vents on the north and south sides of the box. Vents are located 12" (30.5cm) from the bottom of the outer shell.	This box will serve as the reference to which all boxes will be compared.
Vent Removal (VR)	2	The vent removal design is identical to the standard design but lacks vents.	This box will support a warmer microclimate than all other designs and will increase minimum temperatures on cold days.
Chimney (CH)	3	The chimney design is identical to the standard design, but adds a 3' (91.4cm) foot tall, 3" (7.6cm) diameter black PVC chimney to the roof. The hole in the outer roof is 2 1/2" (6.4cm) in diameter.	This box will reduce maximum temperatures by venting heat out of the top of the chimney. The black chimney should facilitate heat rise.
White Tile Roof (WTR)	4	The white tile roof design is identical to the standard design but adds an 8mm thick white glazed ceramic tile to the roof instead of a shingle.	This box will reduce maximum temperatures by reflecting solar radiation with the white roof tile.
External Water Jacket (EXTJ)	5	The external water jacket design adds a 3/4" (1.9cm) chamber around the outer shell. Each side of this new chamber is filled with 3 packets containing 750ml of DI water and foam to support the edges of the packet. This chamber is then sealed to prevent access by vertebrates.	Being buffered by an additional water-filled chamber, this box should provide a more stable microclimate that resists extreme temperatures as water takes longer to heat and cool than air.



Figure 2-2: Placement of water packets within the EXTJ design's insulated shell.



Figure 2-3: Scuffed post and inner shell half prior to inner shell attachment.

Microclimate Data Collection~

For each of the 40 boxes deployed, we recorded internal roost temperature with Thermochron iButtons (Thermochron iButton DS1921G, Maxim Integrated, 0.5°C increments at ± 1.0 °C accuracy, range -40 to 85°C). We placed 12 iButtons inside the outer chamber of each rocket box. We only placed iButtons in the outer chamber because inner chambers are typically more stable than those on the periphery (Brittingham and Williams 2000; Ruegger 2019), and we were fundamentally interested in the thermal extremes experienced by these boxes as temperature extremes are likely to impact suitability. We placed 3 iButtons at the top (5cm beneath the roofline), middle (43cm from the roof), and bottom (7.5cm from bottom) levels along each of the 4 box faces (Figure 2-4).

We set iButtons to record temperature every other hour, programming half of the iButtons to record on even hour intervals and half to record on odd hour intervals. Even and odd hour iButtons were alternated at each level within the roost to ensure that temperature data was collected every hour at every level within the roost (i.e., top, middle, and bottom). Setting the iButtons to record on an every other hour schedule was necessary to conserve memory space (Model #DS1921G can hold 2048 temperature recordings). Our schedule insured that temperature data collection spanned the duration of the study; data collection occurred from 1 April to 15 September 2019.

We placed iButtons inside cages, with the serial number facing outward, to prevent bats from touching the iButton's surface and potentially altering temperature readings (Figure 2-5). We constructed cages from 1/2" (1.3cm) plastic bushings with 1/4" (0.6cm) wire domes added to the top, secured by 24-gauge bailing wire. Wire

domes did not restrict airflow over the surface of the iButton. A square of double-sided mounting tape was used to hold iButtons in place within the cage. Once in cages, we attached iButtons to a 3'6" (91.4cm) strand of 30lbs (13.6kg) nylon-coated steel fishing line using flag crimp rings (Figure 2-5). We attached iButton lines to quick release systems (Figure 2-6) located at the top of the inner chambers. We made quick releases by sinking a 5/8" (1.6cm) eye-screw in the edge of the inner roof board offset 2-3/4" (7cm) from the left edge of the roof. We attached 5/8" (1.6cm) paper clips to iButton lines and looped the paperclips through the eye-screws, securing iButtons in place. We placed a staple at the bottom of each line, flush with the bottom edge of the inner shell to reduce the risk of entangling for bats. Pulling on the bottom of the line opened the paperclip and allowed the iButtons to fall from the roost, allowing for non-invasive iButton removal. Once airborne, iButtons hung down in a straight line in their respective positions.

Prior to deployment, we assessed the influence of plastic bushings on iButton temperature records. We compared hourly air temperatures recorded by 30 iButtons with bushings to 30 iButtons without bushings. We set iButtons to record air temperature hourly within an incubator, which we alternated air temperature between 20°C, 30°C, and 40°C for at least 18 hours for each temperature setting. We compared recorded temperatures for both groups using with a Wilcoxon rank sum test. No significant difference was found in recorded temperature between groups ($p > 0.05$), thus, no temperature correction was needed.



Figure 2-4: Relative placement of iButtons in cages attached to the quick release line prior to box closure.

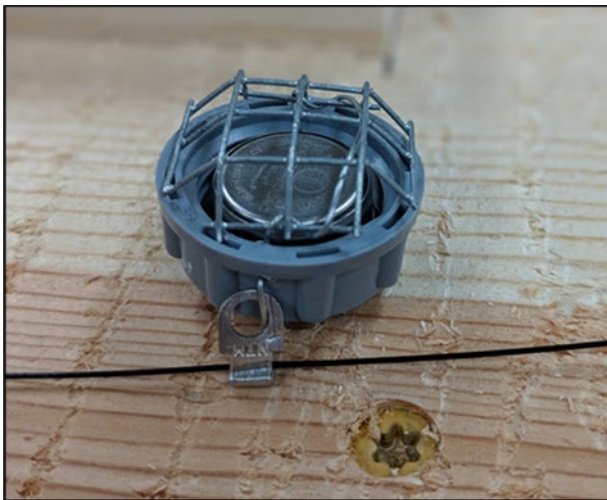


Figure 2-5: iButton cage designed to prevent bats from coming into direct contact with the sensors surface.

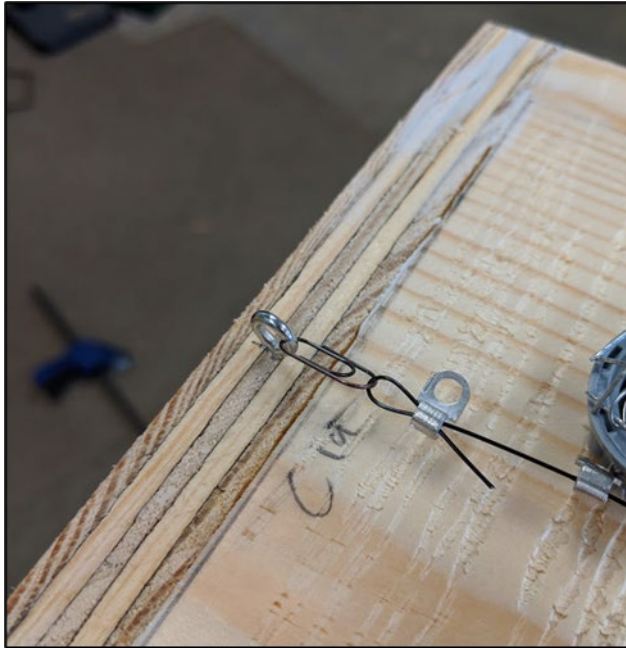


Figure 2-6: iButton quick release system.

Rocket Box Deployment~

All boxes were in place by 1 April 2019. At each field site, rocket boxes were deployed in 4 clusters, with 5 boxes (1 per design) present within each cluster ($n = 8$ total clusters between both field sites). Each box was marked with a unique tree tag with the last digit on the tag identifying its design. Rocket box clusters ran along a north-south axis, and boxes within each cluster were spaced 2m apart. We randomly determined the order of rocket box designs within each cluster. We set boxes in ~1.3m deep holes so that the top of each rocket box was ~6.1m above ground. Boxes were set in 45.4 kg of fast-setting concrete and the above-ground base of each box post was braced with 4 angled 2" x 4" x 4' boards.

We deployed boxes in clusters to facilitate roost discovery, roost switching, and provide bats a variety of available microclimates within one locality (Lewis 1995; Ruegger 2016), from which we could potentially delineate roost design and solar

exposure preference. One “open” cluster was located away from tree lines so that boxes received solar exposure throughout the day. A “forest” cluster was in a closed canopy condition in which boxes would receive little to no direct solar exposure. An “easterly sun” cluster was ~5m from an east-facing tree line such that boxes primarily received morning solar exposure. A “westerly sun” cluster was ~5m from a west-facing tree line such that boxes primarily received afternoon solar exposure. This deployment strategy exposed box designs to varied solar conditions, thus potentially altering the performance of each design in a particular situation.

Weather Data Collection~

To monitor cluster-specific weather conditions, we collected hourly weather data at each cluster via Ambient Weather WS-1201 weather stations powered by a 12v-18amh battery and locked in weatherproof Pelican (Model 1500) cases (4 stations per site, n = 8 total). Each weather station was mounted on a 3.2m tall fence top rail post and was concreted into the ground so that each weather station was 3m above ground. Each station was placed 2m from the south side of each rocket box cluster so that the stations would not be shaded by the boxes.

Weather stations recorded temperature (°F, accuracy $\pm 2^\circ\text{F}$, converted to °C after download), solar radiation (lux, $\pm 15\%$, converted to w/m²), rainfall (inches, \pm accuracy 0.01 inches, converted to mm), and wind speed (mph, accuracy $\pm 2.2\text{mph}$, converted to m/s). While weather stations recorded data hourly, data were not able to be collected on the hour. Rather, stations recorded on a 60-min time interval starting when power was connected to the station. Thus, this interval changed each time the power supply for a

weather station's data receiver was changed (roughly every 2–3 days). Subsequently, we binned data on an hourly basis.

Roost Checks~

To survey all 40 rocket box roosts, of 8 different roost clusters, for the daily presence/absence (P/A) and abundance of Indiana bats, we performed spotlight checks 2–4 times per week at both the Indiana and Kentucky field sites. The number of surveys per week varied based on weather and conflicts with hunting seasons. Spotlight checks began on 6 April 2019 and ended on 15 September 2019 at the Kentucky field site and began on 28 March 2019 and ended on 10 October 2019 at the Indiana field site. Spotlight checks involved shining a ~1000 lumen spotlight (Stanley Fatmax Model #SL10LEDS) up into each roost and visually determining P/A of bats (Whitaker et al. 2006; De La Cruz et al. 2018; Hoeh et al. 2018). When two observers were present, each individually checked the roost and conferred on their assessments. For roosts where bats were present, bats were visually counted to estimate abundance and to aid in determining where to conduct emergence counts. We classified bats to genus visually via spotlight checks and took non-flash photos when conditions were favorable. To minimize stress to bats, spotlight checks typically lasted < 20 seconds. We made a concerted effort to not check roost clusters in the same order in consecutive visits to field sites, this reduced the effect of time of day and solar position on our ability to detect bats in a roost.

We conducted emergence counts 2–4 times per week, weather dependent, at roosts we considered likely to contain the most bats based on spotlight checks and guano accumulation. Emergence counts help to reduce the error in abundance estimates

based on data collected from spotlight checks, given that bat counts from spotlight surveys are less accurate for larger colony sizes. Observers arrived at roosts ~30 min before sunset and stayed at least 10 min after the last bat emerged or 30 min after sunset if no bats emerged (Arndt et al. 2018; Hoeh et al. 2018; Oyler-McCance et al. 2018). Observers recorded the roost ID number, time of first emergence, time of last emergence, and total number of bats emerged for each roost watched. Each observer typically watched ~3 roosts within a cluster during emergence counts, varying based on weather and visibility. The total number of roosts counted per night varied with personnel availability.

iButton Removal~

We removed iButton data loggers at the end of the study following 3 consecutive days of no bat detections at each field site (4 November 2019 at the Indiana site and 19 November 2019 at the Kentucky site). We removed iButtons from roosts using a gaff consisting of a blunted wire hook attached to a telescoping painter's pole. We used the gaff to hook the lowest iButton within the roost and pulled downward to break the quick release system, thus, causing the iButtons to fall from the roost. All roosts were spotlight checked for bats immediately before removal took place; all iButtons were successfully recovered.

Calculation of Daily Availability, Variability, and Suitability~

All analyses and visualizations were conducted in R (version 3.6.2; R Core Team 2019). Daily roost temperature variability, defined as the range of temperature experience by a roost over the course a day (daily $T_{MAX}-T_{MIN}$), was calculated for each rocket box. We calculated hourly roost availability, defined as the range of temperature

available within a roost in a given hour (hourly $T_{\text{MAX}}-T_{\text{MIN}}$), for every 24hr day of data collection. Hourly availability values were then averaged providing the mean daily availability for each roost. We defined roost suitability following Tillman (2019), with roost temperatures between 15–40°C considered suitable. These suitable temperature thresholds are buffered from potentially lethal/harmful values as Licht and Leitner (1967) found that temperatures $> 40^{\circ}\text{C}$ resulted in heat stress response from 3 species of bats and prolonged exposure to these temperatures often resulted in mortality. Further, the entry and arousal costs of torpor are higher with decreasing ambient temperature (Davis and Reite 1967; Wojciechowski et al. 2006). Hourly recordings were marked as suitable if they were within this range or unsuitable if they were outside this range. We calculated daily suitability for each roost by dividing the total count of suitable hourly recordings for each day by the total number of recordings for each day, resulting in the proportion of suitable roosting space. All means are reported as $x \pm \text{SE}$ unless otherwise stated.

Analysis~

Roosts at the Kentucky field site were opened for bats on 4 April; thus, no microclimate readings were used before this date for this site. Additionally, we note that on 25 June the easterly sun EXTJ roost (Box1605) at the Indiana field site was damaged, thus, no microclimate readings for this roost were used on or after this date. Additionally, due to damage to Box1605, the middle tier iButton of the west box face was damaged and data was not recoverable; all data prior to 25 June for Box1605 comes from 11 iButtons. Lastly, on 19 August the east aspect strand of 3 iButtons fell from the westerly sun REF box at the Indiana site, subsequently, no temperature data

points were used from this date on for that strand and all remaining recordings from this roost resulted from 9 remaining iButtons.

We conducted 3 microclimate analyses. We followed an information theoretic approach to compare competing models for all 3 analyses (Burnham and Anderson 2002). All models were based on ecologically relevant hypotheses attempting to explain drivers of roost microclimate. The first analysis, East/West, modeled daily rocket box availability, variability, and suitability for the easterly and westerly sun clusters during the months of June, July, and August. These solar treatments were primarily chosen to assess the impact of roost occupancy on our response variables. Open and forest solar treatments were not used in this analysis, as bats rarely used these roosts. We chose the months of June–August because bat occupancy peaked during these months at each site; in this analysis, we did not use data for the cooler months with lower occupancy which occurred earlier and later in the season. We compared 17 candidate models (Table 2-2). Each model included the fixed effects of box design and solar treatment along with some combination of these covariates: total bats, mean daily temperature (°C; AvgTemp), daily ambient temperature range (°C; TaRange), mean daily solar radiation (w/m^2 ; AvgSolRad), and mean daily windspeed (m/s; AvgWind).

The second analysis, Open/Forest, modeled daily rocket box availability, variability, and suitability for the open and forest solar treatments from April–September. Because these roosts experienced little to no usage during the field season, we deemed it appropriate to model the effects of box design, solar treatment, and weather on these treatments that were opposite in terms of solar exposure. We compared 8 candidate models (Table 2-3). Each model included the fixed effects of box

design, and solar treatment along with some combination of these covariates: mean daily temperature, daily ambient temperature range, mean daily solar radiation, and mean daily wind speed. We did not include total bats as a covariate because bats were largely absent from these solar treatments; we excluded data from days where we detected > 2 bats in the forest solar treatments.

The third analysis, Spring, involved modeling the daily suitability of all roost solar treatments during April and May, when roost use was low across all solar treatments. We chose to only model suitability during this time period as it has been shown that roosts often become entirely unsuitable during cold weather conditions (Hoeh et al. 2018); availability and variability in an entirely unsuitably cold roost would have little meaning. The months of April and May correspond to the coolest months of the study period (See Appendix A). This analysis allowed comparison of the effectiveness of designs during cool weather conditions and assesses the interaction of design performance in relation to landscape position. We compared 5 candidate models (Table 2-4). The Spring analysis only considered box design and solar treatment, as this analysis was aimed specifically at detailing the effectiveness of box designs in different solar treatments during the coldest period of the study.

For all 3 analyses, we ranked models via AIC_C (Akaike's Information Criterion corrected for small sample sizes) and considered models to be competing if they were within $\Delta AIC_C \leq 2$ of the best ranked model. We made inferences from the top ranked model if it had substantial support (i.e., $w_i \geq 0.90$; Burnham and Anderson 2002) and no models within $\Delta AIC_C \leq 2$. If competing models existed, we constructed a 90% confidence set and averaged models using the R package MuMIN (Barton 2020), basing

inference on parameters included in the competing models. We identified informative parameters as those for which 85% confidence intervals did not overlap zero, as this practice has been found to be less likely to exclude biologically relevant model parameters (Arnold 2010). Means are reported as $x \pm \text{SE}$ and 85% confidence intervals are displayed unless otherwise stated. Weather parameters are not discussed unless they interacted with total bats, box design, or solar treatment. Loess smoothed regression lines are shown for relationships that were not strictly linear.

This research was approved by Eastern Kentucky University IACUC protocol number 01-2019.

Table 2-2: Candidate set of 17 models used in the East/West analysis.

Model	<i>K</i>	Included predictors
Null	2	-
m2	7	Total Bats + Design
m3	4	Total Bats + Solar Treatment
m4	7	Design + Solar Treatment
m5	8	Total Bats + Design + Solar Treatment
m6	11	Total Bats + Design + Total Bats*Design
m7	5	Total Bats + Solar Treatment + Total Bats*Solar Treatment
m8	11	Design + Solar Treatment + Design*Solar Treatment
m9	13	Total Bats + Design + Solar Treatment + Total Bats*Design + Total Bats*Solar Treatment
m10	11	Total Bats + Design + AvgTemp + TaRange + AvgSolRad + AvgWind
m11	8	Total Bats + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind
m12	11	Design + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind
m13	12	Total Bats + Design + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind
m14	18	Total Bats + Design + AvgTemp + TaRange + AvgSolRad + AvgWind + Total Bats*Design + Total Bats*AvgTemp + Total Bats*AvgWind + Total Bats*AvgSolRad
m15	12	Total Bats + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind + Total Bats*Solar Treatment + Total Bats*AvgTemp + Total Bats*AvgWind + Total Bats*AvgSolRad
m16	20	Design + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind + Design*Solar Treatment + Design*TaRange + Solar Treatment*AvgWind
m17	23	Total Bats + Design + Solar Treatment + AvgTemp + TaRange + AvgSolRad + AvgWind + Total Bats*Design + Total Bats*Solar Treatment + Total Bats*AvgTemp + Design*TaRange + Solar Treatment*AvgWind

Table 2-3: Candidate set of 8 models used in the Open/Forest analysis.

Model	<i>K</i>	Included predictors
Null	2	-
m2	11	Solar Treatment + Design + Solar Treatment*Design
m3	9	Solar Treatment + AvgTemp + AvgWind +TaRange + Solar Treatment*AvgTemp + Solar Treatment*AvgWind +Solar Treatment*TaRange
m4	21	Design + AvgTemp + AvgWind + TaRange + Design*AvgTemp + Design*AvgWind + Design*TaRange
m5	10	Solar Treatment + Design + AvgTemp + TaRange + AvgWind
m6	14	Solar Treatment + Design + AvgTemp + TaRange + AvgWind + Solar Treatment*Design
m7	17	Solar Treatment + Design + AvgTemp + AvgWind +TaRange + Solar Treatment*Design + Solar Treatment*AvgTemp + Solar Treatment*AvgWind + Solar Treatment*TaRange
m8	26	Design +Solar Treatment + AvgTemp + AvgWind + TaRange + Design*Solar Treatment + Design*AvgTemp + Design*AvgWind + Design*TaRange

Table 2-4: Candidate set of 5 models used in the Spring Month analysis.

Model	<i>K</i>	Included predictors
Null	2	-
m2	5	Solar Treatment
m3	6	Design
m4	9	Solar Treatment + Design
m5	21	Solar Treatment + Design + Solar Treatment*Design

RESULTS

Weather~

At the Indiana site, from 11 April (date of weather station installation for IN) to 10 October 2019, ambient air temperature (T_a) across roost clusters ranged from 1.2–34.7°C (mean = 19.7°C). Hourly wind speeds ranged from 0–10.4 m/s (mean = 0.51 m/s) across roost clusters, though gusts likely exceeded the recorded hourly wind speed. Total rainfall accumulation for the study period at the Indiana site amounted to 677.7

mm. Solar radiation ranged from 0–1116 w/m² (mean = 154.03 w/m²) across roost clusters. Differences in tree line density and forest composition likely influenced all microsite weather parameters.

At the Kentucky site, from 5 April (date of weather station installation for KY) to 15 September 2019, T_a across roost clusters ranged from 2.5–36.4°C (mean = 20.8°C; See Appendix A). Hourly wind speeds ranged from 0–9.9 m/s (mean = 0.46 m/s) across roost clusters. Total rainfall accumulation for the study period was 803.7 mm. Solar radiation ranged from 0–1138 w/m² (mean = 168.93) across roost clusters. Differences in tree line density and forest composition likely influenced all microsite weather parameters.

Microclimate Overview~

From 1 April to 15 September 2019 our iButtons collected 980,992 hourly microclimate recordings. Precluding lost or discarded data, we were left with 945,060 raw microclimate recordings across all 40 roosts. Across both sites, a total of 9,171 unsuitably hot hourly temperature recordings were logged (< 1% of recordings; Figure 1-2: A). The Kentucky site logged 6,303 unsuitably hot records and the Indiana site logged 2,868 unsuitably hot records. The majority of unsuitably hot temperature recordings were logged in VR designs (3,288 recordings), and the fewest were logged in EXTJ designs (651 recordings). Most unsuitably hot recordings occurred in the easterly and westerly solar treatments (3,657 and 3,328 recordings, respectively), with the fewest occurring in the forest solar treatments (25 recordings; all of which occurring in Kentucky). Further, most unsuitably hot events occurred at the top positions within roosts (8,594 recordings; 93.7% of observations; Figure 2-7: C); 6.1% were in the

middle layer (561 recordings) and only 0.2% were at the bottoms of roosts (16 recordings). In contrast, 140,398 unsuitably cold hourly temperature records were logged (14.9% of recordings; Figure 2-7: B). CH designs logged the most unsuitably cold temperature events (29,789), while EXTJ designs logged the fewest (24,044). Most unsuitably cold recordings occurred in the westerly (35,324 recordings) and easterly solar treatments (35,214 recordings). The open and forest solar treatments recorded similar numbers of unsuitably cold temperatures (34,888 and 34,972, respectively). Unsuitably cold recordings most often occurred at the bottom roost positions (52,345 recordings; 37.3%), though similar numbers were recorded at the middle (44,693 recordings) and top positions (43,360 recordings) (Figure 2-7: D). No boxes completely overheated during the study (i.e., no instances where all 12 iButtons simultaneously recorded temperatures $\geq 40^{\circ}\text{C}$). However, there were 115 instances when the daily maximum box temperature did not exceed 15°C (93 events at the Indiana site and 22 at the Kentucky site).

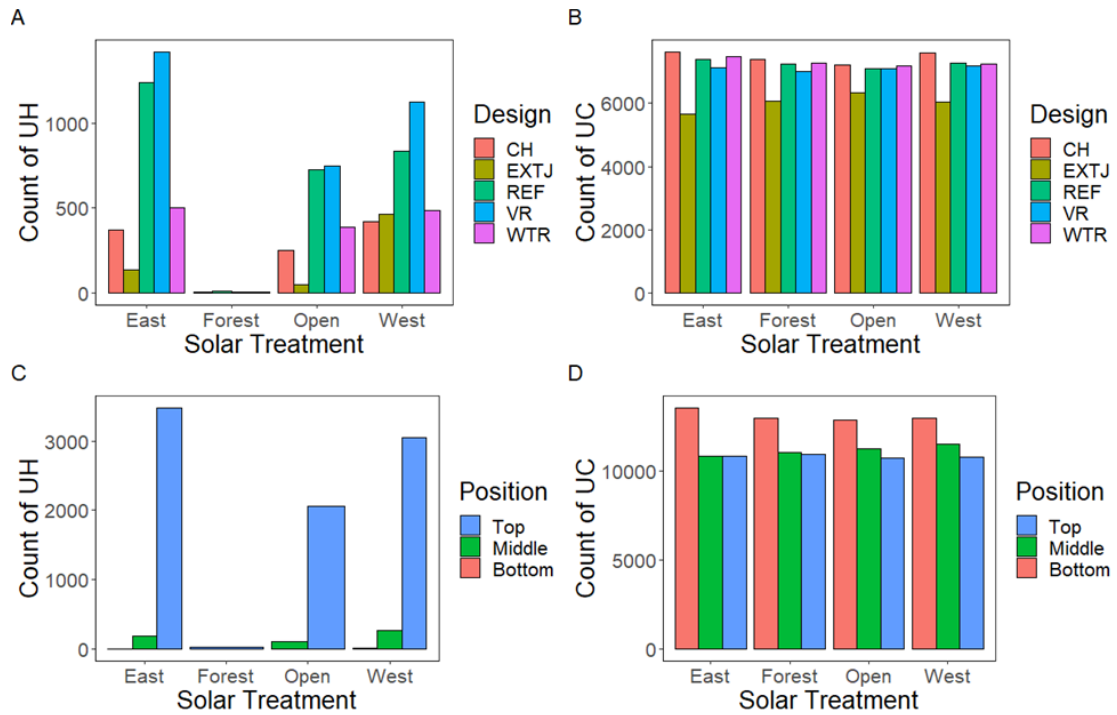


Figure 2-7: Count of unsuitably hot (UH) and unsuitably cold (UC) hourly microclimate recordings by solar treatment and design (A, B) and by solar treatment and position (C, D).

East/West Analysis~

Daily Availability:

We accumulated 795 observations of mean daily roost availability for our East/West analysis. When we examined models predicting availability in the East/West solar treatments, we found that model 17 received top rank with 97.4% of the cumulative Akaike weights (Table 2-5). There were no competing models within 2 AIC_c units of model 17. The evidence ratio (w_1/w_i) for our top ranked model compared to the 2nd highest ranked model is 37.5 to 1, indicating substantial support for model 17 as the best overall model for this candidate set. Based on overwhelming support

for model 17, we based all inference on this model for daily availability and identified 9 informative parameters based on their 85% confidence intervals not overlapping 0 (Table 2-6).

From informative parameters, we delineate several trends. As the total number of bats in a roost increased, the availability within the roost increased (Figure 2-8). The WTR and EXTJ designs had larger increases in mean daily availability with increasing numbers of bats as compared to the REF design. Though not substantially different from the REF design, mean daily availability was typically 2°C lower in the CH design (Figure 2-8). At low mean daily temperatures ($< 20^{\circ}\text{C}$), small (≤ 29 bats) and large (≥ 30 bats) groups of bats tended to promote higher mean daily availability when compared to unoccupied boxes (Figure 2-9). At mean daily temperatures below 20°C, mean daily availability could be ~4°C higher in roosts with large colony sizes compared to empty roosts (Figure 2-9). As mean daily temperature increased, large groups of bats tended to decrease mean daily availability. Small groups of bats exerted less influence over roost availability and generally roosts containing small groups tracked changes in availability due to increasing mean daily temperature. As ambient air temperature range increased, availability was ~2°C lower in the CH design than in the REF design (Figure 2-10). All other designs seemingly mirrored the REF design when the ambient temperature range increased. Increasing mean daily wind speeds had a greater negative impact on the westerly sun clusters than the easterly sun clusters, due to the west cluster experiencing greater wind speeds (Figure 2-11).

Table 2-5: AIC_C ranks of the 17 candidate models for mean daily availability (East/West analysis; June-August 2019).

Model Name	ΔAIC_C	K	w_i
m17	0.0	23	0.9740
m14	7.3	18	0.0260
m13	28.6	12	<0.001
m10	35.0	11	<0.001
m15	101.1	12	<0.001
m11	109.7	8	<0.001
m16	111.8	20	<0.001
m12	119.4	11	<0.001
m9	229.6	13	<0.001
m6	242.6	11	<0.001
m5	249.7	8	<0.001
m2	261.0	7	<0.001
m7	305.0	5	<0.001
m3	305.4	4	<0.001
m8	334.2	11	<0.001
m4	338.0	7	<0.001
Null	440.0	2	<0.001

Table 2-6: Parameter estimates and 85% confidence intervals for the top-ranked daily availability model (East/West analysis; June-August 2019; informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	0.023	-0.861	0.906
Total.Bats	0.062	0.037	0.087
DesignCH	-0.117	-0.937	0.703
DesignEXTJ	0.373	-0.470	1.215
DesignVR	-0.015	-0.855	0.826
DesignWTR	-0.066	-0.880	0.749
ClusterWest	-0.203	-0.411	0.006
AvgTemp	0.161	0.132	0.190
TaRange	0.199	0.150	0.247
AvgSolRad	0.000	-0.002	0.001
AvgWind	-0.837	-1.330	-0.344
Total.Bats:DesignCH	-0.001	-0.017	0.014
Total.Bats:DesignEXTJ	0.021	0.005	0.037
Total.Bats:DesignVR	-0.001	-0.008	0.006
Total.Bats:DesignWTR	0.026	0.018	0.034
Total.Bats:ClusterWest	0.002	-0.006	0.009
Total.Bats:AvgTemp	-0.002	-0.003	-0.001
DesignCH:TaRange	-0.090	-0.152	-0.028
DesignEXTJ:TaRange	-0.051	-0.116	0.013
DesignVR:TaRange	0.010	-0.053	0.074
DesignWTR:TaRange	-0.062	-0.124	0.000
ClusterWest:AvgWind	-0.697	-1.271	-0.123

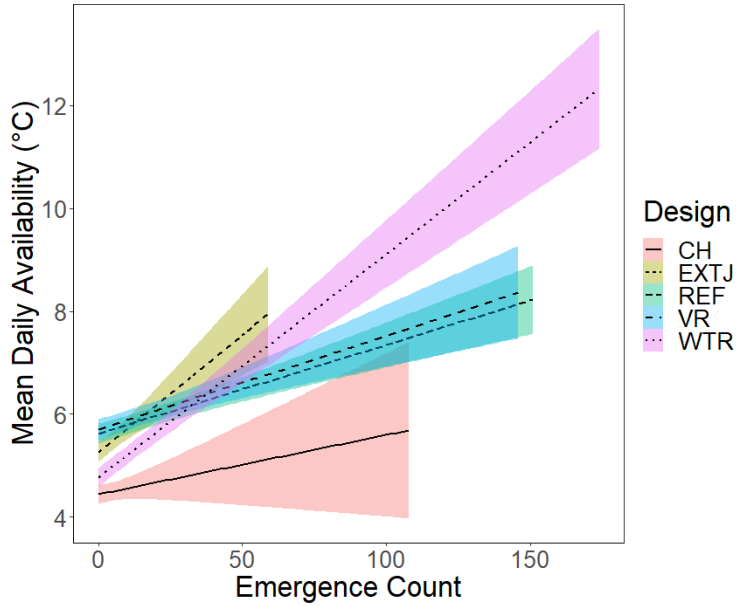


Figure 2-8: Regression lines and 85% confidence intervals for the interactive effect of box design and emergence count on mean daily availability (85% confidence intervals are displayed, as informative parameters were selected based on 85% confidence intervals; not 95%).

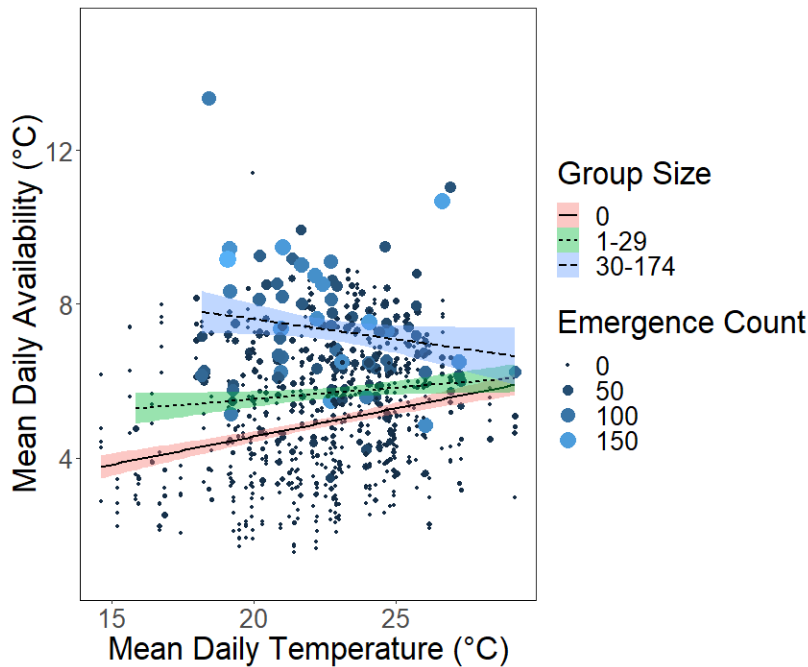


Figure 2-9: Regression lines and 85% confidence intervals showing the interaction of unoccupied (0), small (≤ 29), and large groups of bats (≥ 30) and mean daily temperature on mean daily box availability.

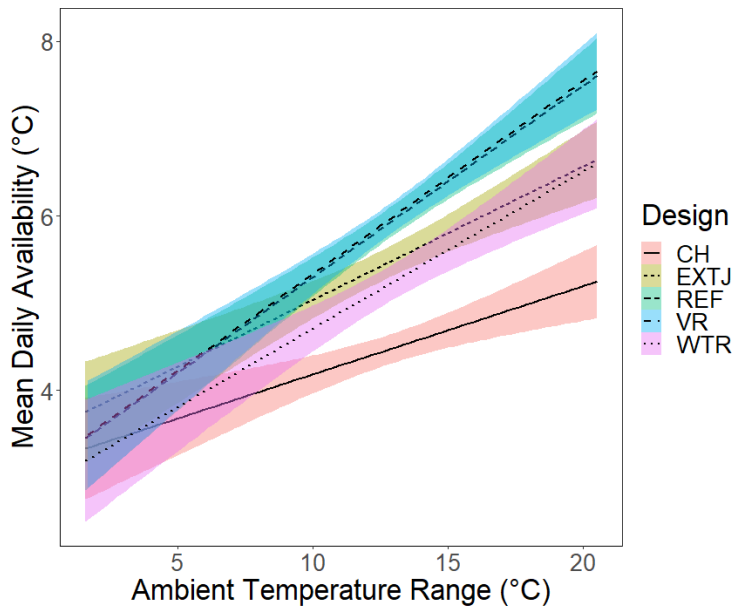


Figure 2-10: Regression lines and 85% confidence intervals showing the interaction of box design and ambient temperature range on mean daily availability.

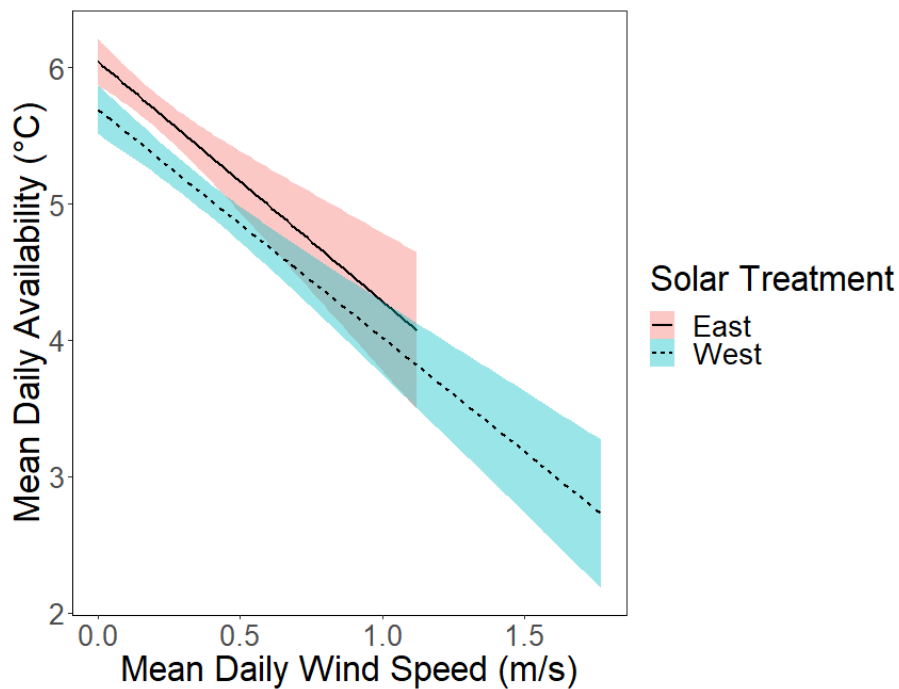


Figure 2-11: Regression lines and 85% confidence intervals showing the interaction of roost solar treatment (cluster) on mean daily availability.

Daily Variability:

We accumulated 795 observations of daily roost variability for our East/West analysis. When we examined models predicting variability in the East/West clusters, we found that model 14 received top rank with 53% of the cumulative model weights. Model 10 was competing, with a ΔAIC_C of 1.4 from model 14 (Table 2-7). The evidence ratio of model 14 to model 10 is 1.97 to 1. Based on the existence of competing models and no substantial support for a single model, we constructed a 90% candidate set of models for averaging based on Akaike weights. This confidence set included models 14, 10, and 13. From the model averaged results, we identified 8 informative parameters contained within competing models (Table 2-8).

When compared to the REF design, the VR design performed similarly, but EXTJ, WTR, and CH designs generally supported lower daily variability (Figure 2-12). Large and small groups of bats increased the variability of all designs with decreasing mean daily temperature (Figure 2-13), differing from empty roosts by $\sim 5^\circ\text{C}$ when mean daily temperatures were $\leq 20^\circ\text{C}$. Furthermore, as mean daily temperature increased, variability became similar across empty and occupied roosts. Both large and small groups of bats increased daily variability, but when mean daily solar radiation was $> 300\text{w/m}^2$, large groups of bats increased variability by $\sim 5^\circ\text{C}$ as compared to empty roosts (Figure 2-14)

Table 2-7: AIC_C ranks of the 17 candidate models for daily variability (East/West analysis; June-August 2019).

Model Name	ΔAIC_C	K	w_i
m14	0.0	18	0.5329
m10	1.4	11	0.2704
m13	2.3	12	0.1702
m12	7.7	11	0.0113
m16	7.8	20	0.0105
m17	9.5	23	0.0046
m15	143.4	12	<0.001
m11	146.3	8	<0.001
m2	275.7	7	<0.001
m5	276.8	8	<0.001
m6	279.7	11	<0.001
m9	282.4	13	<0.001
m4	288.7	7	<0.001
m8	293.6	11	<0.001
m3	379.7	4	<0.001
m7	381.3	5	<0.001
Null	406.6	2	<0.001

Table 2-8: Model averaged parameter estimates and 85% confidence intervals for the 90% confidence set daily variability models (East/West analysis; June-August 2019; informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	8.515	6.062	10.969
Total.Bats	0.041	-0.031	0.112
DesignCH	-3.395	-4.162	-2.628
DesignEXTJ	-5.658	-6.478	-4.838
DesignVR	0.547	-0.253	1.348
DesignWTR	-2.388	-3.166	-1.611
AvgTemp	0.353	0.251	0.455
TaRange	0.775	0.675	0.875
AvgSolRad	-0.001	-0.006	0.005
AvgWind	-3.671	-4.573	-2.768
DesignCH:Total.Bats	0.019	-0.035	0.073
DesignEXTJ:Total.Bats	0.028	-0.027	0.084
DesignVR:Total.Bats	0.011	-0.013	0.035
DesignWTR:Total.Bats	0.007	-0.019	0.032
AvgTemp:Total.Bats	-0.006	-0.010	-0.002
AvgWind:Total.Bats	0.042	-0.008	0.092
AvgSolRad:Total.Bats	0.0003	0.0002	0.0005
ClusterWest	0.384	-0.139	0.907

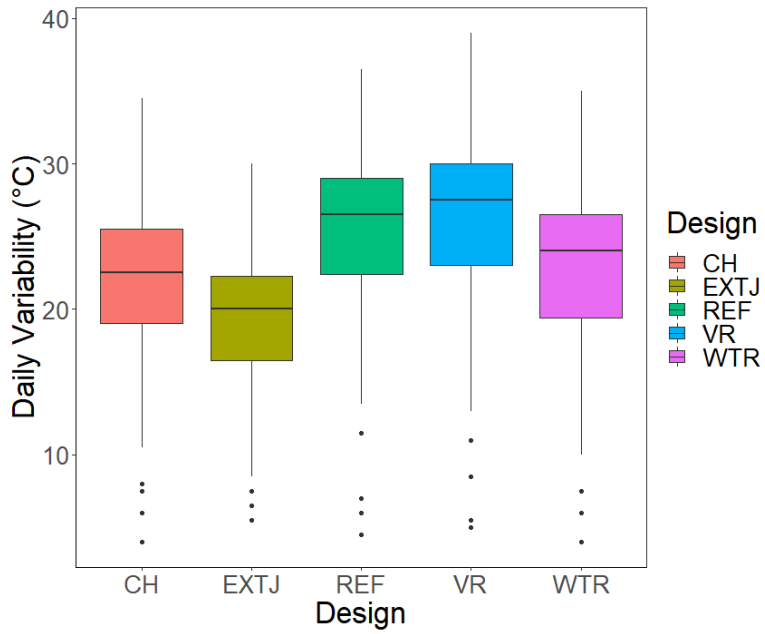


Figure 2-12: Box and whisker plot showing the effect of box design on daily variability.

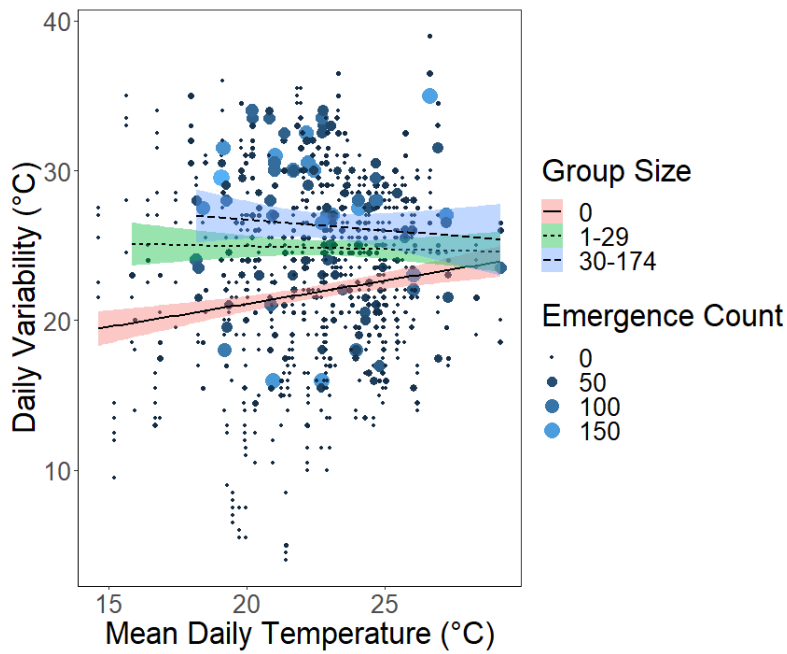


Figure 2-13: Regression lines and 85% confidence intervals showing the interactive effect of emergence count size and mean daily temperature on daily variability.

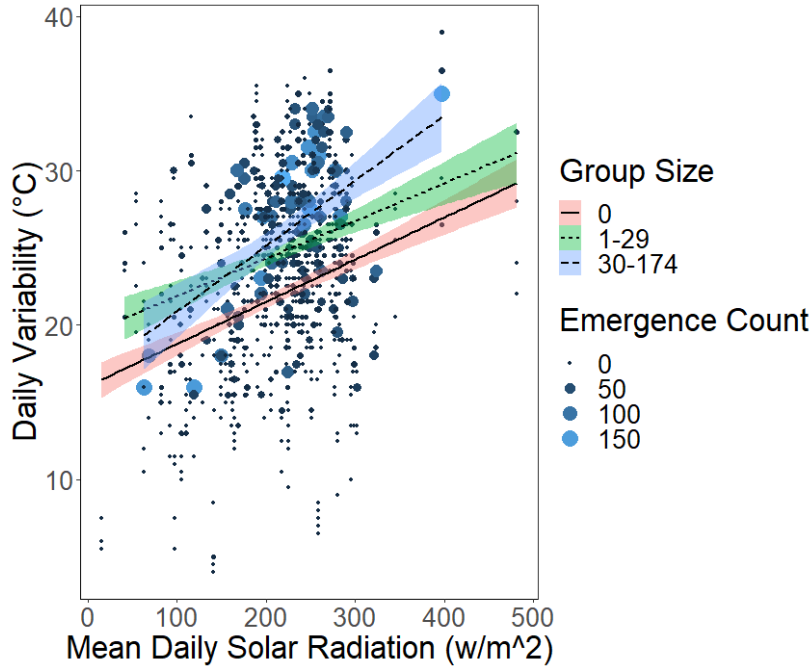


Figure 2-14: Regression lines and 85% confidence intervals showing the interactive effect of emergence count size and mean daily solar radiation on daily variability.

Daily Suitability:

We accumulated 795 observations of daily roost suitability for our East/West analysis.

When comparing daily suitability models for the East/West clusters, we found that model 12 received top rank, carrying 44% of the model weights. Additionally, we found support for models 10 and 13, which were within ΔAIC_C of ≤ 2 of the top ranked model (Table 2-9). The evidence ratio of the top ranked model (model 12) compared to the 2nd highest ranked model (model 10) was 1.82 to 1. Due to the presence of these competing models and the lack of substantial support for the top ranked model, we established a 90% confidence set for model averaging. This confidence set included models 12, 10, 13, and 14, from which we identified 7 informative parameters within competing models (Table 2-10).

From our 7 informative parameters, we found the EXTJ, WTR, and CH designs all generally provided higher daily suitability than the REF design (Figure 2-15). Further, westerly solar treatments generally supported 100% suitable microclimates more frequently than easterly solar treatments (Figure 2-16).

Table 2-9: AIC_C ranks of the 17 candidate models for daily suitability (East/West analysis; June-August 2019).

Model Name	ΔAIC_C	K	w_i
m12	0.0	11	0.4353
m10	1.2	11	0.2391
m13	1.4	12	0.2195
m14	4.2	18	0.0525
m16	4.5	20	0.0459
m17	8.1	23	0.0077
m15	33.0	12	<0.001
m11	38.6	8	<0.001
m2	101.8	7	<0.001
m5	103.1	8	<0.001
m4	103.4	7	<0.001
m8	106.2	11	<0.001
m6	108.5	11	<0.001
m9	111.7	13	<0.001
m3	130.3	4	<0.001
m7	131.7	5	<0.001
Null	135.3	2	<0.001

Table 2-10: Model averaged parameter estimates and 85% confidence Intervals for the 90% confidence set daily suitability models (East/West analysis; June-August 2019; informative parameters **bolded).**

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	2.902	2.399	3.406
DesignCH	0.441	0.290	0.593
DesignEXTJ	0.579	0.417	0.741
DesignVR	-0.046	-0.195	0.104
DesignWTR	0.295	0.146	0.444
ClusterWest	0.108	0.003	0.212
AvgTemp	0.032	0.012	0.051
TaRange	-0.127	-0.148	-0.107
AvgSolRad	0.002	0.001	0.003
AvgWind	0.084	-0.103	0.270
Total.Bats	0.002	-0.012	0.015
DesignCH:Total.Bats	-0.005	-0.017	0.006
DesignEXTJ:Total.Bats	0.007	-0.005	0.018
DesignVR:Total.Bats	-0.003	-0.007	0.002
DesignWTR:Total.Bats	0.001	-0.003	0.006
AvgTemp:Total.Bats	-0.001	-0.002	0.000
AvgWind:Total.Bats	-0.002	-0.011	0.008
AvgSolRad:Total.Bats	-0.00004	-0.00007	-0.00001

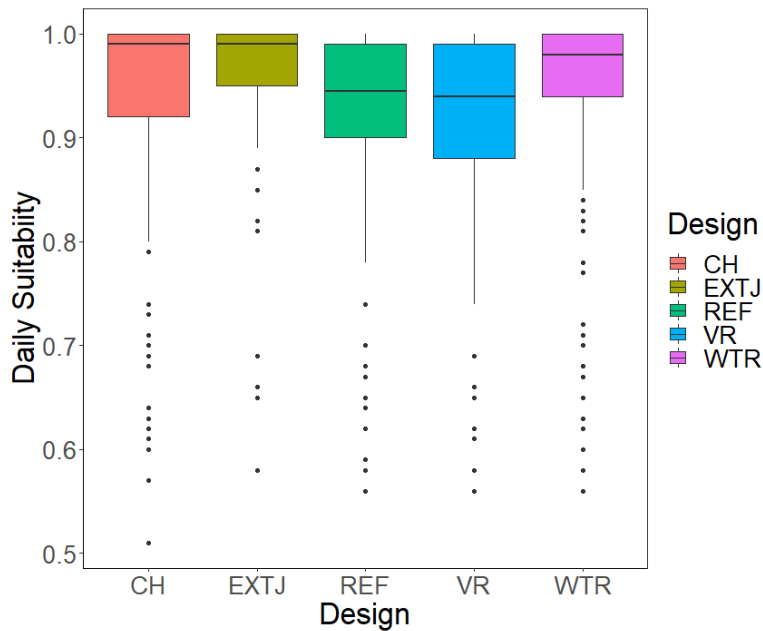


Figure 2-15: Box and whisker plot showing the effect of box design on daily suitability.

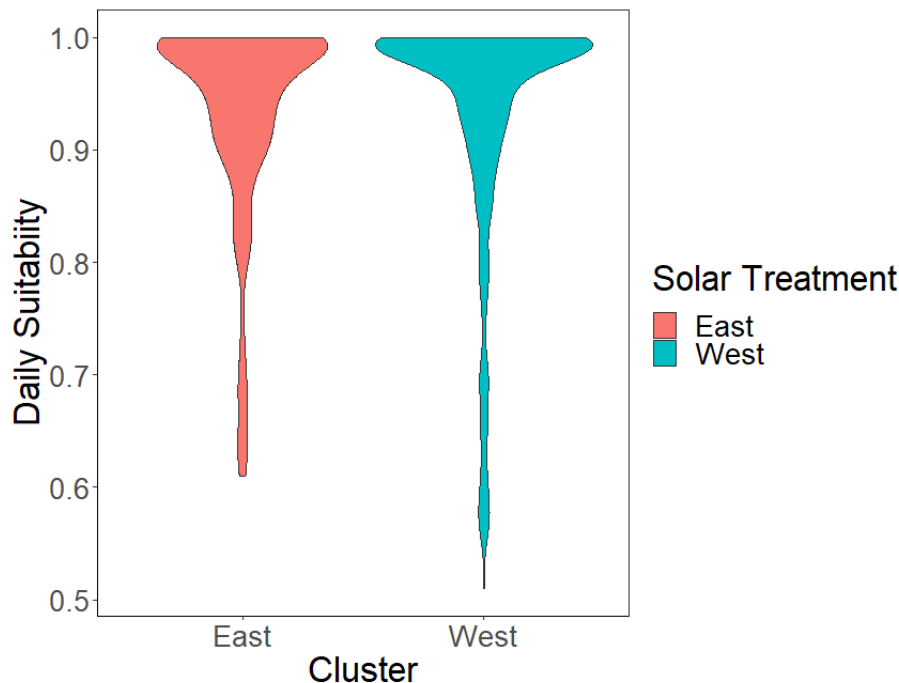


Figure 2-16: Violin plot showing the relative frequency of suitability recordings in the easterly and westerly sun solar treatments (wider colored areas indicate a higher recorded frequency of occurrence).

Open/Forest Analysis~

Daily Availability:

We accumulated 1144 observations of mean daily roost availability for our Open/Forest analysis. When comparing models predicting availability in the Open/Forest clusters, we found that, model 7 received top rank with 100% of the model weights (Table 2-11). No competing models were present within the candidate set. The 2nd highest ranked model was 34.3 AIC_C units away from the top rank model. Based on overwhelming support for model 7, we based all inferences on its 13 informative parameters (Table 2-12).

From informative parameters, we found that all box designs supported higher mean daily availability in the open solar treatments when compared to the forest solar treatments (Figure 2-17). The EXTJ and WTR designs typically supported lower availability than the REF design in the open solar treatments. The VR design in the open solar treatment generally supported the highest mean daily availability. In contrast, the EXTJ design in the forest solar treatments generally supported the highest availability. As the mean daily temperature increased, mean daily availability remained around 2°C in the forest solar treatments, but increased rapidly for open solar treatment boxes, such that there was a difference of $\geq 3^{\circ}\text{C}$ between the open and forest treatments at a mean ambient temperature of 25°C (Figure 2-18). Roosts in open solar treatments experienced higher mean daily windspeeds than the forest solar treatment roosts, and responded with a strong decrease in mean daily roost temperature availability (Figure 2-19).

Table 2-11: AIC_C ranks of the 8 candidate models for daily availability (Open/Forest analysis; April-September 2019).

Model Name	ΔAIC_C	K	w_i
m7	0.0	17	1.0000
m6	34.3	14	<0.001
m8	48.0	26	<0.001
m5	81.6	10	<0.001
m3	95.3	9	<0.001
m2	451.7	11	<0.001
m4	753.5	21	<0.001
Null	1290.1	2	<0.001

Table 2-12: Parameter estimates and 85% confidence intervals for the top ranked daily availability model (Open/Forest analysis; April-September 2019; informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	0.921	0.790	1.051
ClusterOpen	0.281	0.090	0.472
DesignCH	-0.123	-0.177	-0.069
DesignEXTJ	0.108	0.054	0.162
DesignVR	-0.125	-0.181	-0.068
DesignWTR	-0.067	-0.122	-0.011
AvgTemp	0.007	0.001	0.012
AvgWind	0.282	0.017	0.548
TaRange	0.037	0.032	0.043
ClusterOpen:DesignCH	-0.070	-0.145	0.006
ClusterOpen:DesignEXTJ	-0.233	-0.309	-0.158
ClusterOpen:DesignVR	0.160	0.082	0.237
ClusterOpen:DesignWTR	-0.105	-0.182	-0.028
ClusterOpen:AvgTemp	0.029	0.022	0.036
ClusterOpen:AvgWind	-0.499	-0.767	-0.231
ClusterOpen:TaRange	-0.002	-0.009	0.005

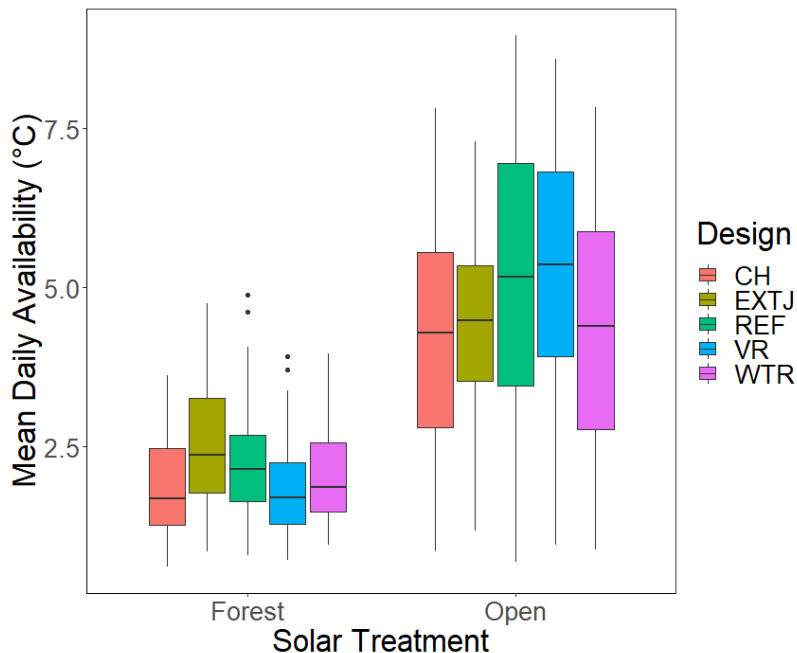


Figure 2-17: Box and whisker plot showing mean daily roost temperature availability as a function of each design within the open and forest solar treatments.

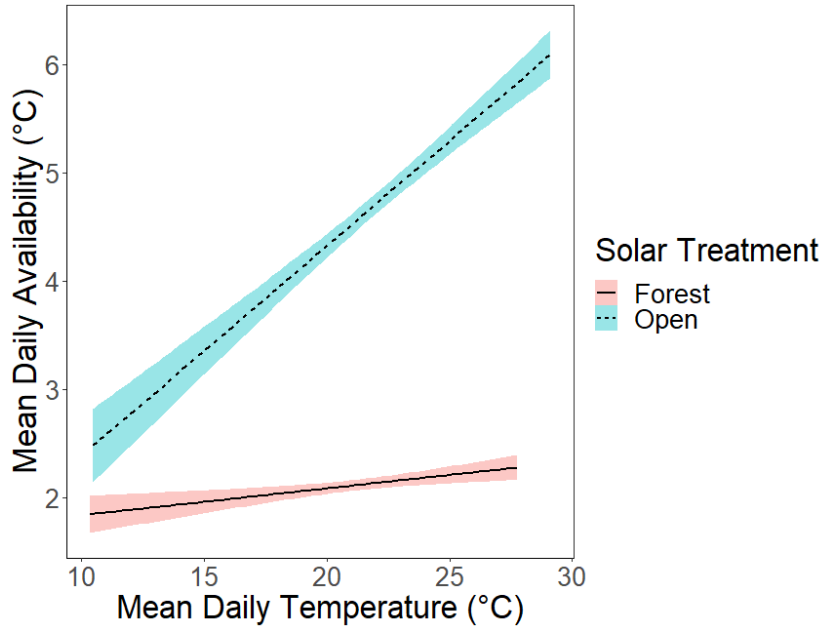


Figure 2-18: Regression lines and 85% confidence intervals showing the interactive impact of mean daily air temperature and solar treatment on mean daily availability within our rocket boxes.

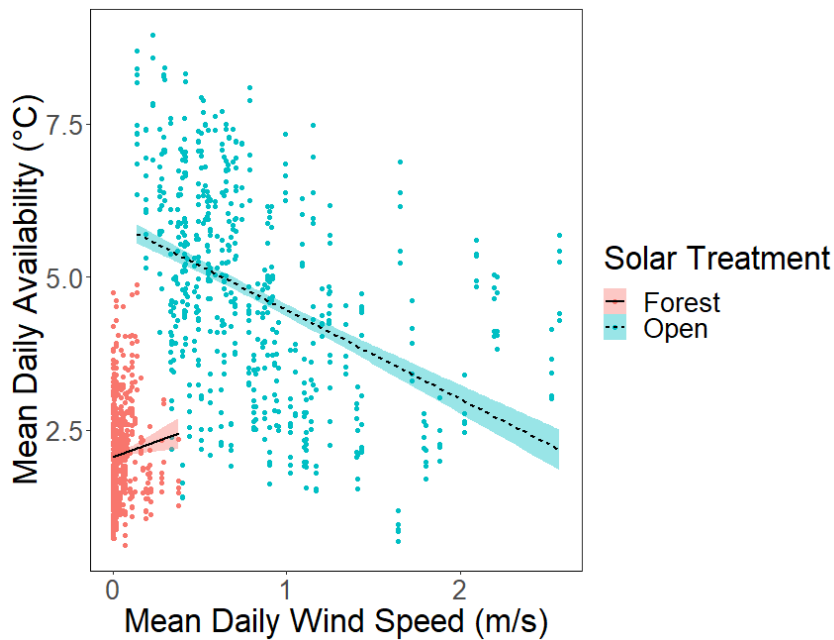


Figure 2-19: Regression lines and 85% confidence intervals showing the interactive effect of mean daily wind speed and solar treatment on mean daily roost temperature availability (data points are shown to highlight the positive slope exhibited by the forest solar treatment is likely an artifact of low experienced wind speeds).

Daily Variability:

We accumulated 1144 observations of daily roost variability for our Open/Forest analysis. When we examined models that predicted variability in the Open/Forest clusters, we found that model 7 received top rank, carrying 100% of the cumulative model weights (Table 2-13). No competing models were within $\Delta AIC_C \leq 2$ units of the top model. The 2nd highest ranked model was 24.5 AIC_C units away from the top ranked model. Based on the overwhelming support for model 7 as the best overall model from this candidate set, we based all inference off this model and identified 9 informative parameters (Table 2-14).

From these informative parameters, we note open solar treatment roosts experienced greater variability than forest solar treatment roosts (Figure 2-20). The CH and EXTJ designs within the open solar treatment were more stable (less variable) than the REF design. Roosts in the open cluster showed a greater change in daily roost temperature variability with increasing mean ambient temperature than was observed for roosts in the forest solar treatment (Figure 2-21). Finally, increasing mean daily wind speeds had a strong negative impact on the daily variability experienced in open solar treatment roosts (Figure 2-22).

Table 2-13: AIC_C ranks of the 8 candidate models for daily variability (Open/Forest analysis; April-September 2019).

Model Name	ΔAIC_C	K	w_i
m7	0.0	17	1.0000
m6	24.5	14	<0.001
m8	34.0	26	<0.001
m5	48.8	10	<0.001
m3	146.6	9	<0.001
m4	369.9	21	<0.001
m2	582.8	11	<0.001
Null	1062.0	2	<0.001

Table 2-14: Parameter estimates and 85% confidence intervals for the top ranked daily variability model (Open/Forest analysis; April-September 2019; informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	-0.019	-1.903	1.866
ClusterOpen	5.673	2.921	8.426
DesignCH	-0.541	-1.322	0.240
DesignEXTJ	-1.990	-2.770	-1.211
DesignVR	-0.150	-0.966	0.665
DesignWTR	-0.108	-0.908	0.692
AvgTemp	0.218	0.139	0.296
AvgWind	10.370	6.535	14.204
TaRange	0.819	0.743	0.896
ClusterOpen:DesignCH	-1.417	-2.508	-0.326
ClusterOpen:DesignEXTJ	-3.272	-4.362	-2.183
ClusterOpen:DesignVR	0.800	-0.315	1.916
ClusterOpen:DesignWTR	-0.838	-1.942	0.266
ClusterOpen:AvgTemp	0.191	0.083	0.299
ClusterOpen:AvgWind	-12.601	-16.469	-8.733
ClusterOpen:TaRange	-0.067	-0.174	0.040

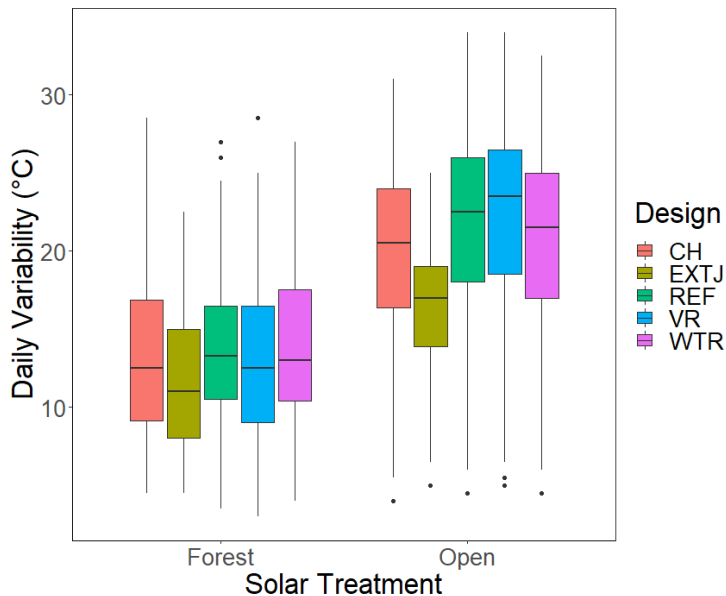


Figure 2-20: Box and whisker plot showing the interactive effect of box design within solar treatment on daily variability.

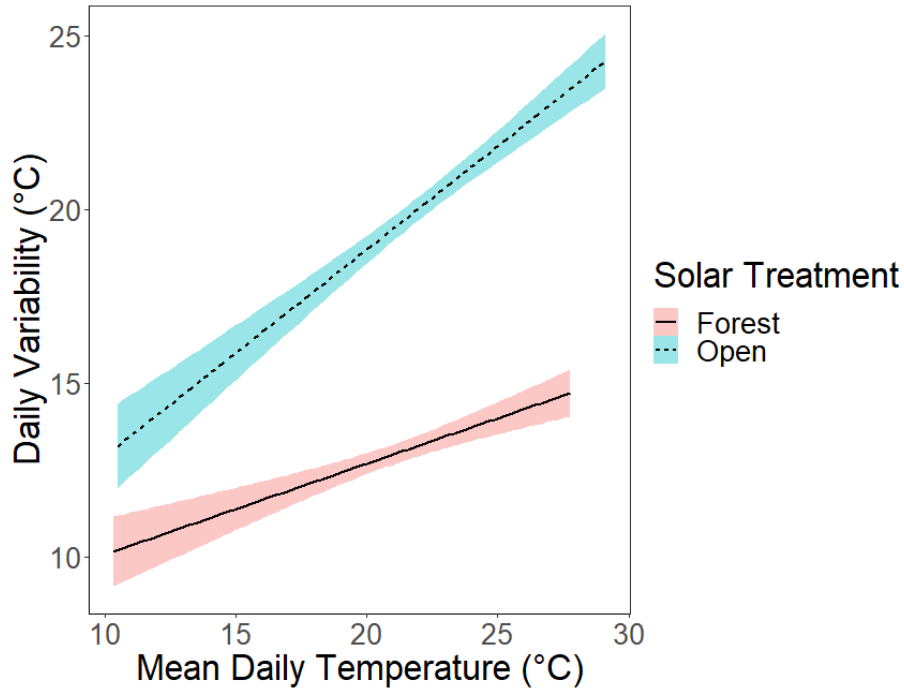


Figure 2-21: Regression lines and 85% confidence intervals showing the interactive effect of solar treatment and increasing mean daily air temperature on daily box variability.

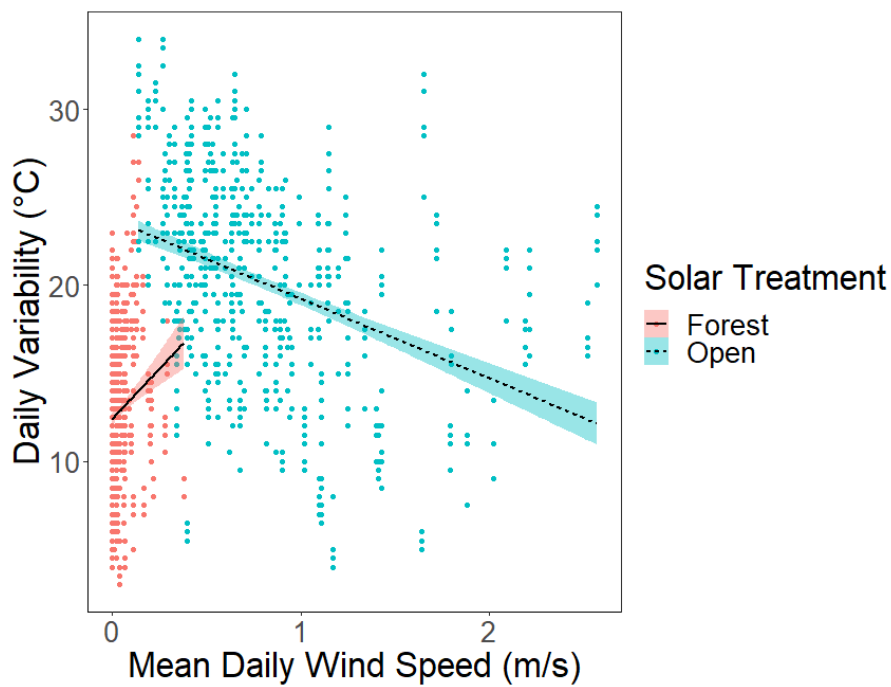


Figure 2-22: Regression lines and 85% confidence intervals showing the interactive effect of solar treatment and mean daily wind speed on daily box variability.

Daily Suitability:

We accumulated 1144 observations of daily roost suitability for our Open/Forest analysis. When comparing models predicting suitability within the Open/Forest clusters, we found that model 3 received top rank, carrying 52% of the cumulative model weights (Table 2-15). Model 7 was a competing model, being 0.2 AIC_C units away from the top model and carrying 48% of the cumulative model weights. The evidence ratio comparing these 2 models is 1.08 to 1. Thus, we constructed a 90% confidence set, including models 3 and 7, for model averaging. We identified 7 informative parameters based on model averaged results (Table 2-16).

From informative parameters, we note both solar treatments generally increased in suitability with increasing mean daily temperature, though the forest solar treatment has a stronger positive slope from ~15–20°C (Figure 2-23). The open solar treatments generally were less suitable for bats than the forest solar treatments. When mean daily air temperature exceeded ~21°C, both solar treatments level off in suitability as days become subsequently warmer. Increasing mean daily wind speeds decrease daily suitability in both solar treatments, with the forest solar treatments experiencing a more extreme negative response at low wind speeds (Figure 2-24). Roosts in the forest solar treatment generally were more suitable at low ambient temperature ranges compared to the open solar treatment roosts (Figure 2-25), though both solar treatments show decreased suitability when ambient temperature ranges exceed ~7°C.

Table 2-15: AIC_C ranks of the 8 candidate models for daily suitability (Open/Forest analysis; April-September 2019).

Model Name	ΔAIC_C	K	w_i
m3	0.0	9	0.5200
m7	0.2	17	0.4800
m5	21.7	10	<0.001
m6	26.7	14	<0.001
m4	39.9	21	<0.001
m8	43.4	26	<0.001
m2	247.8	11	<0.001
Null	261.2	2	<0.001

Table 2-16: Parameter estimates and 85% confidence intervals for the top ranked daily suitability model (Open/Forest analysis; April-September 2019; informative parameters bolded).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	-2.512	-2.999	-2.024
ClusterOpen	2.075	1.364	2.786
AvgTemp	0.236	0.215	0.257
AvgWind	-1.950	-2.954	-0.947
TaRange	-0.021	-0.040	-0.001
AvgTemp:ClusterOpen	-0.089	-0.117	-0.060
AvgWind:ClusterOpen	1.725	0.713	2.738
ClusterOpen:TaRange	-0.044	-0.072	-0.016
DesignCH	-0.026	-0.229	0.177
DesignEXTJ	0.144	-0.058	0.345
DesignVR	0.035	-0.176	0.247
DesignWTR	-0.009	-0.216	0.199
ClusterOpen:DesignCH	0.174	-0.110	0.459
ClusterOpen:DesignEXTJ	0.272	-0.011	0.555
ClusterOpen:DesignVR	-0.073	-0.364	0.218
ClusterOpen:DesignWTR	0.071	-0.217	0.358

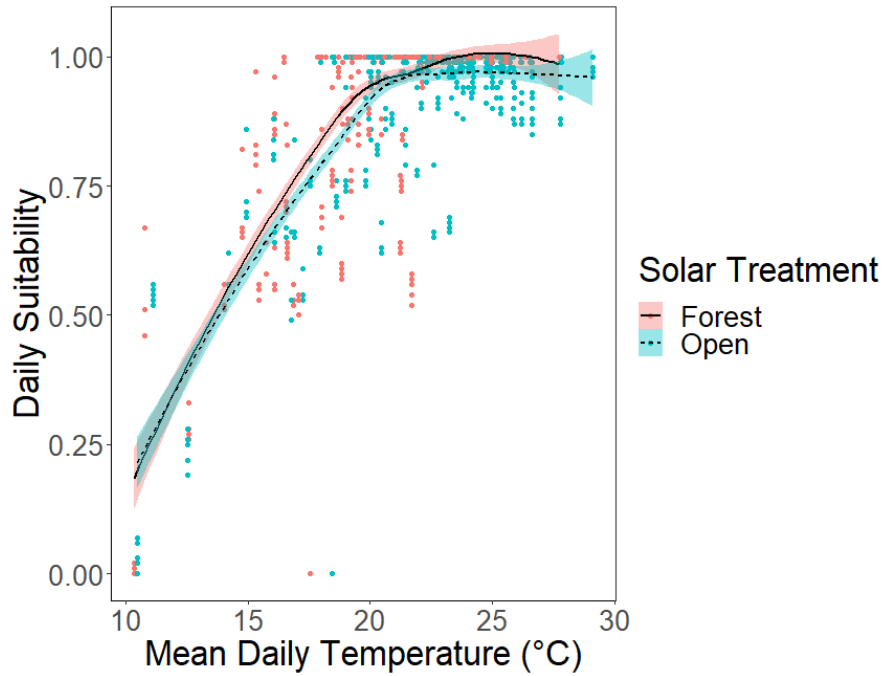


Figure 2-23: Loess smoothed regression lines and 85% confidence intervals showing the interactive effect of solar treatment and mean daily air temperature on daily box suitability.

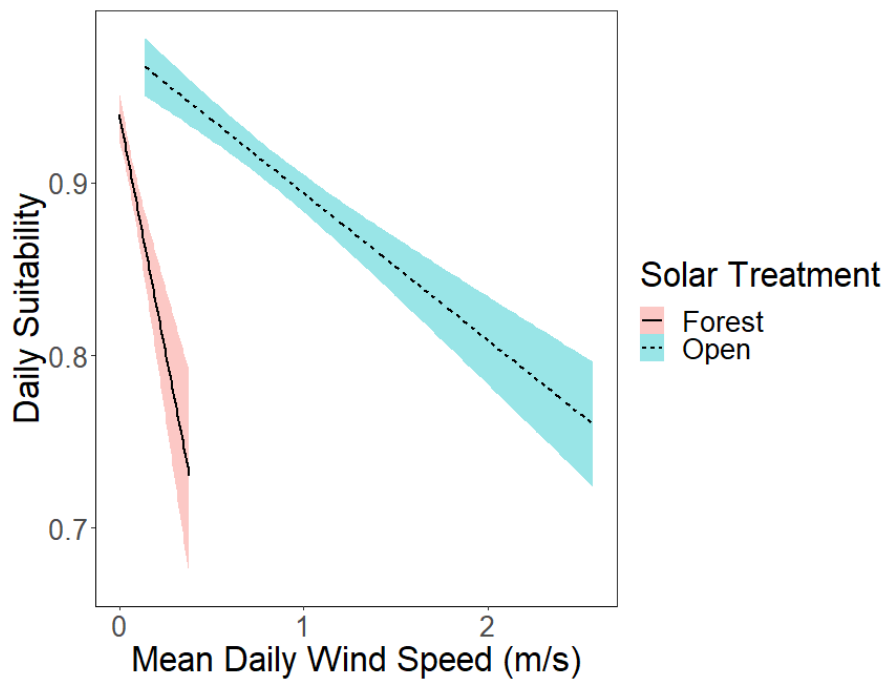


Figure 2-24: Regression lines and 85% confidence intervals showing the interactive effect of solar treatment and mean daily wind speed on daily box suitability.

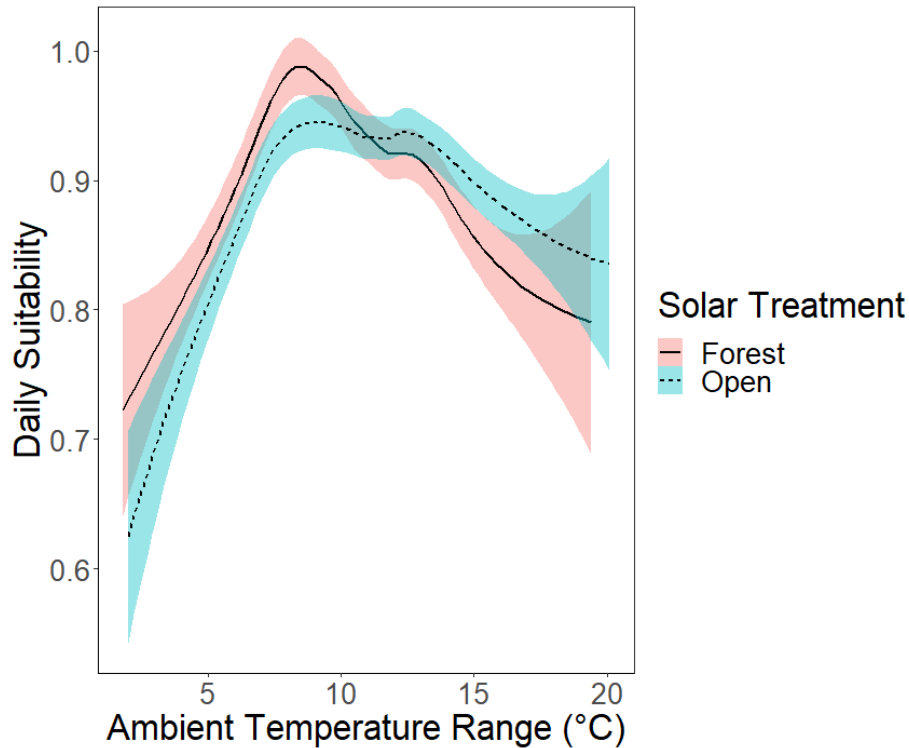


Figure 2-25: Loess smoothed regression lines and 85% confidence intervals showing the interactive effect of solar treatment and ambient temperature range on daily box suitability.

Spring Analysis~

Daily suitability:

We accumulated 463 observations of daily suitability for our Spring analysis. Based on AIC_C model selection, the null intercept model was the top ranked model with ~90% of the cumulative model weights (Table 2-17). There were no competing models within 2 AIC_C units of this top model, and the evidence ratio for the top model compared to the 2nd highest rank model is 12.4 to 1. Based on the strong support for the null model, we infer that box design and solar treatment had little influence on daily suitability (Table 2-18; Figure 2-26), and that all boxes provided similar suitability under springtime conditions.

Table 2-17: AIC_C ranks of the 5 candidate models for daily suitability (Spring analysis; April-May 2019).

Model Name	ΔAIC_C	K	w_i
Null	0.0	2	0.8997
m2	5.0	5	0.0723
m3	7.1	6	0.026
m4	12.2	9	0.0021
m5	37.5	21	<0.001

Table 2-18: Parameter estimate and 85% confidence intervals for the top ranked daily suitability model (Spring analysis; April-May 2019).

Parameter	Estimate	85% Confidence Interval	
		Lower	Upper
(Intercept)	0.977	0.879	1.075

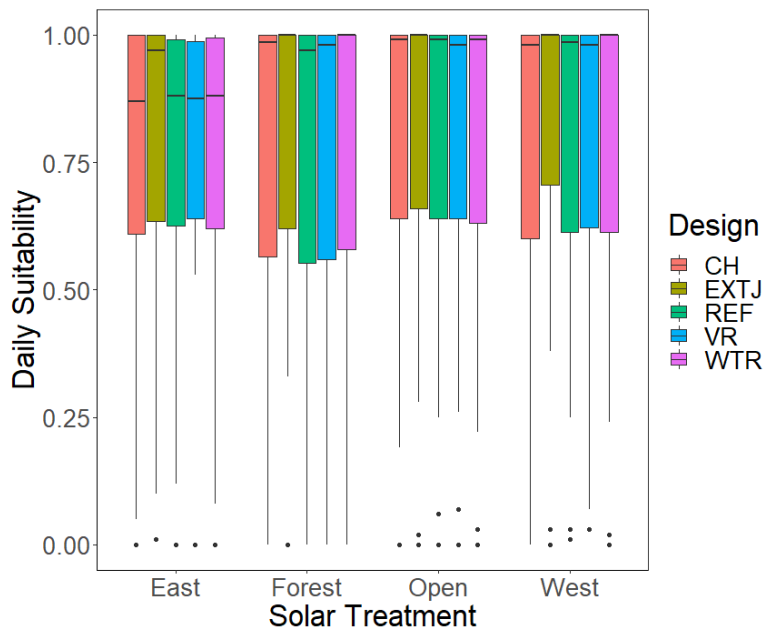


Figure 2-26: Box and whisker plot showing the daily suitability of box designs within each solar treatment.

DISCUSSION

Artificial roosts are often deployed by resource managers as tools for conservation of at-risk bat species. These structures have been successful rehousing displaced maternity colonies (Brittingham and Williams 2000; Garland et al. 2017; Arias et al. 2020), in addition to supplementing a lack of natural roosts (Flaquer et al. 2006; Adams et al. 2015). Thus, artificial roosts are showing promise as mitigation tools for bats in varied situations. Even so, several studies suggest improper deployment of potentially suitable designs can lead to limited occupancy, and poor designs in inappropriate locations can lead to unsuitable microclimates potentially harmful to bats (Whitaker et al. 2006; Bideguren et al. 2018; Rueegger et al. 2019). To complicate matters, strong design preference in conjunction with the influence of solar exposure has been documented for several species (Brittingham and Williams 2000; Mering and Chambers 2012; Doty et al. 2016; Hoeh et al. 2018). Roost preferences are likely species specific and should be evaluated on this basis. For example, northern long-eared bats (*Myotis septentrionalis*) are more likely to roost in cavities, live trees, and in areas with higher canopy cover as compared to the Indiana bat (Foster and Kurta 1999); this difference in roost selection should be reflected in targeted artificial roost deployments (Mering and Chambers 2014). Uncertainty and lack of guidance regarding proper roost design and deployment may lead to poor management decisions and negative long-term outcomes for bats (Rueegger et al. 2019). Herein we show that roost design, placement, and occupancy can alter artificial roost microclimate. Further, we demonstrate that some roost designs, have varying performance, depending on the deployment location.

Design has been repeatedly documented as a critical factor influencing the risk of overheating in artificial roosts (Lourenço and Palmeirim 2004; Bideguren et al. 2018; Hoeh et al. 2018). Our results expand on previous studies, demonstrating that simple design alterations can have a considerable impact on the microclimate provided to bats (this study; Tillman 2019). For example, the VR and REF designs recorded the highest frequency of unsuitably hot temperatures, potentially due to a lack of adequate ventilation, lower mass (compared to EXTJ), or small, ineffective vents. In contrast, CH, EXTJ, and WTR designs accounted for considerably fewer overheating events. Thus, CH, EXTJ, and WTR designs hold promise for reducing the risk of overheating events in warm climate regions or during heat waves. Though further modification and testing is merited, these designs could be useful, as climate change may increase the frequency of heat waves (Meehl and Tebaldi 2004) and may exacerbate the risk of overheating occurring in bat boxes (Bideguren et al. 2018).

Following a common trend, all designs in our study performed poorly during cold weather periods, with entire roosts frequently supporting temperatures below 15°C. Hoeh et al (2018) similarly note that all artificial roost styles tested in their study did not effectively buffer against cold temperatures, with roosts showing low suitability at ambient temperatures below 10°C. Further, Kerth et al. (2001) found that artificial roosts supported significantly different temperature profiles during the day, but that all supported virtually identical microclimates roughly 1–3 hours after sunset. Lourenço and Palmeirim (2004) and Bartonicka and Rehak (2007) similarly note the lack of heat retention by roosts of different types. Even though limited knowledge is available on natural tree roost microclimates, one recent study shows that nighttime temperature

variance under exfoliating bark can differ by as much as 4.5°C among tree species and shows that larger diameter trees radiate heat longer into the night compared to trees of lower mass (Lacki et al. 2013). Further, nest boxes deployed for marsupials in Australia were more variable in temperature and overheated more often than naturally occurring tree hollows (Rowland et al. 2017). These findings, in conjunction with our own, highlight the widespread pattern that artificial roost designs are generally inadequate at retaining heat captured during the day and may not be adequate surrogates for natural roosts. As such, we suggest future work designing and testing artificial roosts is necessary to mitigate against negative energetic effects of cold roosts, as cold conditions are not favorable to pup development (Hoying and Kunz 1998; Wilde et al. 1999; Lausen and Barclay 2006). We note our EXTJ design exhibited some capacity to reduce the number of unsuitably cold temperature recordings, but we judge this unlikely to be effective during extended cold periods, as the EXTJ design requires warm temperatures to build up heat. The EXTJ design is likely effective at buffering against short duration drops in temperature (i.e., lasting no more than a day). For example, minimum temperature availability within the EXTJ design was typically reached 4–5 hours later in the morning (mode occurrence at 0900 hours) compared to all other designs. Prolonged buffering against cold ambient temperatures would likely require roosts to be heated (Wilcox and Willis 2016). Even so, marginal gains in cold weather suitability could lead to substantial energetic savings for reproductively active bats.

While the EXTJ design holds promise as a roost resistant to unsuitably hot and cold temperatures, we note a structural flaw that must be addressed to enhance durability and utility of the design. Due to the increased mass of this design, the roofs of

the EXTJ design began to separate from the outer shell boards. This led to the outer shells of 2 boxes (25% of total), 1 in Indiana and 1 in Kentucky, to separate and slide down the 4"x4" posts. Though no bats were injured during these 2 events, this structural flaw poses a serious threat to roosting bats. As a result, all 8 EXTJ boxes were removed from our field sites at the end of the study. Subsequent reconfiguration and improvement of this design will be undergone before reinstallation at our sites. This highlights that long-term maintenance and construction costs should be carefully considered when designing and deploying novel roost designs (Rueegger 2016), as short-lived, high-cost roosts are not practical for effective conservation.

Artificial roost positioning on the landscape is critical to providing bats with safe and effective alternative roosting options. Solar exposure, in relation to landscape position, is a key determinant of Indiana bat natural and artificial roost selection (Callahan et al. 1997; Hammond et al. 2016; Bergeson et al. 2018). We found that easterly and westerly sun treatments logged the most overheating events. In contrast, roosts in forest solar treatments rarely experienced overheating events, likely due to canopy shading reducing the ambient temperature and blocking solar radiation. Open solar treatments, though receiving all-day solar exposure, experienced fewer overheating events than the easterly and westerly sun roosts, which only receive partial solar exposure. A plausible explanation of this observation is that convective cooling was more extreme at the open solar treatments, as recorded mean daily wind speeds were greater at the open solar treatments as compared to the easterly and westerly sun clusters (~0.5 m/s greater; Appendix A). High winds leading to strong convective cooling likely reduce roost temperature and overheating risk. Our observations align

with Tillman (2019), who noted greater wind speeds decrease roost temperature availability and variability across rocket box designs. Open solar treatment roost deployments could feasibly reduce the risk of overheating events and be effective deployments if the focal species is amenable to roosting in such locations.

Though forest and open solar treatments experience fewer unsuitably hot and cold temperatures compared to easterly and westerly sun treatments, bats still preferred to roost in forest edge treatments (See Results Chapter 2). Bats avoided open solar treatments and rarely used forest solar treatments. We posit bats likely avoided forest solar treatment roosts due to inadequate solar exposure leading to cooler-less optimal maternity roosting conditions, as pup development is enhanced by warm conditions (Zahn 1999; Lausen and Barclay 2006). Further, Indiana bats generally select maternity roost that receive high amounts of solar exposure (Callahan et al. 1997; Britzke et al. 2003; O’Keefe and Loeb 2017). We suspect Indiana bats likely avoided open solar treatments, as they are a relatively slow-flying, clutter-adapted species, and may perceive a higher predation risk when flying and emerging from roosts on open landscapes (Lesiński et al. 2009; Lima and O’Keefe 2013). For example, Arndt et al. (2019) show that Indiana bats emerge later relative to sunset with increasing proximity to open habitats. This trade-off between microclimate and predation risk likely led to bats’ preference for easterly and westerly sun roosts, as these placements allow for both solar exposure and quick access to cover upon emergence.

Groups size influences microclimate~

To date, most artificial roost microclimate studies focus on the impact of design, placement, and region on roost microclimate without examining the potential influence

of bats on roost microclimate (Brittingham and Williams 2000; Griffiths et al. 2017; Bideguren et al. 2018; Hoeh et al. 2018; Ruegger 2019). For bats that roost under poorly insulated exfoliating bark, like the Indiana bat, insulation resulting from social thermoregulation could be increasingly important for energy savings (Russo et al. 2017). While exclusion studies are necessary to assess roost safety prior to large scale deployment for bats, researchers should further consider evidence that bats may substantially impact microclimate and subsequent suitability of roosts. We found that large primary maternity groups and smaller groups of Indiana bats, in a field-based setting, substantially altered the hourly availability and daily variability of temperature within rocket boxes, in addition to having varying microclimate effect strengths-based roost design. This is similar to the results of Willis and Brigham (2007), who note the presence of bats can alter roost temperature by as much as 7°C. Further, artificial roosts occupied by Bechstein's bats (*Myotis bechsteinii*) supported roost temperatures that were on average 4.6°C higher than ambient temperature when compared to unoccupied roosts, which only supported mean temperatures 0.5°C higher than ambient (Pretzlaff et al. 2010). These authors noted that the energetic benefits of social thermoregulation were greater on cold weather days, which also corroborates our findings. The impact of bats on the “realized” roost microclimate should be considered when selecting a design for deployment.

With decreasing mean daily ambient temperature, large primary and small non-primary groups of bats increased mean daily availability and variability in roosts, as compared to unoccupied roosts. Body heat collectively generated by bats on cooler days likely results in a larger vertical temperature gradient in roosts. This result highlights the

potential metabolic advantages associated with social thermoregulation by large groups of bats during the maternity season (Trune and Slobodchikoff 1976; Willis and Brigham 2007; Pretzlaff et al. 2010; Russo et al. 2017). Similarly, big brown bats have been shown to aggregate in larger numbers when the difference between roost and ambient temperature is low, presumably attempting to negate the negative effects of a cold roost through social thermoregulation (Webber and Willis 2018). In our study, large and small groups of bats increased daily variability as mean daily solar radiation increased. A possible explanation for this is that roosts cool significantly at night (Kerth et al. 2001; Lourenço and Palmeirim 2004; Bartonicka and Rehak 2007) when bats are likely out foraging; the subsequent arrival of bats to roosts at dawn combined with high levels of solar radiation during the day likely result in a large increase in maximum roost temperatures as compared to overnight minimums.

Expanding upon our results, bats had a stronger warming effect in 2 designs that could either not effectively vent heat generated internally or that reflected radiant heat (i.e., EXTJ and WTR). The WTR design is intended to reflect radiant heat from the sun thus has no mechanism to buffer metabolic heat generated within. The EXTJ design likely traps internal heat generated by the bats due to increased mass and the lack of vents. The CH design typically supported the lowest mean daily availability and variability, likely because of the design's capacity to dissipate internal metabolic heat production by bats through the chimney. This result highlights that bats cannot be expected to have the same effect across all types of roost structures (Kurta 1985). Designs that better retain heat generated by bats (i.e., EXTJ and WTR) may be more valuable for promoting the development of pups during the maternity season, as heat

retention by roosts is a trait often selected for by maternity roosting bats (Sedgeley 2001; Lausen and Barclay 2002, 2006). Designs that dissipate internal heat (like CH) may negate the benefits of social thermoregulation, but this does not discount the utility of the CH design as this style could serve as a temporary refugia during heat waves and could be a more suitable roost design to use in warmer and more humid environments. While roost designs in our study provided the same volume and entrance area, we expect that bats would have a proportionally stronger influence on the microclimates of small volume roosts as opposed to large volume roosts (Kurta 1985).

Further investigation into the relative humidity within rocket boxes is merited. We suspect the CH design will support lower humidity, through warm, moist air venting through the chimney, which could lower the heat index but conversely increase evaporative water loss (EWL) of roosting bats. This effect could pose serious health risks for bats, as up to 30% of their body mass could be lost daily through EWL at low (< 20%) humidity (Webb et al. 1995). At ambient temperatures of 25°C EWL by bats is 65% lower under high humidity conditions compared to low humidity conditions (Webb et al. 1995). Further, some bat species often occupy roosts that support higher humidity than ambient conditions (Sedgeley 2001; Bartonicka and Rehak 2007), though this humidity could be generated by EWL from bats through respiration.

We note that daily suitability within easterly and westerly sun treatments was not substantially influenced by occupancy, but rather by box design and weather. This is likely because bats are most influential during cold weather conditions (Pretzlaff et al. 2010), whereas this analysis focused on the warmest months. While bats can increase minimum roost temperature (e.g., Willis and Brigham 2007), they cannot decrease

maximum temperatures. Westerly sun clusters generally had higher frequency of 100% suitability as compared to the easterly solar treatments, likely due to greater wind speeds at the west clusters increasing convective cooling and decreasing the risk of overheating.

Design, location, and weather influence microclimate~

Solar exposure is a critical determinant of artificial roost microclimate, and is a roost trait often influencing selection by bats (Brittingham and Williams 2000; Mering and Chambers 2012). For reproductively active Indiana bats, high solar exposure is important to roost habitat selection (Britzke et al. 2003; Hammond et al. 2016; Bergeson et al. 2018). Open solar treatment roosts, which provided a higher gradient of temperature than forest solar treatments offered bats a wider variety of roosting temperatures from which they could attempt to balance their energetic budgets (Williams and Brittingham 1997; Brittingham and Williams 2000; Lourenço and Palmeirim 2004; Ruegger 2019). Increasing wind speeds substantially reduced roost temperature availability within open solar treatments, however this effect was not observed within forest solar treatments. This observation is likely the result of dense forest vegetation buffering against high wind speeds, thus, reducing the impact of convective cooling. For example, foliage-roosting hoary bats (*Lasiurus cinereus*) select southeast-facing roosting positions where the vegetation buffers prevailing winds; this lessen the costs of convective cooling on metabolic heat production (Willis and Brigham 2005). Our results also highlight that the risk of windthrow at forest interior roosts may be less and could offer bats with refugia during windy spring and fall periods, when Indiana bats migrate to and from maternity sites (Pettit and O'Keefe

2017). Further, less canopy closure during spring months may mitigate the microclimatic effects of reduced solar exposure (i.e., cooler temperatures) typically experienced by forest solar treatments. The EXTJ roost within the forest solar treatment typically supported the highest mean daily availability, though only marginally so. Within open solar treatments, the EXTJ, CH, and WTR designs typically supported lower availability than the REF design. This is likely because these 3 designs can buffer against high temperatures and, thus, do not support as large of a temperature gradient from top to bottom within the roost.

Open solar treatment roosts were more variable than forest solar treatment roosts, likely due to higher average temperatures and associated increases in solar radiation for the unshaded by open solar treatment. The high variability provided by open solar treatment roosts may allow bats to passively rewarm in the morning and evening (Hamilton and Barclay 1994; Lacki et al. 2013). Further, non-reproductive females and male bats may also take advantage of the relatively low variability experienced by forest clusters, which could promote cooler overall temperatures and facilitate deeper bouts of torpor (Hamilton and Barclay 1994; Lacki et al. 2013). Higher mean windspeeds decreased variability in roosts in the open solar treatment, likely as a result of heat loss through convective cooling.

Roost temperature stability can have major implications on bat fitness and life history (Lausen and Barclay 2003a; Russo et al. 2017; Bideguren et al. 2018). Roosts offering stable microclimates may also be better at buffering highly variable ambient temperatures. For instance, in Australia, when ambient temperatures exceeded 48°C, a little broad-nosed bat (*Scotorepens greyii*) roosting in a poorly insulated slender branch

(30 cm circumference) abandoned the roost 3.2 hours after it began to actively thermoregulate (Bondarenco et al. 2014). On the same day a male inland freetail bat (*Mormopterus* spp.) roosting within the main trunk of a larger river red gum tree (130 cm in circumference) was able to remain within this better-insulated roost during this extreme temperature event, and was largely able to thermoconform at an elevated body temperature (Bondarenco et al. 2014). These observations highlight the critical importance of roost selection when ambient temperature is extreme. The higher stability, relative to the REF design, of the EXTJ (via increased mass) and CH designs (via a heat venting chimney) could be valuable to keep bats safe from heat waves as these roosts were better at buffering highly variable ambient temperature. Our 2 most variable box designs, REF and VR, recorded the hottest temperatures seen during the study (53.5 and 54.5°C, respectively). Likewise, Hoeh et al. (2018) found that of 3 artificial roost designs tested in a side-by-side comparison, the roost that generally supported the highest variability (up to 40°C) on 0% cloud cover days, also recorded the highest maximum roost temperature of 61°C. This supports the idea that roosts prone to high variability may be more likely to subject bats to lethal temperatures. The well insulated EXTJ design, alongside the CH design that can vent excess heat through its chimney, should be further investigated as potentially valuable mitigation tools for bats especially with the increasing threat of climate change.

While supporting greater suitability, the cooler microclimates of forest solar treatment roosts might not be ideal for maternity colonies. For example, Lourenço and Palmeirim (2004) found soprano pipistrelles routinely shifted to the warmest positions within an attic roost just below their theoretical upper thermal tolerance threshold of

40°C. This suggests that some bat species may seek roost temperatures just below their theoretical critical limits, as such conditions should minimize metabolic energy lost to generating body heat. Further, it has been shown that bats often preferentially select artificial roost designs that promote warm microclimates (Lourenço and Palmeirim 2004; Doty et al. 2016; Wilcox and Willis 2016). Forest solar treatment roosts rarely reached temperatures $\geq 40^\circ\text{C}$, likely as a result of increased canopy shading, suggesting that forest deployments of a varied box designs may serve as refugia during periods of extreme heat. The forest solar treatment was generally more suitable than the open solar treatment with increasing ambient temperature range likely due to decreased roost variability experienced by the forest buffering against extreme temperature fluxes; though increased variability may allow open solar treatments to reach suitable temperatures faster on cold days. If bats can seek refugia within artificial roosts during extreme temperature events, artificial roosts are less likely to function as ecological traps, at least in terms of microclimate. Researchers and resource managers should carefully weigh the risks of deploying roosts in locations that increase the risk of overheating with the potential benefits associated with warmer maternity roosting conditions.

Cold temperatures homogenize roost microclimate~

The capacity of bats to locate suitable springtime roosting habitat that maximizes energetic savings immediately after emergence from hibernation is thought to be critical for the recovery of WNS-affected bats (Wilcox and Willis 2016). By conserving energy, bats may be able to build greater fat stores and, thus, potentially increase their overwinter survival probability when experiencing WNS infection (Cheng

et al. 2018). Further, as bats impacted by WNS may leave hibernacula earlier than expected in search of food, the confounding effects of variable spring weather could be detrimental to female survival and fecundity (Norquay and Willis 2014). These considerations underscore the need for enhanced spring roosting habitat to minimize the energetic expenditure of WNS weakened bats.

From our Spring analysis of all roosts and solar treatments for the months of April and May, we found that roost design and position had no discernable impact on microclimate suitability when assessed at this scale (though subtle differences in roost design microclimate likely exist). Predominantly cooler weather conditions (such as spring and nighttime conditions), likely homogenized the microclimates of each roost, thus resulting in similar microclimates (Kerth et al. 2001; Lourenço and Palmeirim 2004; Bartonicka and Rehak 2007). This cooling effect is similar to that documented by Hoeh et al. (2018), who found that cloudy days resulted in roost microclimates indistinguishable across the roost designs tested, even though designs promoted significantly different microclimates under clearer skies and warmer conditions. We note, however, that even small difference in roost microclimate could have substantial biological importance and should be investigated. In the absence of artificially heating roosts during cold weather periods (e.g., Wilcox and Willis 2016; Webber and Willis 2018), we caution against the construction of roosts that can naturally generate enough heat (i.e., absorption of solar radiation) to reach suitable temperatures during cold periods, as such roosts may prove dangerous during summer months as the risk of overheating could be exacerbated. For example, in a controlled setting black artificial roosts provide normothermic bats with substantial energetic savings when compare to

cooler microclimate white roosts and were preferentially selected by Gould's long-eared bats (*Nyctophilus gouldi*) (Doty et al. 2016); however, black roost designs are at higher risk of overheating in certain climates (Bideguren et al. 2018; Rueegger 2019). While they should provide warmer microclimates during cold weather periods, black artificial roosts could potentially function as an ecological trap (as defined by Battin 2004) in which bats may preferentially select them and subsequently experience fitness decline or mortality resulting from an unsuitably hot microclimate during warm weather conditions. We suggest that researchers develop and test roost designs that can insulate, like our EXTJ design, and be more efficient at buffering both hot and cold ambient temperatures. Insulated artificial roosts could be key to retaining body heat generated by bats, thus potentially increasing roost temperature on cold weather days.

Management considerations~

It is clear that managers must account for a variety of complex issues when considering if and where to deploy artificial roosts. Regional climate should be evaluated in relation to roost microclimate (e.g., Bideguren et al. 2018). We note that while mean ambient temperature at the Kentucky field site was 1.1°C higher than that at the Indiana site, the Kentucky site logged over twice as many unsuitably hot temperature recordings. Which shows that even slight differences in local climate could severely impact roost microclimate. The relative ease of modification makes the rocket box adaptable across an array of environmental conditions. Managers in warm, arid regions should consider the benefits of deploying roosts like the WTR, EXTJ, and CH designs tested in this study, as these designs may reduce the risk of overheating events. In cool climates, managers should consider deploying insulated roosts similar to the

EXTJ design or other roosts with higher thermal mass, as such roosts may help bats reduce their energetic expenditure during the maternity season, without substantially increasing the risk of overheating events.

We suggest that resource managers think critically about the life history traits of their focal species and evaluate what deployment strategies would be most effective for maximizing energetic benefits. Specifically, the typical colony sizes of a bat species should be considered when selecting a roost design. We show that large colony sizes can have a substantial impact on roost microclimate, but if a species generally forms smaller maternity groups (i.e., < 30 individuals) resource managers should consider deploying smaller volume roosts that could potentially enhance the social thermoregulatory benefits of a smaller group (Kurta 1985). In addition, deployment locations on the landscape should be carefully scrutinized. For example, forest deployments, while potentially less optimal for pup rearing, may yet offer refugia during heat waves. Alternatively, deploying roosts along forest edges could provide bats with optimal solar exposure while also decreasing the perceived (and presumable) risk of predation.

Flight morphology is likely a key trait determining the appropriateness of a deployment strategy. In our case, Indiana bats possess relatively low wing loading and low aspect ratios (Norberg and Rayner 1987); their clutter-adapted traits may contribute to their perception of a higher risk of predation in open habitats (Lima and O’Keefe 2013; Arndt et al. 2018). In contrast, species with high wing loading and high aspect ratios (e.g., *Eptesicus fuscus*) may perceive a lower risk when flying in open areas (Lima and O’Keefe 2013) and may be more likely to select roost in open locations.

We recommend that resource managers first consider the need for artificial roosts on their landscape by assessing the quality of natural roosting habitat and foraging space, in addition to considering the long-term goals for the site. Ideally, artificial roosts will be phased out as natural roosting habitat is restored. If artificial roosts are deemed necessary, we recommend that resource managers deploy a variety of roost designs, in clusters, in a variety of locations on the landscape (e.g., tree line and forest interior deployments). This cluster and design strategy would provide bats with a variety of microclimates within one microsite and could facilitate the discovery of roosts in addition to facilitating the ease of roost switching (Lewis 1995; Mering and Chambers 2012; Rueeggger 2016). Deploying a variety of designs in a variety of locations could give bats refugia during weather extremes and thus potentially increase fitness and survival. Further, by providing multiple roosts on the landscape, bats would be able to switch between structures to potentially avoid high parasite loads associated with large colony sizes and long-term roost use (Bartonička and Gaisler 2007; Bartonička and Růžicková 2012, 2013).

Future work~

Though our work has shed light on a variety of topics, we have also delineated areas that warrant further investigation. None of our roost designs were effective at combating cold weather conditions, which is a common trend across artificial roost studies (Kerth et al. 2001; Lourenço and Palmeirim 2004; Bartonicka and Rehak 2007; Hoeh et al. 2018; Rueeggger 2019); A more define, nuanced investigation is needed to delineate biologically meaningful differences on a day to day basis under variable cool weather conditions. Further development and testing of additional roost designs is

needed to address this issue, as enhanced cold weather and springtime roosting habitat could be critical for the survival and reproduction of bats weakened by WNS (Wilcox and Willis 2016; Webber and Willis 2018). Our finding that bats still preferred to roost in clusters that experience the most overheating events highlights the need for developing roost designs that can combat these extreme temperatures to protect roosting bats. The potential exists that bats' preference for warm roosts that overheat often could result in an ecological or evolutionary trap (Schlaepfer et al. 2002; Battin 2004). Though our observation is likely the result of a predator/microclimate trade-off, reducing the frequency and intensity of overheating events is critical with the increasing risks of climate change. Additional work profiling the microclimates of both novel and commercially available artificial roost designs is needed, as concerns have increased regarding the potential for overheating events in bat boxes (Flaquer et al. 2014; Bideguren et al. 2018). The proliferation of inappropriate roost designs, be it by retailer, environmental consultants, or well-intentioned but misinformed conservationists, could lead to negative long-term consequences for bats across the globe. Lastly, artificial roosts potentially provide Indiana bats with roosting microclimates that are very different from that of natural roosts and, thus, further research is needed assessing this paucity of information on natural roost microclimate in addition to measures of reproductive success and survival in artificial roosts. Demographic statistics will be critical to support or refute the future use of artificial roosts on our landscapes.

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APPENDICES

Appendix A: Report of the mean and range (min/max) of weather parameters by cluster and season for each field site.

Parameter	Season	Site-Solar Treatment							
		IN-East	IN-Forest	IN-Open	IN-West	KY-East	KY-Forest	KY-Open	KY-West
T _a (°C)	All	19.6 (1.3–34.0)	20.0 (2.9–31.2)	20.5 (1.5–33.6)	20.1 (1.5–34.7)	20.7 (2.6–36.0)	20.5 (2.5–34.8)	21.1 (2.7–35.4)	21.0 (2.5–36.4)
							10.9 (1.4–21.7)		
T _a Range (°C)	All	11.7 (1.6–22.2)	9.6 (1.6–19.1)	11.2 (1.7–19.8)	12.8 (2.6–21.5)	12.2 (1.6–22.2)	21.7	11.5 (1.6–21.1)	11.8 (1.4–21.1)
		188.5 (0.0–1104.0)	21.9 (0.0–709.2)	213.7 (0.0–1088.0)	203.6 (0.0–1116.0)	186.9 (0.0–1065.0)	64.2 (0.0–854.6)	223.8 (0.0–1138)	197.5 (0.0–1075.0)
Solar Radiation (w/m ²)	All						0.13 (0.0–4.7)		
		0.42 (0.0–7.6)	0.05 (0.0–2.3)	1.16 (0.0–10.4)	0.40 (0.0–7.1)	0.30 (0.0–6.2)		0.78 (0.0–8.8)	0.62 (0.0–9.9)
Wind Speed (m/s)	All								
T _a (°C)	Apr–May	15.2 (1.3–31.5)	15.8 (2.9–29.7)	16.0 (1.6–30.6)	16.0 (1.5–31.1)	17.0 (2.6–31.0)	17.1 (2.7–31.1)	17.3 (2.7–30.8)	17.4 (2.5–31.1)
T _a Range (°C)	Apr–May	12.4 (2.5–22.2)	10.8 (2.3–19.1)	11.1 (2.6–19.8)	11.7 (2.6–21.5)	11.9 (2.8–20.9)	11.6 (2.9–21.7)	11.2 (2.9–21.1)	11.1 (2.6–21.1)
		160.6 (0.0–1065.0)	54.03 (0.0–584.2)	183.9 (0.0–1012.0)	164.6 (0.0–1011.0)	178.4 (0.0–1035.0)	90.1 (0.0–853.7)	194.7 (0.0–957.3)	178.16 (0.0–1017.0)
Solar Radiation (w/m ²)	Apr–May						0.28 (0.0–4.7)		
		0.70 (0.0–7.6)	0.15 (0.0–2.0)	1.75 (0.0–10.4)	0.69 (0.0–7.1)	0.58 (0.0–6.2)		1.18 (0.0–8.8)	1.00 (0.0–8.6)
Wind Speed (m/s)	Jun–Aug								
T _a (°C)	Jun–Aug	22.3 (6.5–34.0)	21.5 (7.1–31.2)	22.7 (7.3–33.4)	22.1 (5.0–34.1)	22.7 (6.9–34.2)	22.3 (8.1–33.9)	23.0 (7.4–34.8)	22.8 (8.0–35.7)
							10.1 (1.4–14.9)		
T _a Range (°C)	Jun–Aug	13.5 (3.2–19.8)	9.0 (1.6–16.6)	11.1 (1.7–18.3)	13.1 (3.3–20.5)	11.8 (1.6–17.4)	14.9	11.4 (1.6–16.7)	11.9 (1.4–17.2)
		209.2 (0–977.5)	12.9 (0.0–302.4)	231.1 (0.0–993.4)	226.7 (0.0–1064.0)	206.1 (0.0–1065.0)	52.1 (0.0–719.7)	244.2 (0.0–1030.0)	244.1 (0.0–1030.0)
Solar Radiation (w/m ²)	Jun–Aug						0.04 (0.0–1.6)		
		0.29 (0.0–3.6)	0.01 (0.0–1.1)	0.93 (0.0–8.3)	0.29 (0.0–3.9)	0.18 (0.0–4.7)		0.58 (0.0–4.0)	0.43 (0.0–5.3)
Wind Speed (m/s)	Jun–Aug								

Appendix B: Representative hot ($T_a > 30^\circ\text{C}$) and cold ($T_a < 15^\circ\text{C}$) weather days for the open and forest solar treatment clusters at both the Indiana and Kentucky field sites.

