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RESEARCH ARTICLE

Design modifications affect bat box temperatures and suitability as maternity habitat

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Abstract

1. Artificial roosting structures (e.g. bat boxes) are widely used as conservation tools for many animals, including bats. Although it is relatively easy to monitor bat box temperatures, we know little about the effect of design on temperatures within a box.
2. Box microclimate affects energy budgets and physiological processes and, thus, suitability as a roost. Optimal temperature varies during the period when reproductive females aggregate to rear pups; warm roosts enhance pup development during gestation and lactation, while cool roosts facilitate energy savings by torpor, which is often important during post-lactation.
3. To better understand the relation of design to internal temperature, we simultaneously compared 20 box designs (19 variations of a rocket box and one three-chamber flat box) in an open site, May to September 2018. We measured temperatures at the top, middle and bottom of each box and tallied counts of daytime and nighttime cool (≤30°C; T_{COOL}), permissive (30.1–39.9°C; T_{PERM}) and stressful (≥40°C; T_{STRS}) temperature observations. We also measured temperature, solar radiation and wind speed at the site. We used generalized linear models with negative binomial distributions to test the effects of design, environmental variables and their interactions.
4. Adding an external jacket or decreasing ventilation increased daytime and nighttime counts of T_{PERM}. Increasing box volume (i.e. lengthening box by 50%) also positively affected daytime counts of T_{PERM}, whereas decreasing box volume (by 50%) had the opposite effect.
5. Adding an external water jacket was the only modification we tested that decreased counts of T_{COOL} at night. Counts of T_{STRS} were elevated by warmer, sunnier and less windy conditions outside, but these effects were lessened by increasing roof shading or reflectivity, adding ventilation or external jackets, or decreasing box volume.

6. These results inform the development and implementation of novel bat box designs as conservation and management tools for maternal colonies of bats, with consideration for the effects of weather on internal temperatures.

KEYWORDS
air temperature, artificial roost, bats, box, global radiation, internal temperature, wind speed

1 | INTRODUCTION

Artificial habitat structures are important conservation tools that are substituted for natural structures to provide habitat for birds (Ropert-Coudert et al., 2004; Wachob, 1996), invertebrates (Lye et al., 2011), lizards (Grillet et al., 2010) and small mammals (Burger, 1969; Rueegger, 2016). In many parts of the world, bat boxes are deployed as habitat for cavity- and crevice-roosting bats (e.g. Brittingham & Williams, 2000; Flaquer et al., 2006; Neilson & Fenton, 1994). During the warmer months in temperate climates, cavity- and crevice-roosting bats naturally use a diverse set of roosts ranging from exfoliating bark and tree cavities to rock crevices and mines (Campbell et al., 2010; Johnson & Lacki, 2014; Kunz & Lumsden, 2003). Such bat species sometimes use bat boxes in lieu of natural roosts when boxes are provided by landowners and conservation practitioners as surrogates for natural habitat. For example, federally threatened northern long-eared bats (*Myotis septentrionalis*) formed maternity colonies in bat boxes deployed as mitigation for forest clearing in West Virginia, USA (De La Cruz et al., 2018) and a maternity colony of federally endangered Indiana bats (*M. sodalis*) transitioned from roosting only in trees to using both trees and numerous bat boxes supplied during tree clearing and urban development in central Indiana, USA (Whitaker et al., 2006). Bats are most likely to occupy bat boxes during critical life stages (pregnancy, lactation and pup development) that occur during the warmer months of the year, so it is crucial to assess the efficacy of bat boxes as surrogates for natural tree and rock roosts.

Bats spend ~15 h per day at roosts (Kunz & Lumsden, 2003), so internal temperature is a critical aspect of bat box design. Here, we consider the costs and benefits of using bat boxes for female Indiana bats (*M. sodalis*) and their pups during the maternity period, which occurs from ~April to September (Pettit & O'Keefe, 2017). Adult females arrive at maternity sites in early pregnancy and are faced with cold and variable April weather. During this period, Indiana bats use bat boxes in the forest interior (Crawford, 2020); presumably, bats use torpor (i.e. heterothermy; Willis et al., 2006) in these shaded roosts during periods of harsh weather and low insect availability to conserve energy and to synchronize foetal development with other females (Racey, 1973). In the latter half of pregnancy, female Indiana bats move into tall, solar-exposed roosts (O'Keefe & Loeb, 2017) and use only short torpor bouts and on fewer than 30% of days tracked (Bergeson et al., 2021); staying normothermic should promote the final stages of foetal development. Lactating females face higher energetic demands for milk production versus foetal development (Kurta et al., 1989) and heterothermic behaviours allow energy savings. Lactating female Indiana bats use torpor on about 50% of days, alternating between solar-exposed and shaded roosts and spending an average of 6.7 h per day in torpor (Bergeson et al., 2021). Solar-exposed roosts are also important for developing pups, as warmer temperatures should facilitate faster growth. During post-lactation, greater energetic savings are realized from the use of torpor (Willis et al., 2006) and, thus, post-lactating females tend to select roosts with cooler microclimates (e.g. shaded trees; Bergeson et al., 2020) and to use torpor more often than pregnant or lactating individuals (Bergeson et al., 2021; Lausen & Barclay, 2003).

Because bats' energetic demands vary across the maternity season, it is important to consider whether bat boxes provide optimal internal temperatures for normothermic and heterothermic processes. There is ample evidence that bat boxes in solar-exposed locations will provide warm temperatures during the day (Kerth et al., 2001; Lourenço & Palmeirim, 2004; Rueegger, 2019), which could promote energy savings when it is advantageous to be normothermic. Herein, we assume bats maintain normothermia when roost temperatures are in a 'permissive' temperature range (modified terminology from Mitchell et al., 2018) of 30.1–39.9°C, a range that should encompass the thermoneutral zone of adult and juvenile Indiana bats (based on data for 50–60 bat species; Speakman & Thomas, 2003). Tall bat boxes offer a gradient of temperatures and bats can move around a spacious box to find an optimal temperature. However, on warm days late in the reproductive period (i.e. during post-lactation), bats may avoid roosting in warm bat boxes if it is more advantageous to roost in a cooler location that facilitates heterothermy (Bergeson et al., 2021), namely where roost temperatures are ≤30°C. Furthermore, bat boxes are prone to reaching stressful (≥40°C) or lethal temperatures (≥45°C) on warm, sunny days (Flaquer et al., 2014; Hoeh et al., 2018; Martin Bideguren et al., 2018), which could kill the occupants if they are unable to move into a cooler roost space (Crawford & O'Keefe, 2021). Extremely hot temperatures are particularly dangerous for young pups, which are inefficient at thermoregulation (Klug & Barclay, 2013), less likely to move, and more likely to overheat due to their small size. Pup deaths have been reported for artificial roosts in Spain (Alcalde et al., 2017) and Australia (Griffiths, 2021).

We must also consider the role of the microclimate parameters acting on the box – air temperature, global radiation, thermal radiation, and wind speed – which determine heat exchange between the outer surface of the box and the environment (Gates, 1980). Air temperature is a convenient starting point, with solar and thermal radiation absorbed by the box creating a temperature increment or decrement modified by wind speed (Bakken, 1992, eqs. 1–2,). Variation in radiation, particularly solar radiation, may be responsible for more variation in heat transfer over the course of a day than variation in air temperature. A bat box placed in the shade may be heated by diffuse sunlight penetrating clouds or a leaf canopy (Gates, 1980), sometimes creating surprisingly high temperatures (43.5°C; R. Crawford et al., unpublished data, 2020). While wind speed is not typically mentioned in studies of bat box internal temperatures, it plays a major role in modulating radiation heating. Higher wind speeds reduce daytime operative temperatures and, thus, temperatures within bat boxes (Crawford, 2020) and thereby decrease overheating risk.

Many design factors have been shown to affect internal temperatures in bat boxes. Box colour, shape and orientation could enhance or diminish heat transfer as a function of solar radiation. For example, the maximum temperature in a black box is 3–9°C warmer than in a white box (Doty et al., 2016; Lourenço & Palmeirim, 2004; Rueegger, 2019). External insulation (including construction materials) or additional chambers could slow the transfer of heat to the box interior. For example, boxes made of rice cement are cooler than wooden boxes with similar colouration (Martin Bideguren et al., 2018) and black wood cement boxes are cooler than black plywood boxes (Rueegger, 2019). In multi-chambered boxes, the chamber facing the sun may be >3.5°C warmer than inner chambers (Brittingham & Williams, 2000; Rueegger, 2019). Hot air is less dense, so it will rise within a box, creating a vertical temperature gradient; for example the top of a 0.9-m tall box is >10°C warmer than the bottom on a clear and moderately warm (26°C) day (Hoeh et al., 2018). Modifications to ventilation could trap or vent hot air along the length of a box, though we are unaware of any systematic tests of different ventilation schemes for bat boxes.

We investigated the effects of design variations and environmental variables on bat box internal temperatures. We characterized bat box internal temperatures in a four-sided, two-chamber rocket-style reference box in the absence of bats. Because rocket-style boxes are typically 0.9 m tall, we predicted that rising warm air would create vertical temperature gradients. Concurrently, we tested experimental increases and decreases to volume, airflow, heat capacity and insulation and shading of the reference box, which we predicted would affect temperatures within the box; we also tested a three-chamber, flat-fronted box, which is a typical style offered to bats. We classified temperatures at 12 positions within bat boxes as cool (≤30°C), permissive (30.1–39.9°C) or stressful (≥40°C) and relate daytime and nighttime counts of temperatures in these categories to box design and daily maximum global radiation, daily maximum wind speed, and daily maximum outside air temperature. We predicted that design modifications that altered shading, external layers, ventilation and volume would interact with environmental variables to affect the counts of cool, permissive and stressful temperatures.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study took place from May to September 2018 on a ~0.5-ha plot on private property in Vigo County, Indiana (39.538764, −87.235827). The site was along a gravel road with agricultural fields to the north and south, and conifer-hardwood forest 100 m to the west and 70 m to the east. Mean monthly air temperature (T_a) was 25.3°C (May, only the last 6 days), 24.0°C (June), 23.7°C (July), 23.6°C (August) and 22.3°C (September) (range 11.6–35.4°C). The site received 52.2 cm of total precipitation (mean daily precipitation was 0.34 cm, range 0–2.0 cm; data from National Oceanic and Atmospheric Administration (NOAA) weather station 10.5 km away).

2.2 | Bat boxes

We built a single flat-faced box with three chambers (similar to Stebbings & Walsh, 1991; hereafter, TCB), and 19 variations of a two-chambered rocket-style box (Figure 1a, Table 1; Hoeh et al., 2018). The rocket-style box (Figure 1b) was the reference design (hereafter, REF) because of its previous use by the endangered Indiana bat (Hoeh et al., 2018) and the threatened northern long-eared bat (De La Cruz et al., 2018).

Seventeen designs had the same volume (Table 1). Internal structures were identical, except in designs with modified shape and volume (LONG, SHORT, TCB; Table 1). Each rocket-style box included eight wooden blocks (3.2 cm × 10.2 cm × 2.5 cm) per side to maintain chamber width and a 2.54 cm-diameter hole between chambers per side. We constructed boxes with 1.91-cm thick untreated pinewood, excepting the composite material design (hereafter, COMP; 2.54-cm thick ChoiceDek Wood-Polymer Composite Lumber Product Springdale, AR, USA) and TCB (1.9-cm thick ACX plywood). Plywood (1.9-cm thick) was used for roofs, but because we have observed plywood roofs deteriorating over multi-year deployments, we do not recommend them for long-term box deployment. We sealed each box with paintable latex caulk with silicone and painted the outside with two coats of flat exterior paint; to reduce the number of design variations, we used the same medium brown colours for all boxes, though we suspect the house wrap used on one design functioned similarly to white paint. We attached each box to an untreated wooden post (10.2 cm × 10.2 cm), with the top at ~4.9 m above ground. Vents, if present, were oriented north–south to be consistent with Hoeh et al. (2018). Bats were excluded by covering openings with 0.6-cm wire mesh that did not appreciably hinder air flow.

We built only one of each of the 20 designs, devoting our resources to box structural modifications rather than replication. Excluding bats eliminated variation due to heating by the metabolism of a variable number of bats. To ensure nearly identical external weather conditions, we installed the boxes in one row (REF near center), oriented east–west, with 2 m separation between boxes (Figure 1a). The open location offered high solar exposure with brief and infrequent shading by trees (>70 m to nearest tree) or adjacent boxes. We assume internal temperature differences among boxes are due to design modifications and not environmental variation.

2.3 | Box comparison

We used temperature-only iButton data loggers (DS1921G Thermochron iButton Device, Maxim Integrated, San Jose, CA, USA) to measure box temperatures in 0.5°C increments. Data were recorded

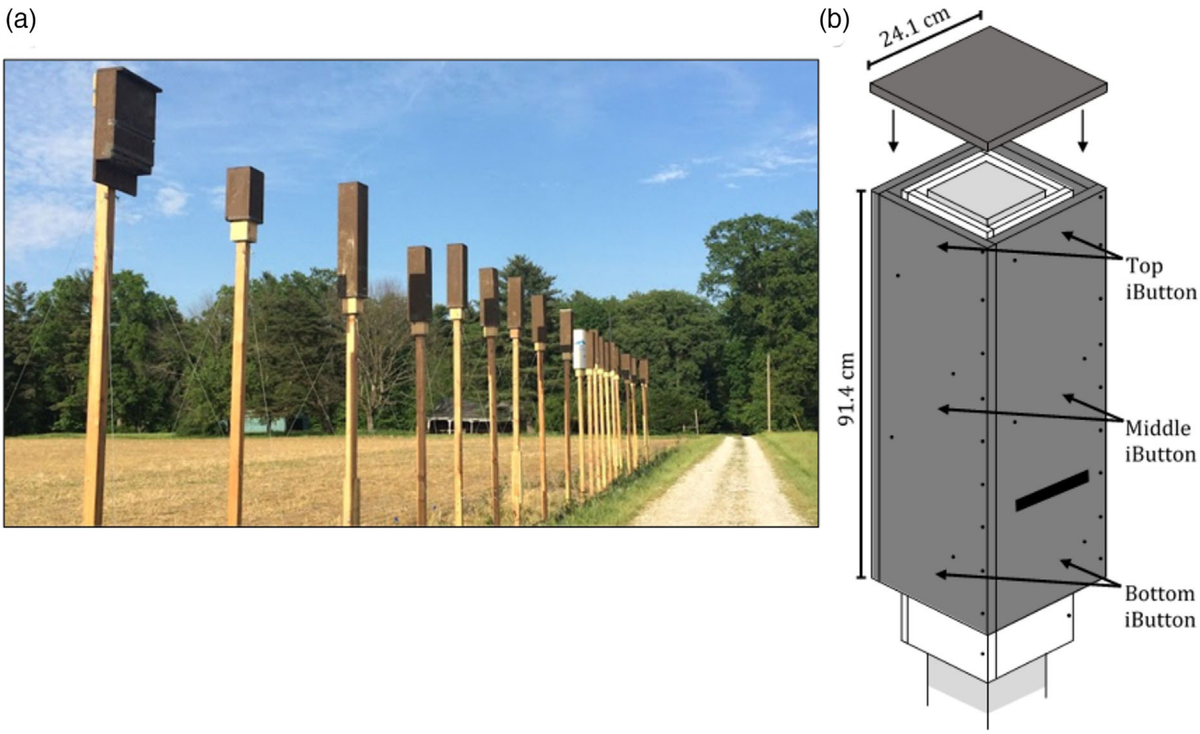

FIGURE 1 (a) Twenty bat box designs installed in Vigo County, Indiana, May–September 2018. (b) Schematic with dimensions of a reference rocket-style bat box and iButton temperature data logger locations. Data loggers were placed between the outer (dark grey) and inner (white) sleeves. To maintain chamber widths, wooden blocks were placed between the outer and inner sleeves and the post (light grey) and inner sleeve

from 24 May to 14 September 2018 (accuracy ± 1°C). We placed 12 iButtons between the inner and outer sleeves (Figure 1b; hereafter, 'outer chamber') of each rocket-style box. We only measured temperatures of the outer chamber due to a limited number of iButtons, recognizing that temperatures in internal chambers are more stable and thus less informative about box differences (Brittingham & Williams, 2000; Rueegger, 2019). In each box, we placed iButtons oriented with the serial number facing outward in three vertical zones (top, middle and bottom; Figure 1b). Each zone had an iButton on north-, south-, east- and west-facing sides. For the TCB box, we used nine iButtons, placed top, middle and bottom in each of the three chambers. To allow data storage for the entire season, the iButtons recorded every 2 h, with half of the iButtons recording during even hours and half during odd. We assume iButton recordings were an accurate indicator of box air temperatures but recognize that recordings may have been influenced by thermal radiation from nearby surfaces. We took down boxes and retrieved iButtons on 22 September 2018.

To determine study site T_a, we averaged T_a measurements from four HOBO temperature data loggers (HOBO UA-002-64, Onset Computer Corporation, Bourne, MA, USA) recording in solar shields 1.5 m above ground. We installed a weather station (CR10, Campbell Scientific, Logan, UT, USA) to measure wind speed (m/s) and solar radiation (W/m^2). Hourly wind speed was calculated by averaging values from sensitive cup anemometers (model 901-LED, C. W. Thornthwaite Associates, Centerton, NJ, USA) at the eastern and western ends of the box arrangement (2 m from the nearest box at box level). A storm on 8 September 2018 damaged the eastern anemometer, so wind speed values after this date are from the western anemometer only. We measured solar radiation near the center of the box array via one black and white pyranometer (model 8-48, Eppley Laboratory, Inc., Newport, RI, USA).

2.4 | Temperature variables

Mean (a mean of mean daily values; T_{box}), maximum (T_{max}), and minimum (T_{min}) daily box temperatures were based on values recorded by all temperature data loggers in a box. For each 24-h day, we calculated the average hourly range of box temperatures and the daily range of box temperatures. We present means ± 1 SE for each design in a table (Table S1 in the Supporting Information), but do not use mean values in our analyses. Within R (R Core Team, 2018; version 3.6.1), we used the tidyr (version 1.1.3) and dplyr (version 1.0.6) packages to tally the number of daytime and nighttime cool (≤30°C; T_{COOL}), permissive (30.1–39.9°C; T_{PERM}) and stressful (≥40°C; T_{STRS}) temperature observations; each bihourly recording by an iButton was treated as an observation. Cool temperatures represent times when bats are likely to use torpor, permissive temperatures when bats are likely to be normothermic and stressful when bats should begin showing signs of heat stress (O'Farrell & Studier, 1970).

TABLE 1 Descriptions, box codes and approximate habitable volumes of a reference rocket-style bat box, 18 modified rocket-style designs and one three-chamber bat box design tested in 2018

Box design	Box code	Approximate habitable volume	Description
Reference design	REF	24,538 cm^3	Standard two-chambered, four sided, rocket box 1.0 m tall with vents on north and south sides 0.3 m from bottom of box, 1.9 cm chamber opening at bottom.
	Modifications changing ventilation		
Chimney design	CHIM		0.9 m black PVC chimney (6.4 cm internal diameter) added to roof to maximize ventilation, particularly by free convection on sunny days.
Upper vent design	UV		Move vents higher to 0.3 m from top of box.
Double vent design	DV		Four vents, two vents each on north and south sides
Vent removal design	VR		No vents to decrease ventilation
Reduced opening design	OW		1.3 cm wide chamber opening at bottom.
	Modifications changing solar heating		
House wrap design	HR		Outer surface covered with two layers white house wrap
White gloss roof design	WG		Roof painted with white gloss enamel rather than brown
South roof shade design	SRS		Flat 1.2 m E-W × 0.6 m S shade roof
Two-inch roof design	TWO		Two inch roof overhang on all sides of box
	Modifications changing internal heat storage capacity		
Empty cavity design	ICE		Air space in center of box 8.9 cm × 8.9 cm × 0.9 m.
Foam cavity design	ICF		As above, but space filled with insulating foam
Water cavity design	ICW		As above, but space filled with water-filled, heat sealed, freezer bags.
	Modifications changing external heat capacity, external insulation, or both		
Composite material design	COMP		Constructed with dense synthetic decking board
Empty jacket design	EJE		A rocket box surrounded by an empty wooden jacket creating 1.9-cm-wide-air space between outer wall and outer chamber. No vents.
Foam jacket design	EJF		As above, jacket filled with foam insulation.
Water jacket design	EJW		As above, jacket contains 12 water-filled packets; each packet is a heat-sealed freezer bag filled with 750 mL water.
	Modifications to shape and volume		
Long design	LONG	36,779 cm^3	Rocket box with vertical dimension 1.4 m
Short design	SHORT	12,296 cm^3	Rocket box with vertical dimension 0.5 m
Three-chambered design[a]	TCB	20,549 cm^3	Commonly used flat three-chamber box

[a]Flat-front box.

2.5 | Data analysis

We conducted statistical analyses in R, using parametric statistics after assessing normality and homogeneity of variances with qq-plots and histograms. To determine how each environmental variable – maximum daily air temperature, maximum daily global radiation and maximum daily wind speed – affected the counts of daily and nightly T_{COOL}, T_{PERM} and T_{STRS} observations, we developed 30 a priori generalized linear models with negative binomial distributions (five per temperature category and time period). These models were combinations of box design, maximum daily temperature ($T_a$max), maximum daily solar radiation (G_{max}), maximum daily wind speed (μ) and their interactions (Table 2). Because it had fewer observations and a different configuration, we did not include data for the TCB box in our models. We used the R packages MASS (version 7.3-53.1) and bbmle (version 1.0.23.1) to compare models and considered models competitive if ΔAICc $\lessapprox 2$. We evaluated significance of variables within competitive models at $p < 0.05$. For ease of interpretation, we present graphical representations of model results only for boxes that differed significantly from the REF. To visualize the spatiotemporal variation in temperature across each design, we used the geom_tile function in ggplot to map temperature data for 4 July 2018, which was a warm day with low cloud cover.

TABLE 2 All models tested to explain daytime and nightly permissive (P; 30.1–39.9°C), cool (C; ≤ 30°C),and stressful (S; ≥ 40°C) temperature observations in 19 rocket-style bat boxes where bats were excluded, in Vigo County, Indiana, May–September 2018. Temperature observations were taken bihourly via 12 iButton temperature data loggers per box. The best-fit models were determined by Akaike information criterion (AIC) value comparison. Degrees of freedom (df), relative model differences (ΔAIC), and model weight are presented for day and night models. Models that best explain the data (ΔAIC ≤ 2.1) have ΔAIC and weight in bold

Model	Explanatory variables	df	ΔAIC day	Weight day	ΔAIC night	Weight night
Permissive						
P.null		2	30940.7	<0.001	39498.1	<0.001
P1	Box	20	3934.3	<0.001	1601.2	<0.001
P2	Box + Daily max wind speed + Box:Daily max wind speed	39	3971	<0.001	1636.3	<0.001
P3	Box + Daily max air temperature + Box:Daily max air temperature	39	1051.4	<0.001	98.9	<0.001
P4	Box + Daily max global radiation + Box:Daily max global radiation	39	2790.8	<0.001	1466.8	<0.001
P5	Box + Daily max wind speed + Daily max air temperature + Daily max global radiation + Box:Daily max wind speed + Box:Daily max air temperature + Box:Daily max global radiation	77	**0**	**1**	**0**	**1**
Cool						
C.null		2	2509.8	<0.001	5585.6	<0.001
C1	Box	20	2471.4	<0.001	432.9	<0.001
C2	Box + Daily max wind speed + Box:Daily max wind speed	39	2478.2	<0.001	404.1	<0.001
C3	Box + Daily max air temperature + Box:Daily max air temperature	39	250.7	<0.001	**0**	**0.74**
C4	Box + Daily max global radiation + Box:Daily max global radiation	39	2062.4	<0.001	144.6	<0.001
C5	Box + Daily max wind speed + Daily max air temperature + Daily max global radiation + Box:Daily max wind speed + Box:Daily max air temperature + Box:Daily max global radiation	77	**0**	**1**	**2.1**	**0.26**
Stressful						
S.null		2	2320.5	<0.001	7254.4	<0.001
S1	Box	20	1923.8	<0.001	102.8	<0.001
S2	Box + Daily max wind speed + Box:Daily max wind speed	39	1747.2	<0.001	133.5	<0.001
S3	Box + Daily max air temperature + Box:Daily max air temperature	39	1070.8	<0.001	**0**	**0.95**
S4	Box + Daily max global radiation + Box:Daily max global radiation	39	1727.3	<0.001	139.9	<0.001
S5	Box + Daily max wind speed + Daily max air temperature + Daily max global radiation + Box:Daily max wind speed + Box:Daily max air temperature + Box:Daily max global radiation	77	**0**	**1**	5.9	0.05

(:) Indicates interactions between variables.
(+) Indicates additive effects.

3 | RESULTS

3.1 | Spatiotemporal representation of box microclimate

In the REF box, we recorded a minimum temperature of 12°C and a maximum temperature of 52°C. Mean T_{box} was 25–26°C for all designs (Table S1 in the Supporting Information), but there was substantial spatiotemporal variation within and across designs that can be visualized via heat maps (Figure S1 in the Supporting Information). On 4 July 2018, a sunny (G_{max} = 944 W/m^2) and warm ($T_a$max = 35°C) day, the entire REF box was coolest before 1000 h and warmest in the evening, 1800–1900 h (Figure 2). On this day, top and middle zone temperatures began to rise above T_a in late morning and by late afternoon the top zone of the box was in the T_{STRS} category (≥40°C; Figure 2), with the warmest temperatures on the west side. Top-zone iButtons accounted for 96.5% of heat stress observations across our entire dataset. The patterns observed in the REF design were repeated across most of the

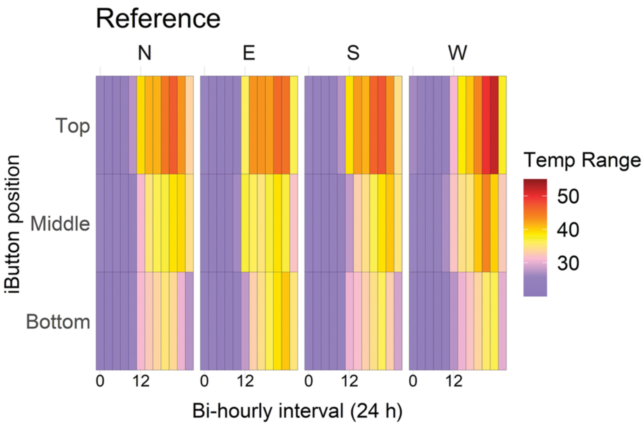

FIGURE 2 Heat map detailing bihourly temperatures recorded by 12 iButton temperature data loggers in a reference rocket-style bat box (REF) on 4 July 2018. On this day, $T_a$max was 35°C, daily wind speed max was 12.5 m/s and daily global radiation max was 944 W/m^2. Each block represents the temperature at the iButton position in the middle of that zone (top, middle or bottom) on each side of the box (N, E, S or W)

other designs on a warm, sunny day, but with noticeable variability in the occurrence of stressful temperatures in the top zone (Figure S1).

3.2 | Effects of box design and environmental variables on counts of cool, permissive and stressful temperatures

For both daytime and nightly counts of T_{PERM}, Model P5 was the only plausible model (Table 2). Some box designs were significantly different from the REF, and interactions with all three environmental variables were significant. For 11 designs, daytime counts of T_{PERM} were significantly lower than in the REF design; however, for the LONG and VR designs, counts were significantly higher (Figure 3a; Table S2 in the Supporting Information). Wind negatively affected daytime counts of T_{PERM} and daily T_{a}max and solar radiation had positive effects (Table S2). For the SHORT design, there was a significant negative effect of wind; while the SHORT design always had fewer daytime counts of T_{PERM} than the REF, on very windy days counts of T_{PERM} were even lower than expected in the SHORT design (Figure 3b). Compared to the REF design, on days when T_{a}max was <33°C, counts of T_{PERM} were higher in the LONG and VR designs and lower in 11 other designs (Figure 3a). However, on the warmest days (>33°C), most designs had T_{PERM} counts similar to the REF, but counts were lower in the LONG and VR designs (Figure 3a).

Compared to the REF, nighttime counts of T_{PERM} were significantly higher in the COMP and EJW designs and significantly lower in the HR design (Table S3 in the Supporting Information). Wind speed and daily T_{a}max had negative and positive effects, respectively, on nighttime counts of T_{PERM}. On days >29°C, the EJE, EJW and COMP designs had higher nighttime counts of T_{PERM} than the REF, with the most pronounced effect in the EJW design (Figure 4a). While the EJW and EJE generally had more nighttime counts of T_{PERM} than the REF design, the difference was greater than expected on nights following days with solar radiation >800 W/m^2 (Figure 4b).

For nighttime T_{COOL}, Model C3 was most plausible, but the ΔAICc for Model C5 was 2.1 (Table 2). In both models T_{a}max was a significant factor, and in Model C5 the interaction between box design and T_{a}max was significant. Counts of nighttime T_{COOL} were significantly higher in the EJW design compared to the REF design (Table S4 in the Supporting Information), but this effect varied with daytime air temperatures. Following cool days (<25°C), the EJW design had higher counts of T_{COOL} than the REF design (Figure 5; Table S4) due to the greater thermal inertia of the EJW design. Increasing T_{a}max negatively affected counts of nighttime T_{COOL} for all designs (Table S4); however, and on days when T_{a}max was >25°C the EJW had significantly fewer nighttime counts of T_{COOL} than the REF design (Figure 5).

Model S5 was the only plausible model explaining daytime counts of T_{STRS} (Table 2). For the EJW, HR, and SRS designs, daytime counts of T_{STRS} were significantly lower than in the REF design; this effect was most pronounced for the HR design (Table S5 in the Supporting Information). Both daily T_{a}max and global radiation had positive effects on daytime counts of T_{STRS}, particularly on days with higher than average values for these two environmental variables (Figure 6a,b). However, six designs buffered the effects of T_{a}max (Figure 6a) and three designs buffered the effects of global radiation (Figure 6b). The SHORT and WG designs buffered both T_{a}max and global radiation such that on warm, sunny days both designs had lower counts of daytime T_{STRS} than the REF. The LONG and VR designs always had higher daytime counts of T_{STRS} than the REF design, but this difference was most pronounced on days with wind >10 m/s due to lower air circulation in these two designs compared to the REF (Figure 6c).

In total, we observed only 83 total counts of T_{STRS} at night, which likely explains why the T_{STRS} night models did not converge (Table S6 in the Supporting Information). For the T_{COOL} day scenario, box design was not important and there were no significant interaction effects. However, daytime counts of T_{COOL} were positively affected by wind speed and negatively affected by daily T_{a}max (Table S7 in the Supporting Information).

4 | DISCUSSION

We compared the microclimates in 20 different bat box designs, most of which varied only slightly from our REF design. Ours is the most comprehensive study of bat box microclimates to date and sheds light on how small changes to box design can affect box suitability as roosting habitat for a maternity colony of bats. We showed that it is possible to increase daytime and nighttime counts of T_{PERM} by adding an external jacket, decreasing ventilation or increasing volume. Critically, adding an external water jacket was the only modification we tested that decreased counts of T_{COOL} at night, but this was true only on days reaching >25°C. Finally, we showed that T_{STRS} counts were driven up by warmer and sunnier conditions outside, but these effects were lessened by changes to the solar conditions of the box, adding ventilation

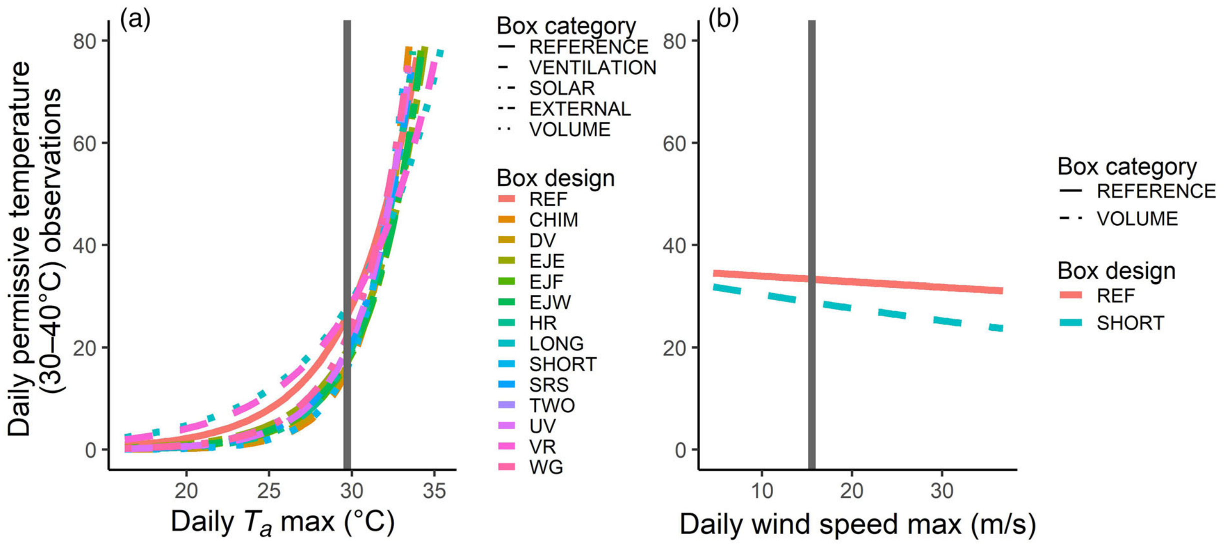

FIGURE 3 Negative binomial fit line graphs of observations of daily permissive temperatures (30.1–39.9°C, rounded in figure) in bat box designs (see Table 1) with responses significantly different from a reference rocket-style bat box design (REF) with respect to (a) daily $T_a$max (°C) and (b) daily wind speed max (m/s). Vertical grey lines indicate mean daily maximum for each environmental variable

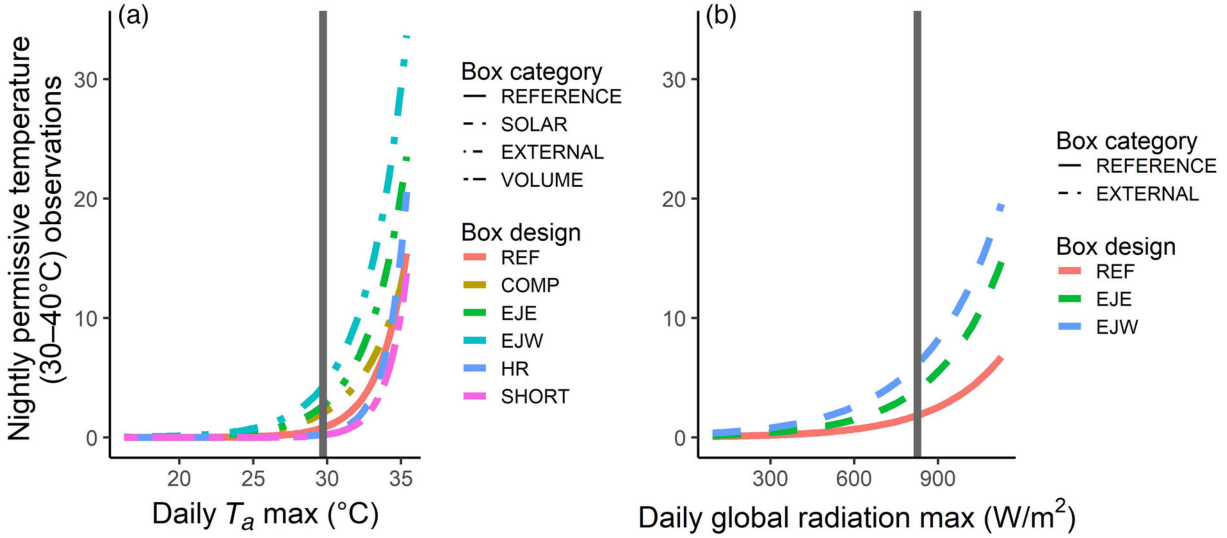

FIGURE 4 Negative binomial fit line graphs of nightly permissive temperature (30.1–39.9°C, rounded in figure) observations in bat box designs (see Table 1) with responses significantly different from a reference rocket-style bat box design (REF) with respect to (a) daily $T_a$max (°C) and (b) daily global radiation max (W/m^2). Vertical grey lines indicate mean daily maximum for each environmental variable

or external jackets or decreasing volume. Together our results suggest that even without changing box colour, which has been tested in many prior bat box studies, making slight changes to structural aspects of design can have a significant impact on a box's suitability as bat maternity habitat.

Previous work attempting to enhance bat boxes for bats has largely focused on changing box colour (e.g. Doty et al., 2016; Griffiths et al., 2017; Lourenço & Palmeirim, 2004) or compared designs so different that it was impossible to isolate significant factors affecting box microclimate (e.g. Hoeh et al., 2018; Martin Bideguren et al., 2018); but see four material × colour combinations in Rueegger (2019) and vertical versus horizontal boxes in Brittingham and Williams (2000). However, in this study, we systematically changed ventilation, external mass, shading or volume of boxes and, in doing so, we identified modifications that significantly impacted counts of T_{PERM} (30.1–39.9°C). Reproductive bats facing high energetic costs from pregnancy and lactation may seek out roosts with temperatures in the T_{PERM} range to limit metabolic costs (Sedgeley, 2001). Simply lengthening the REF box by 50% to make the LONG design enhanced T_{PERM} counts and likely provided optimal conditions for bats because it supported a larger vertical thermal

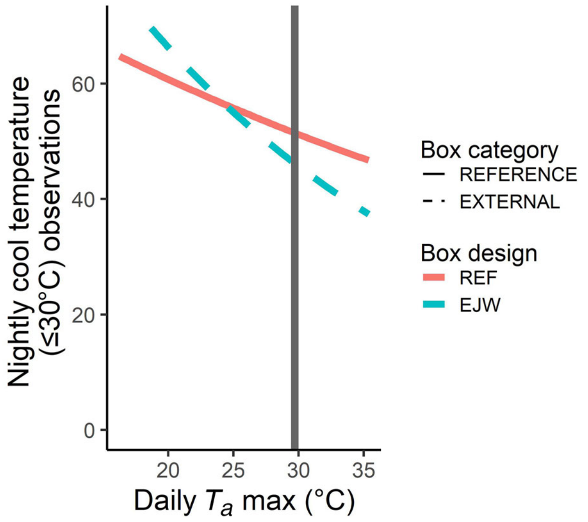

FIGURE 5 Negative binomial fit line graph of nightly cool temperature (≤30°C) observations in reference (REF) and water jacket (EJW) style design, which showed significantly different responses to daily $T_a$max (°C). Vertical grey line indicates mean daily maximum for T_a

gradient (Table S1 in the Supporting Information). Brittingham and Williams (2000) observed that a 76-cm tall box displays a vertical temperature gradient as much as 3.3°C greater than the gradient in a 26-cm tall box. Removing the vents (VR) also enhanced counts of T_{PERM}, but because this design had higher T_{STRS} counts when wind speeds were low (Figure 6a) and has the same volume as the REF design, it is not an improvement over the REF design.

All box designs cooled quickly at night but adding an external jacket (EJW and EJE) yielded higher nighttime counts of T_{PERM} after warm or sunny days (Figure 3). Furthermore, after a moderately warm day (reaching ≥25°C), the EJW was the only design that retained enough heat at night to significantly reduce nighttime counts of T_{COOL} (Figure 3). G.S. Bakken (unpublished data, 2018) found that metabolic costs are lower for an endothermic bat using the EJW due to this thermal phase lag and found this design has an added benefit of reducing the risk of pup mortality from lethally hot temperatures at the top of the box. Following work showing the benefits of heated bat boxes (Wilcox & Willis, 2016), we conceptualized the external jacket design for this study with the goal of enhancing roosting habitat for bats with higher energetic demands, such as bats in the early stages of reproduction or those recovering from white-nose syndrome. Our results suggest there is merit in experimenting more with thermal phase lag designs

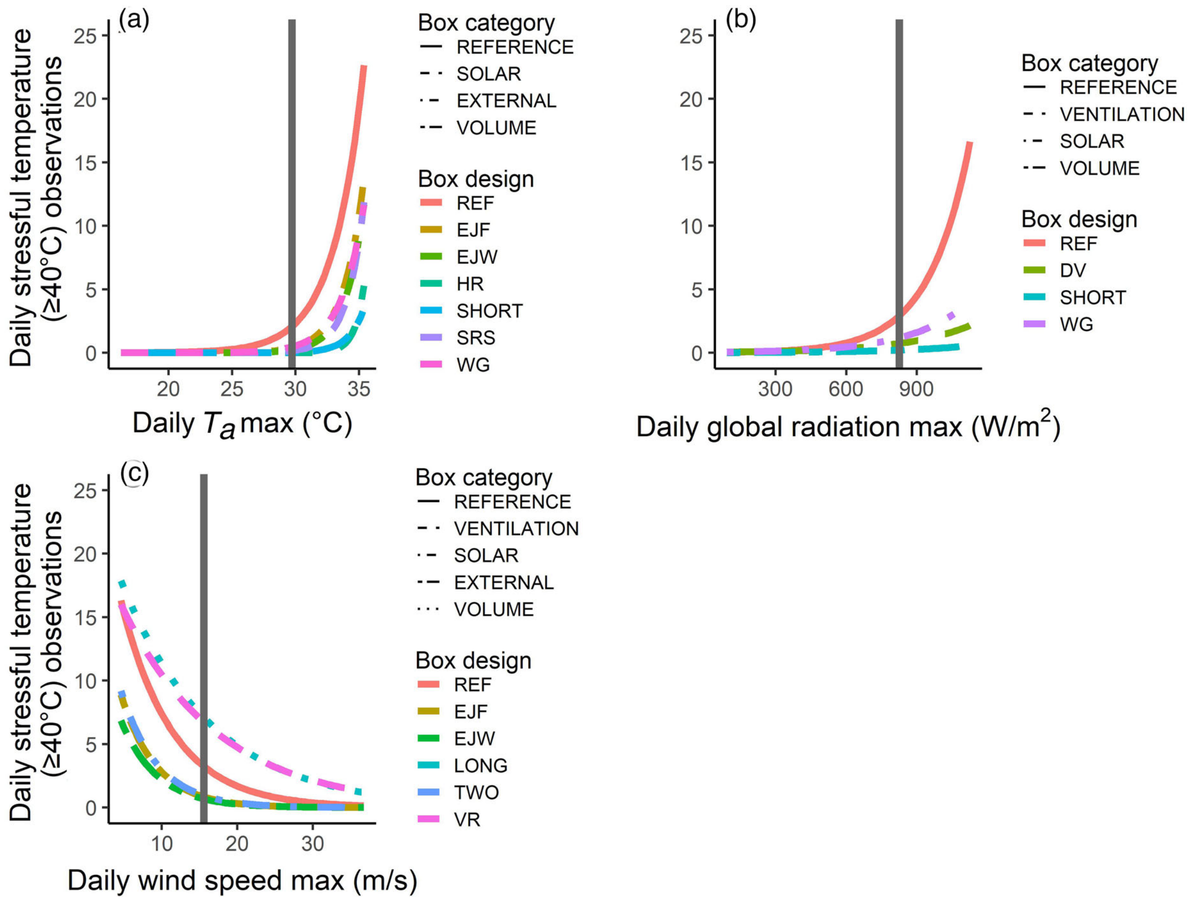

FIGURE 6 Negative binomial fit line graphs of daily stressful temperature (≥40°C) observations in bat box designs (see Table 1) with responses significantly different from a reference rocket-style bat box design (REF) with respect to (a) daily $T_a$max (°C), (b) daily global radiation maximum (W/m^2), and (c) daily wind speed maximum (m/s). Vertical grey lines indicate mean daily maximum for each environmental variable

and colour × design combinations that optimize roost microclimates for bats.

A concern raised repeatedly in the recent literature is that bat boxes are potentially dangerous because of the risk that occupants will overheat (e.g. Alcalde et al., 2017; Crawford & O'Keefe, 2021; Flaquer et al., 2014; Griffiths, 2021; Martin Bideguren et al., 2018). Increasing temperatures and more frequent heat waves driven by climate change could heighten the risk, elevating T_{STRS} counts in bat boxes. We suspect overheating is a risk for which bats are ill-prepared, as the natural tree roosts to which they are adapted have greater heat storage capacity and, hence, should be less prone to overheating; further, tree cavities are more shielded from external conditions and sun, while patches of sloughing bark on a tree trunk should have more ventilation than a typical bat box. Painting bat boxes white or light colours will reduce overheating risks (Griffiths et al., 2017; Martin Bideguren et al., 2018), but light-coloured boxes are not the optimal solution for maternal females in temperate climates, as such roosts may be too cool when outside conditions are cool or cloudy. While we know extremely dark boxes often overheat relative to other colours (Crawford & O'Keefe, 2021; Martin Bideguren et al., 2018), even using medium brown paint (as in this study) was not sufficient to eliminate overheating risk. Design modifications are also critical to reducing overheating. Of the designs we tested, the EJW, WG and LONG will likely be most effective at reducing the risk of overheating while also providing 'permissive' conditions that allow maternal females to save energy and that facilitate pup development during pregnancy and lactation. The LONG design will still have T_{STRS} conditions at the top but offers sufficient space that a colony of bats should be able to move around to avoid lethally hot temperatures.

We acknowledge that gathering temperature data for the internal chambers would provide a more comprehensive understanding of the suitability of different designs to bats. Rueegger (2019) showed that a black four-chamber box averages about 4°C warmer in the chamber facing the sun versus the most interior chamber. It is possible that the inner chamber of our rocketbox designs provided suitable conditions even when the outer chamber overheated, though Rueegger's (2019) work shows that the difference between chambers might be only a few degrees. Allowing bats access to the designs we tested could enhance the suitability of bat boxes on cool or cloudy days as a group of only eight normothermic bats substantially amplifies roost temperature (Pretzlaff et al., 2010). Likewise, however, a group of bats could also elevate overheating risk in an already hot bat box on warm, sunny days. A rocketbox can hold >200 Indiana bats (Hoeh et al., 2018); such a mass of warm bodies could increase roost temperatures from stressful to lethal on hot days when bats are normothermic.

We compared the internal temperatures of 20 different bat boxes and found that, while each of the designs provide livable temperatures for bats, the temperatures in each box responded differently, when compared to a reference rocket style box, to environmental variables. Simple modifications to box volume, airflow, shading and heat capacity had significant effects on the available temperatures within a box. We recommend use of bat boxes that maximize permissive temperatures and that reduce overheating risk via design modifications and suggest placing boxes in different microhabitats (i.e. full shade, partial sun and full sun) to meet the changing energetic demands of reproductive bats across the maternity season. Our work highlights the importance of considering environmental conditions (air temperature, global radiation and wind speed) when designing and installing bat boxes. Furthermore, we contribute easily implementable box design modifications that can improve roost suitability for bats.

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CONFLICT OF INTEREST

The authors will not receive a direct financial benefit from this publication and have no conflict of interest to declare. Our funding agency is acknowledged below.

AUTHORS' CONTRIBUTIONS

FET, GSB, and JMO conceived the research. FET collected data, did the analyses, and wrote the paper with JMO and input from GSB. All authors approved the final publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data from this study are publicly available and stored in the Illinois Data Bank at the University of Illinois at Urbana-Champaign: https://doi.org/10.13012/B2IDB-7904190_V1 (Tillman et al., 2021).

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SUPPORTING INFORMATION

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