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Too hot or not? The influence of colour and material on temperature and relative humidity in flat, single-chambered bat boxes in the Netherlands

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Published: 15 November 2020

Abstract: Bat boxes have become the most popular compensation and mitigation measure in the last few decades and large numbers are being sold by specialized companies. Although bats seem to prefer warm bat boxes, in particular maternity colonies, overheating in southern countries is becoming a problem under the influence of climate change. Literature with regards to this subject in the Netherlands is scarce but there are indications that overheating of bat boxes might also occur in this country. Therefore this study aimed to get more insight into the microclimate of single-chambered, flat bat boxes that can serve as summer or mating roosts. At two locations near Borculo and Neede, the Netherlands, black and wood-coloured woodcrete, Douglas wood and plywood bat boxes were placed on poles. With the help of data loggers, temperature and relative humidity were measured in these unoccupied bat boxes for 90 days during the summer of 2019. Bat box colour significantly influenced daily temperature response variables and also daily minimum bat box relative humidity. Also daily fluctuation of temperature and relative humidity within a bat box were influenced significantly by bat box colour. Bat box material only significantly influenced relative humidity response variables. Wood-coloured bat boxes reacted more slowly to changes in ambient microclimate than black bat boxes. In particular woodcrete bat boxes had a higher buffer capacity of ambient circumstances than bat boxes from Douglas wood and plywood. Although all models experienced overheating (bat box temperature >= 40 ºC), wood-coloured bat boxes were found to encounter significantly less (70,6%) overheating events than black bat boxes. Material did not have a significant effect on the number of overheating events. Nonetheless, the black Douglas wood and black plywood bat box had a lower ambient-temperature-threshold for causing overheating (20,5 ºC) than the black woodcrete bat box (27 ºC). The lower this threshold, the sooner a bat box experienced overheating. This threshold was highest for all wood-coloured bat boxes (32,5-33,5 ºC). Dark-coloured, single-chambered bat boxes can rapidly experience overheating when exposed to direct sunlight; at such locations light-coloured bat boxes are recommended. The risk of fatal overheating events occurring in the Netherlands will likely increase due to climate change and should not be underestimated, therefore overheating should be included as a subject in new guidelines for choosing and placing bat boxes. When selecting and placing bat boxes, a situation-dependent approach is recommended, taking local microclimate and environment into account.

Keywords: bat box, microclimate, temperature, relative humidity, overheating.

1. Introduction

Because of the lack of guidelines, monitoring and knowledge of bat boxes, their efficiency as a replacement for natural roost sites is still relatively unknown and probably limited (Collins et al., 2020; Griffiths et al., 2020; Berthinussen et al., 2019; Dekker & Korsten, 2019; Michaelsen, 2016; Korsten, 2012; Whitaker et al., 2006; Kerth et al., 2001). Occupancy rates (for different species) vary greatly; rates as low as 14% in summer were found in the Netherlands (Boerrigter et al., 2011). But also rates as high as 40-95% during the breeding season have been reported in the Czech Republic and Spain (Chytil, 2014; Flaquer et al., 2005). Internal bat box microclimate is known to play a big part in influencing these occupancy rates (Shek et al., 2012; Fukui et al., 2010).

Bats, in particular maternity colonies, seem to prefer warm bat boxes that receive many hours of direct sunlight (Brittingham & Williams, 2000). But bats also seem to have a thermal limit of 40 degrees Celsius, a temperature located above their thermal neutral zone (Dillingham et al., 2003; Bonaccorso et al., 1992). Overheating events in bat boxes with temperatures of more than 40 ºC have been reported in arid areas. Bartonička and Řehák (2007) from the Czech Republic report that bat boxes with temperatures above 40 ºC were unoccupied. In 2008, a maternity colony of 42 individuals of soprano pipistrelle (*Pipistrellus pygmaeus*) was found dead inside a bat box in Spain without explanation. In 2013, 22 bats were observed falling out a west-facing bat box surrounded by trees at the same location in late afternoon (Flaquer et al., 2014). Similar events were reported in Australia (O'Shea et al., 2016) where bat boxes, designed to improve bat populations, turned into death traps.

Since bats rarely leave their roost during daytime, unable to drink water, relative humidity might also be an important factor for bat box success (Rueegger, 2019; Boerrigter et al., 2011; Bartonička & Řehák, 2007; Sedgeley, 2001). Bartonička and Řehák (2007) even found in their models that internal relative humidity was a better predictor for bat numbers in bat boxes during pregnancy and lactation than was internal temperature, although it was unclear if bat respiration was an influencing factor. Because of their morphology, bats lose much water though their respiratory system and wing membrane (Russo & Ancillotto, 2015; Thomas & Cloutier, 1992). Webb et al. (1995) mentioned that relative humidity directly influenced evaporative water loss in brown long-eared bats (*Plecotus auritus*) and Daubenton's bat (*Myotis daubentonii*). Still, Kurta (2014) emphasizes that evaporative water loss cannot be predicted only by relative humidity and recommends using the absolute values of humidity instead of relative humidity as well as the bat's body temperature. Although poorly investigated (Mering & Chambers, 2014), it seems that most bat boxes lack the ability to retain moisture and have a low relative humidity overall compared to ambient circumstances (Boerrigter et al., 2011) and so they insufficiently mimick natural roosts (Rueegger, 2019; Wieser et al., 2018).

There are indications that even in a country with a temperate climate like the Netherlands bat boxes can reach temperatures as high as 53 ºC (J. Beijk, personal communication, March 6, 2019). However, literature regarding this subject in the Netherlands, where all species of bats and their roosts are protected by European legislation (Habitats Directive)(RVO, 2019), is practically absent. Accordingly, this research aims to investigate the basic effects of colour and material on microclimate in unoccupied, single-chambered, flat bat boxes under influence of Dutch climate. Bat boxes made of woodcrete, Douglas wood and plywood painted in black and wood colour were tested. Consequently, the following research questions were formulated:

What is the influence of colour and material on temperature and relative humidity in flat, single-chambered summer bat boxes in the Netherlands?

- What is the influence of bat box colour and material on daily maximum, (daytime) mean and minimum bat box temperature and relative humidity?
- What is the influence of bat box colour and material on the daily fluctuation of temperature and relative humidity within a bat box?
- How do the bat boxes buffer ambient circumstances?
- What are the influences of bat box colour and material on the number of overheating events?

It is expected that black bat boxes have highest daily mean, minimum and maximum temperature and number of overheating events (Bideguren et al., 2018). Darker colours absorb more radiation which is converted into heat (Lourenço & Palmeirim, 2004). Due to the high specific density of woodcrete (Van der Wijden et al., 2014), woodcrete bat boxes are expected to have better moisture-retaining capabilities and thus higher daily maximum, mean and minimum relative humidity than plywood and Douglas wood bat boxes. Higher solar radiation absorbance is thought to result in lower bat box relative humidity (Rueegger, 2019). Wood-coloured plywood, Douglas wood and woodcrete bat boxes are therefore expected to have higher relative humidity than black bat boxes of the same materials. Woodcrete bat boxes are known for having better buffer capacity compared to regular wood (Van der Wijden et al., 2014; Korsten, 2012). Therefore it is expected that woodcrete bat boxes have the least daily fluctuation of temperature and relative humidity within a bat box and have the highest buffer capacity of ambient circumstances of all studied bat box materials. Woodcrete bat boxes are expected to have less overheating events than plywood bat boxes based on anecdotal evidence (J. Beijk, personal communication, March 6, 2019).

2. Materials and methods

2.1 Study sites

To reduce the effect of spatial autocorrelation (Lee, 2017), bat boxes were placed at two study sites (N 52° 8' 16.70" E 6° 30' 57.82" and N 52° 8' 32.369" E 6° 36' 34.32") near Borculo and Neede, Berkelland municipality, Gelderland province, The Netherlands (see Figure 1). These sites were selected based on accessibility for placement and monitoring of the bat boxes, openness for sunny conditions and privacy because of the possibility of vandalism. The bat boxes were placed in three clusters of six where each cluster contained a bat box of each colour/material-combination. Study site A contained one cluster of bat boxes (cluster 1) in grassland (2.260 m^2) that was surrounded by large trees on the northeastern side. These trees had no shadow effect on the bat boxes. Study site B contained two clusters of bat boxes (cluster 2 and 3) in grassland (13.000 m^2) that was surrounded by corn fields on the northern and western side.
Under the influence of a temperate maritime climate (Köppen climate classification: Cfb), average annual temperature is 9,5 ºC and precipitation is 768 mm (Climate-Data, 2019). Borculo is located at an altitude of 14 meters above sea level on sandy soil.

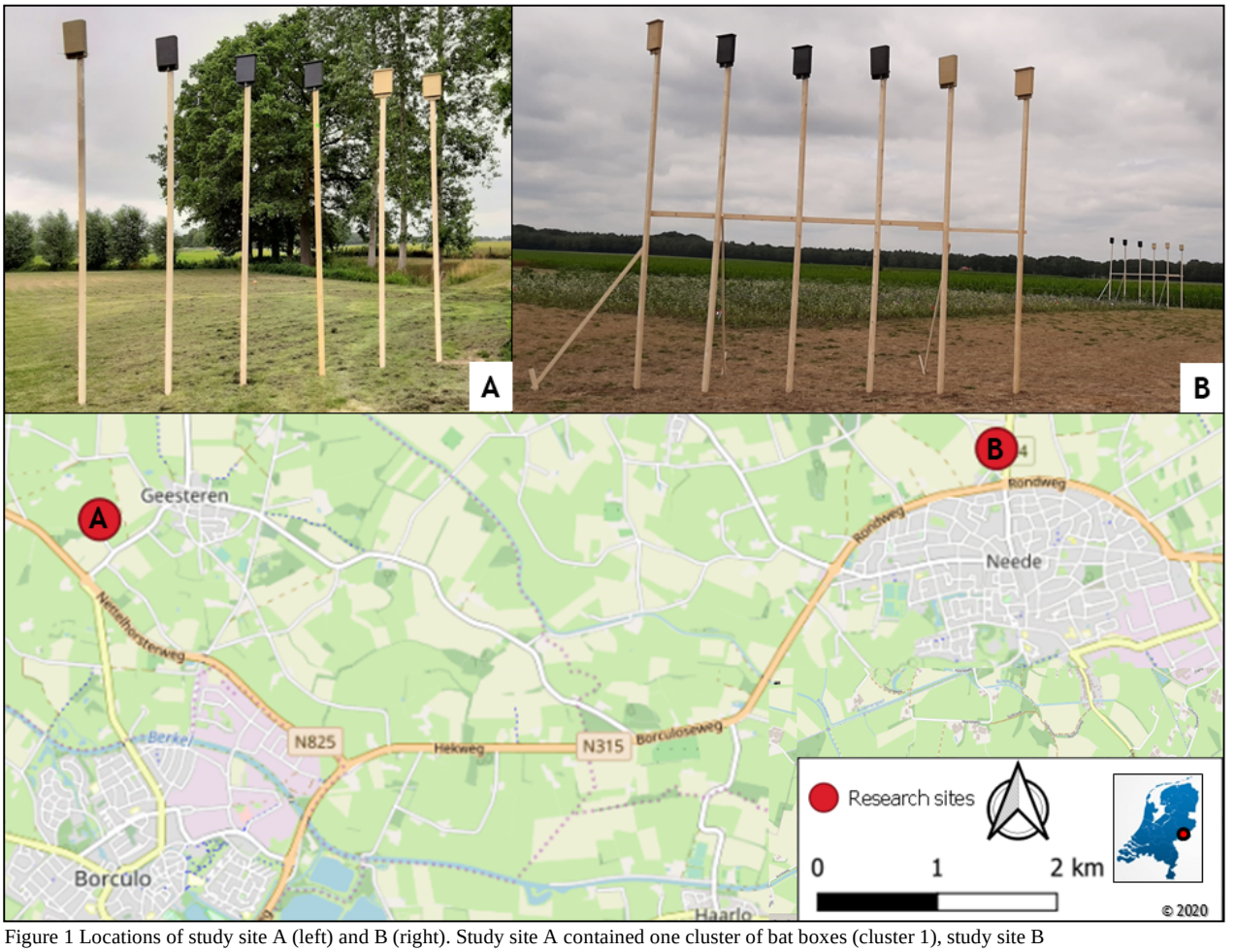

Figure 1 Locations of study site A (left) and B (right). Study site A contained one cluster of bat boxes (cluster 1), study site B two clusters (cluster 2 and 3).

2.2 Bat boxes

Flat, single-chambered bat boxes of different colours and materials were installed. According to Korsten (2012), the type of bat boxes used in this study (small, flat) can function as summer and mating roost for the following species: common pipistrelle (*Pipistrellus pipistrellus*), Nathusius' pipistrelle (*Pipistrellus nathusii*) and brown long-eared bat. Bat boxes were fabricated from woodcrete (15 mm thick), plywood (15 mm thick) and Douglas wood (18 mm thick). The single-chambered woodcrete bat box is a commercial, flat-type model that was used as a template for the other two self-fabricated types (see Figure 2). Inner chamber dimensions of the woodcrete bat box were 32 cm (height) x 23 cm (width) x 2,5 cm (depth). Subsequently, the other two types were fabricated with identical inner chamber dimensions containing the same air volume (Hoeh et al., 2018; Boerrigter et al., 2011). Normally, the chamber of the template bat box is open at the bottom. Bats can enter it and faeces and parasites like bat bugs fall from the bat box (Brittingham & Williams, 2000). However, because bats influence bat box microclimate with their presence (respiration)(Bartonička & Řehák, 2007; Willis & Brigham, 2007), chamber openings of the bat boxes were covered with mesh (size 1,5 mm) during this study. Using this method, normal airflow was still possible but occupation by bats and insects like wasps was prevented. (Hoeh et al., 2018; Fukui et al., 2010). No additional ventilation was present or added. To reduce a possible effect of the paint on microclimatic conditions compared to potential non-painted bat boxes, all studied bat boxes were painted (Larson et al., 2018). The colours black (RAL 9005: Jet Black matt) and wood colour (RAL 1001: Beige matt) were chosen because commercial models are often painted black or remain unpainted (wood colour). All bat boxes were weatherproof (Korsten, 2012; Whitaker et al., 2006; Zoogdiervereniging, s.d.).

Bat boxes were placed on wooden (pine) poles. Poles were chosen instead of walls and trees because heat absorption from walls and canopy cover from trees could have an influence on bat box microclimate (Mering & Chambers, 2014; Korsten, 2012; Flaquer et al., 2005). Without canopy cover from nearby trees surrounding the poles, direct sunlight was assured. The sequence of bat boxes within a cluster was selected randomly. But poles were placed 1 meter from each other so there was no shadow effect between bat boxes. To achieve the maximum quantity of sun hours and consequently the highest effect of sunlight, bat boxes were placed to face a southern exposition (Bideguren et al., 2018). The bat boxes were installed 4 meters above ground level, corresponding with the vertical space bats ideally need to emerge from their roosts (Hoeh et al., 2018; Baucells et al., 2016; Mering & Chambers, 2014; Chytil, 2014; Korsten, 2012; Baranauskas, 2010; Zoogdiervereniging, s.d.).

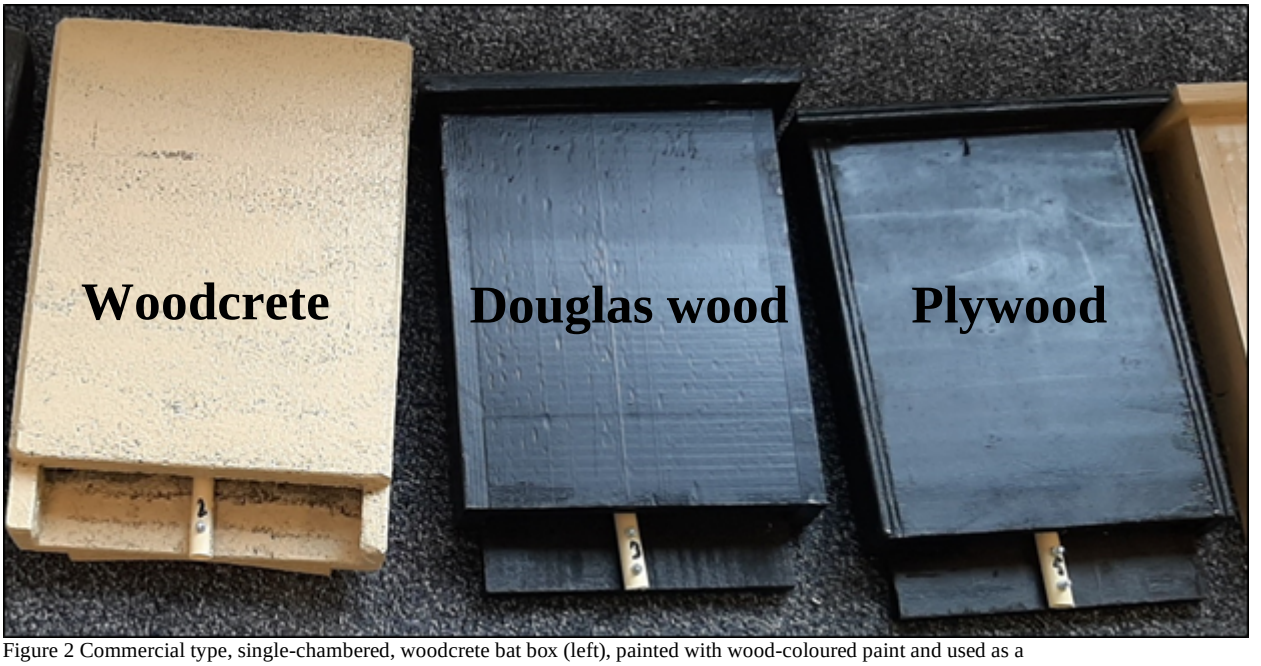

Figure 2 Commercial type, single-chambered, woodcrete bat box (left), painted with wood-coloured paint and used as a template for the Douglas wood (middle) and plywood (right) types.

2.3 Data loggers

For measuring bat box temperature and relative humidity, data loggers were placed inside the inner chambers of the bat boxes (see Figure 3). Because of the relatively small size of the inner chamber, each bat box contained one Lascar Easylog EL-USB 2 data logger. Loggers recorded with an interval of one measurement every 30 minutes and the loggers' internal resolution was 0,5 °C/0,5% RH with an accuracy of ±0.3 °C/±2% RH. Measuring with this specific interval assured sufficient battery longevity during data collection. This was important because the bat boxes were very hard to reach if batteries were needed to be replaced. Using an interval of 30 minutes compared to measuring only once an hour decreased the chance of missing extreme values. The loggers were mounted on a 16 mm PVC dowel (see Figure 3) so that the sensor was placed 8 cm below the roof of each bat box (Rueegger, 2019; Griffiths et al., 2017). Because of the shape of the loggers, the sensor did not touch the wall of the bat boxes (Lourenço & Palmeirim, 2004).
To be able to compare inside and ambient circumstances, indicating buffer capacity of the bat boxes, one logger was placed in each cluster on the back of one of the middle bat boxes. These particular loggers faced north (Griffiths et al., 2017). Before loggers were placed, each one had new, tested batteries to reduce chances of failure during sampling. Sampling took place continuously for 90 days during mid-July, August, September and the first half of October, 2019.

Figure 3 Each PVC dowel with logger was incorporated in the bat box and was mounted to the bat boxes with screws (left). To measure ambient microclimate, each cluster was provided with a north-facing data logger attached to one of the middle bat boxes (right).

3. Data preparation

After extracting data from the loggers, it became clear that 4 of the 21 (19%) loggers had not functioned properly. Two data loggers in Douglas wood bat boxes in cluster 2 and two data loggers that measured ambient circumstances in cluster 2 and 3 failed due to water leakage. Therefore only ambient temperature and relative humidity data from study site A were obtained. Data derived from failed data loggers were omitted from the total dataset. The total dataset was further trimmed down by omitting data from the first three sampling days after placement. Doing this, bat box microclimate had time to settle. This finally resulted in a dataset of 90 sampling days (18 July 2019 – 15 October 2019).
The number of overheating events (Tbox>=40 ºC) for each bat box type were counted (Bideguren et al., 2018). Afterwards, the dataset was imported into SPSS 25.
Data was aggregated with bat box number, date_number, cluster (to determine if there was a location-effect), colour and material as break variables. Aggregated (response) variables for each sampling day were maximum, mean and minimum bat box temperature and relative humidity (TboxMAX, TboxMEAN, TboxMIN, RHboxMAX, RHboxMEAN and RHboxMIN).
A separate, aggregated dataset with the same break and computed variables as the main dataset was created to test the effect on daytime values for daily mean bat box temperature and relative humidity (TboxMEANDAY and RHboxMEANDAY)(Griffiths et al., 2017).
Finally, two new response variables were computed to test the effect on the daily fluctuation of temperature and relative humidity within a bat box: TboxMAX-TboxMIN and RHboxMAX-RHboxMIN (Rueegger, 2019; Griffiths et al., 2017).
Logger measurements were divided into day and night measurements, using sunset and sunrise data from the The Royal Netherlands Meteorological Institute (KNMI, 2019). All response variables included daytime and nighttime values combined except for daily mean daytime bat box temperature and relative humidity.

4. Data analysis

To determine the effect of bat box colour and material on temperature and relative humidity response variables, for each response variable, a first order autoregression (AR-1) Linear Mixed Model (LMM) was fitted. LMM were chosen because dependent variables were normally distributed, multiple measurements took place from the same bat box (no independent data) and there were multiple bat boxes in each cluster (Fox, 2002). Subjects were cluster and bat box number, with date_number as repeated variable. Fixed effects were colour, material, cluster and their interactions. To achieve the best models, fixed effects were omitted stepwise until lowest corrected Akaike Information Criterion (AICc) was accomplished (Vrieze, 2012). Afterwards, models were validated (e.g. normality of residuals)(Steibel et al., 2009). Since there was a significant effect from cluster on multiple response variables (location-effect), ambient data (only available for one of the two study sites) were not used for statistical analysis.
To test the effect of colour and material on the number of overheating events, a Generalized Estimating Equation (GEE) with a negative binomial distribution was fitted to account for dependency of measurements within a cluster (Cui & Feng, 2008). Subject was cluster and within-subjects were colour and material.
Significance was assessed at α=0,05 and results are presented as Estimated Marginal Mean ± SEM.

5. Results

5.1 General

Due to data logger failure, a reduced number of in total 69.120 measurements were recorded for 16 bat boxes and 4320 measurements for ambient circumstances at study site A. Lowest recorded temperature was 1,5 ºC in a wood-coloured plywood and wood-coloured Douglas wood bat box in cluster 1. Highest recorded temperature was 51,5 ºC in a black plywood bat box in cluster 1. The maximum recorded temperature in a black Douglas wood bat box was 51,0 ºC. Black woodcrete bat boxes never exceeded 50ºC with a maximum of 47,5 ºC. Both bat boxes were located in cluster 1. Lowest recorded relative humidity was 18,0% in a black plywood bat box. The highest recorded relative humidity was 107,0% in a black woodcrete bat box. Again, both bat boxes were located in cluster 1. Ambient temperatures ranged from 2,5 ºC to 44,5 ºC. Ambient relative humidity ranged from 19,0% to 105,5%.

5.2 Influence of bat box colour and material on temperature and relative humidity response variables

For comprehending which independent variables were included in the best models for each temperature and relative humidity response variable, see Table 1.

Table 1 Fitted Linear Mixed Models (LMM) for each temperature and relative humidity response variable. Significant effects of independent variables and their interactions on response variables are marked with an asterisk (*).

Category	Response variable	Independent variable	p-value
Temperature	Daily maximum bat box temperature (TboxMAX)	Colour	<0.001*
		Cluster	<0.001*
	Daily mean bat box temperature (TboxMEAN)	Colour	0.147
	Daily mean daytime bat box temperature (TboxMEANDAY)	Colour	0.012*
	Daily minimum bat box temperature (TboxMIN)	Cluster	0.053
	Daily temperature fluctuation within a bat box (TboxMAX-TboxMIN)	Colour	<0.001*
		Cluster	<0.001*
Relative humidity	Daily maximum bat box relative humidity (RHboxMAX)	Material	0.038*
		Cluster	0.120
	Daily mean bat box relative humidity (RHboxMEAN)	Material	0.004*
	Daily mean daytime bat box relative humidity (RHboxMEANDAY)	Material	<0.001*
		Colour * Material	0.043*
	Daily minimum bat box relative humidity (RHboxMIN)	Colour	0.010*
		Material	<0.001*
		Colour * Material	0.022*
	Daily relative humidity fluctuation within a bat box (RHboxMAX-RHboxMIN)	Colour	<0.001*
		Material	<0.001*
		Cluster	<0.001*
		Colour * Material	0.005*
		Cluster * Colour	<0.001*
		Cluster * Material	0.007*

5.2.1 Daily maximum bat box temperature (TboxMAX)

Black bat boxes had a significantly higher daily maximum temperature (27,980±0,514)($F(1,140)=16,542$, $p<0.001$) than wood-coloured bat boxes (25,050±0,514).
Bat boxes in cluster 1 had significantly higher daily maximum temperature (28,507±0,588) than bat boxes in cluster 2 (25,583±0,720)($F(2,140)=8,140$, $p=0.006$) and bat boxes in cluster 3 (25,455±0,588)($F(2,140)=8,140$, $p=0.001$). Daily maximum bat box temperatures between cluster 2 and 3 did not differ significantly ($F(2,140)=8,140$, $p=0.999$).

5.2.2 Daily mean bat box temperature (TboxMEAN)

Although black bat boxes had a higher daily mean temperature (19,042±0,462) than wood-coloured bat boxes (18,082±0,462), this difference was not significant ($F(1,65)=2,158$, $p=0.147$).

5.2.3 Daily mean daytime bat box temperature (TboxMEANDAY)

Black bat boxes had a higher daily mean daytime temperature (21,960±0,458) than wood-coloured bat boxes (20,303±0,458), this difference was significant ($F(1,99)=6,542$, $p=0.012$).

5.2.4 Daily minimum bat box temperature (TboxMIN)

Although bat boxes in cluster 2 (12,536±0,368) and cluster 3 (12,687±0,300) had a higher daily minimum temperature than bat boxes in cluster 1 (11,702±0,300), this difference was not significant ($F(2,125)=3,012$, $p=0.053$).

5.2.5 Daily temperature fluctuation within a bat box (TboxMAX-TboxMIN)

Within black bat boxes, there was a significantly higher daily temperature fluctuation (15,672±0,390)($F(1, 227)=28,449$, $p<0.001$) than within wood-coloured bat boxes (12,756±0,390).

Bat boxes in cluster 1 had significantly higher daily temperature fluctuation (16,839±0,446) than bat boxes in cluster 2 (13,038±0,547)($F(2,227)=24,731$, $p<0.001$) and bat boxes in cluster 3 (12,765±0,446)($F(2,227)=24,731$, $p<0.001$). Daily temperature fluctuation between bat boxes in cluster 2 and 3 did not differ significantly ($F(2,227)=24,731$, $p=0.973$).

5.2.6 Daily maximum bat box relative humidity (RHboxMAX)

Woodcrete bat boxes had a significantly higher daily maximum relative humidity (85,156±0,730) than Douglas wood bat boxes (82,156±0,965)($F(2,141)=3,339$, $p=0.042$) and higher daily maximum relative humidity than plywood bat boxes (83,386±0,730), although not significantly ($F(2,141)=3,339$, $p=0.243$). Plywood bat boxes had a higher daily maximum relative humidity than Douglas wood bat boxes, but also not significantly ($F(2,141)=3,339$, $p=0.673$).
Although cluster ($F(2,141)=2,154$, $p=0.120$) was included in the model, the effect was not significant.

5.2.7 Daily mean bat box relative humidity (RHboxMEAN)

Woodcrete bat boxes had a significantly higher daily mean relative humidity (72,221±1,163) than Douglas wood bat boxes (66,954±1,425)($F(2,107)=5,906$, $p=0.015$) and plywood bat boxes (67,321±1,163)($F(2,107)=5,906$, $p=0.011$). Plywood bat boxes had a higher daily mean relative humidity than Douglas wood bat boxes, but this difference was not significant ($F(2,107)=5,906$, $p=0.996$).

5.2.8 Daily mean daytime bat box relative humidity (RHboxMEANDAY)

Woodcrete bat boxes had a significantly higher daily mean daytime relative humidity (70,058±1,064) than Douglas wood bat boxes (63,774±1,304)($F(2,138)=11,499$, $p=0.001$) and plywood bat boxes (63,494±1,064)($F(2,138)=11,499$, $p<0.001$). Douglas wood bat boxes had a higher daily mean daytime relative humidity than plywood bat boxes, but this difference was not significant ($F(2,138)=11,499$, $p=0.998$).
Black woodcrete bat boxes had a significant higher daily mean daytime bat box relative humidity (71,421±1,505) than black Douglas wood (61,613±1,844)($F(3,138)=2,795$, $p<0.001$) and black plywood bat boxes (61,367±1,505)($F(3,138)=2,795$, $p<0.001$). Daily mean daytime bat box relative humidity did not differ significantly between black Douglas wood and black plywood bat boxes ($F(3,138)=2,795$, $p=0.999$). Although wood-coloured woodcrete bat boxes had a higher daily mean daytime bat box relative humidity (68,696±1,505) than wood-coloured Douglas wood bat boxes (65,934±1,844)($F(3,138)=2,795$, $p=0.575$) and wood-coloured plywood bat boxes (65,622±1,505)($F(3,138)=2,795$, $p=0.388$), these differences were not significant. Daily mean daytime bat box relative humidity did also not differ significantly between wood-coloured Douglas wood and wood-coloured plywood bat boxes ($F(3,138)=2,795$, $p=0.999$).

5.2.9 Daily minimum bat box relative humidity (RHboxMIN)

Wood-coloured bat boxes had a significantly higher daily minimum relative humidity (53,276±0,946)($F(1,180)=6,769$, $p=0.010$) than black bat boxes (49,795±0,946).
Woodcrete bat boxes had a significantly higher daily minimum relative humidity (56,254±1,073) than Douglas wood bat boxes (49,530±1,314)($F(2,180)=13,967$, $p<0.001$) and plywood bat boxes (48,822±1,073)($F(2,180)=5,906$, $p<0.001$). Douglas wood bat boxes had a higher daily minimum relative humidity than plywood bat boxes, but this difference was not significant ($F(2,180)=13,967$, $p=0.966$).
Black woodcrete bat boxes had a significant higher daily minimum relative humidity (57,052±1,517) than black Douglas wood (46,396±1,858)($F(2,180)=3,894$, $p<0.001$) and black plywood bat boxes (45,937±1,517)($F(2,180)=3,894$, $p<0.001$). Daily minimum relative humidity did not differ significantly between black Douglas wood and black plywood bat boxes ($F(2,180)=3,894$, $p=0.997$). Although wood-coloured woodcrete bat boxes had a higher daily minimum relative humidity (55,457±1,517) than wood-coloured Douglas wood bat boxes (52,663±1,858)($F(2,180)=3,894$, $p=0.571$) and wood-coloured plywood bat boxes (51,707±1,517)($F(2,180)=3,894$, $p=0.227$), these differences were not significant. Daily minimum relative humidity did also not differ significantly between wood-coloured Douglas wood and wood-coloured plywood bat boxes ($F(2,180)=3,894$, $p=0.970$).

5.2.10 Daily relative humidity fluctuation within a bat box (RHboxMAX-RHboxMIN)

Within black bat boxes, there was a significantly higher daily relative humidity fluctuation (33,829±0,409)($F(1,419)=41,806$, $p<0.001$) than within wood-coloured bat bat boxes (30,090±0,409).
Plywood bat boxes had a significantly higher daily relative humidity fluctuation within a bat box (34,562±0,472) than woodcrete bat boxes (29,003±0,472)($F(2,419)=35,224$, $p<0.001$) and Douglas wood bat boxes (32,491±0,578)($F(2,419)=35,224$, $p=0.017$). Douglas wood bat boxes had a significantly higher daily relative humidity fluctuation within a bat box than woodcrete bat boxes ($F(2,419)=35,224$, $p<0.001$).
Bat boxes in cluster 3 (32,718±0,472)($F(2,419)=11,723$, $p=0.001$) and cluster 2 (33,473±0,578)($F(2,419)=11,723$, $p<0.001$) had significantly higher daily relative humidity fluctuation than bat boxes in cluster 1 (30,192±0,472).
Black plywood bat boxes had a significant higher daily relative humidity fluctuation within a bat box (37,192±0,668) than black woodcrete (29,582±0,668)($F(2,419)=5,380$, $p<0.001$) and black Douglas wood bat boxes (35,155±0,818), but this difference was not significant ($F(2,419)=5,380$, $p=0.154$). Daily relative humidity fluctuation within a bat box did also differ significantly between black Douglas wood (35,155±0,818) and black woodcrete bat boxes ($F(2,419)=5,380$, $p<0.001$). Although wood-coloured plywood bat boxes had a significantly higher daily relative humidity fluctuation within a bat box (31,932±0,668) than wood-coloured Douglas wood bat boxes (29,827±0,818)($F(2,419)=5,380$, $p=0.134$), and wood-coloured woodcrete bat boxes (28,424±0,668)($F(2,419)=5,380$, $p=0.001$), only the difference with wood-coloured woodcrete bat boxes was significant. Daily relative humidity fluctuation within a bat box did not differ significantly between wood-coloured Douglas wood and wood-coloured woodcrete bat boxes ($F(2,419)=5,380$, $p=0.458$).
In cluster 1, black bat boxes had a significant higher daily relative humidity fluctuation within a bat box (33,733±0,668) than wood-coloured bat boxes (26,651±0,668)($F(2,419)=9,583$, $p<0.001$). In cluster 2, this difference between black bat boxes (34,586±0,818) and wood-coloured bat boxes (32,359±0,818) was not significant ($F(2,419)=9,583$, $p=0.055$). In cluster 3, this difference between black bat boxes (33,420±0,668) and wood-coloured bat boxes (32,017±0,668) was also not significant ($F(2,419)=9,583$, $p=0.138$).
In cluster 1, plywood bat boxes had a higher daily relative humidity fluctuation within a bat box (33,758±0,818) than woodcrete bat boxes (25,233±0,818)($F(3,419)=4,068$, $p<0.001$) and Douglas wood bat boxes (31,586±0,818), but this difference was not significant ($F(3,419)=4,068$, $p=0.172$). In cluster 1, daily relative humidity fluctuation within a bat box did also differ significantly between Douglas wood and woodcrete bat boxes ($F(3,419)=4,068$, $p<0.001$). In cluster 2, plywood bat boxes had a significant higher daily relative humidity fluctuation within a bat box (36,053±0,818) than woodcrete bat boxes (30,892±0,818)($F(3,419)=4,068$, $p<0.001$). Because of logger failure in this cluster, comparison with Douglas bat boxes could not be made. In cluster 3, plywood bat boxes had a higher daily relative humidity fluctuation within a bat box (33,874±0,818) than woodcrete bat boxes (30,884±0,818)($F(3,419)=4,068$, $p=0.030$) and Douglas wood bat boxes (33,396±0,818), but this difference was not significant ($F(3,419)=4,068$, $p=0.967$). In cluster 3, daily relative humidity fluctuation within a bat box did not differ significantly between Douglas wood and woodcrete bat boxes ($F(3,419)=4,068$, $p=0.088$).

5.3 Buffer capacity of ambient circumstances

To indicate the buffer capacity of each bat box model, temperature and relative humidity were plotted in a 24-hour curve for 25 July 2019, when highest mean bat box temperature was measured, and for 20 September 2019, when lowest ambient temperature was measured (see Figure 4).

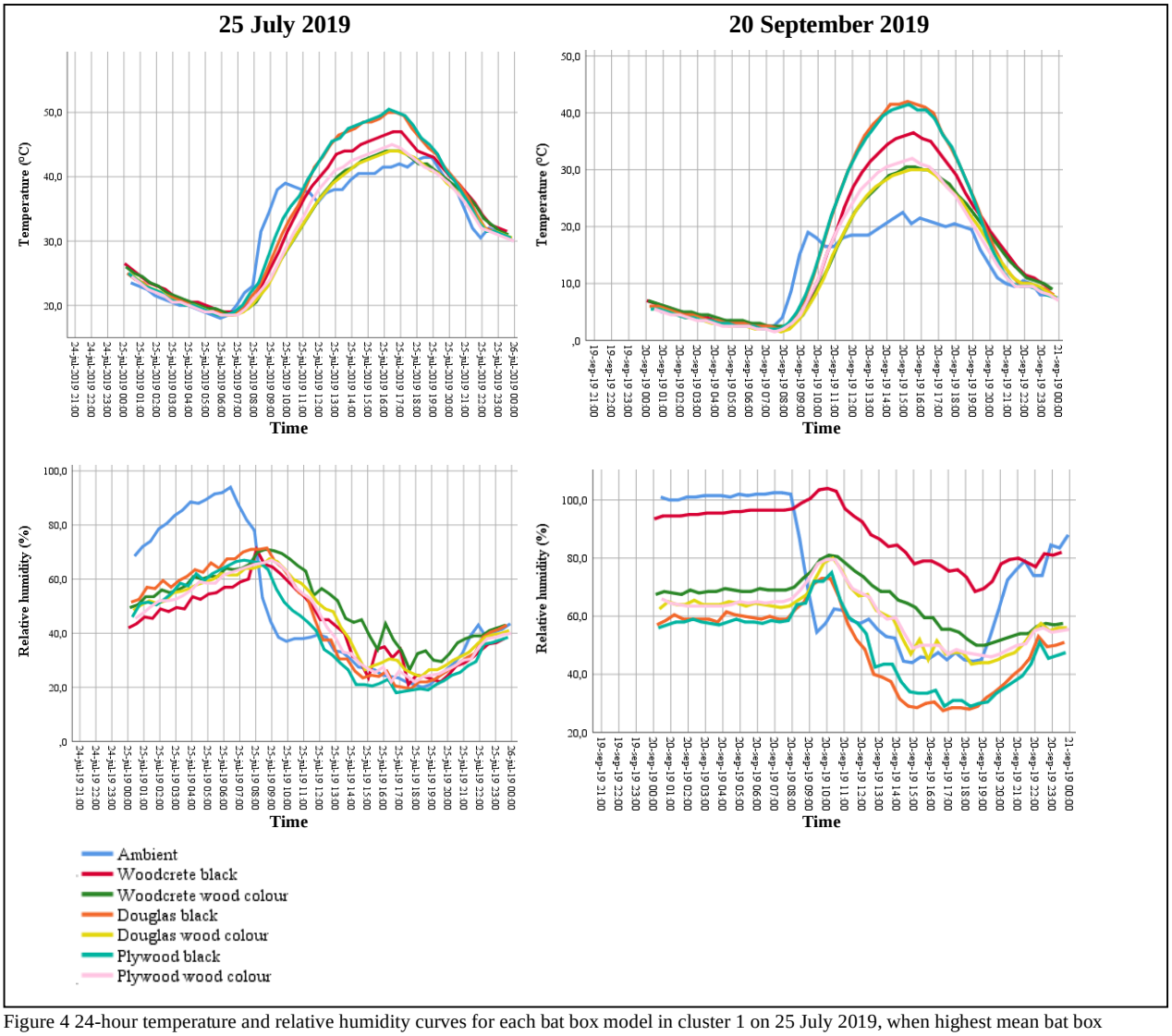

Figure 4 24-hour temperature and relative humidity curves for each bat box model in cluster 1 on 25 July 2019, when highest mean bat box temperature was measured and on 20 September 2019, when lowest ambient temperature was measured. n=1 for each model of bat box and ambient.

5.4 Overheating events

The number of overheating events (Tbox>=40 ºC) in bat boxes were counted for each colour and material. A total of 992 overheating events were counted during a 90-days period. Overheating events ranged from 63 to a maximum of 157 for black bat boxes and from 17 to a maximum of 49 for wood-coloured bat boxes. The highest number of overheating events were accounted to a black Douglas wood bat box (157) and the least number of overheating events were recorded in wood-coloured Douglas wood and plywood bat boxes (17). Most overheating events took place from noon (12:00) until 18:00. Based on data from cluster 1, minimum ambient temperatures between 20,5-33,5 ºC were able to initiate an overheating event of 40 ºC (see Table 2).

A Generalized Estimating Equation (GEE) with a negative binomial distribution indicated that bat box colour had a significant effect on the number of overheating events per bat box ($p<0.001$). Significantly less (70,6%) overheating events occurred in wood-coloured bat boxes (28,260±5,515) than black bat boxes (96,040±18,804)(see Figure 5). Although woodcrete bat boxes experienced less overheating events per bat box (47,939±5,768) than Douglas wood (54,921±13,527) and plywood bat boxes (53,704±13,455), bat box material did not have a significant effect ($p=0.669$).

Table 2 Number of overheating events in bat boxes from all three clusters and minimum ambient temperature to achieve an overheating event. Due to data logger failure, data from Douglas wood bat boxes in cluster 2 and ambient data from cluster 2 and 3 are omitted. Numbers are based on 90 sampling days with n=6 woodcrete bat boxes, n=4 Douglas wood bat boxes and n=6 plywood bat boxes and with n=1 for ambient values.

	Cluster	**Black**	**Wood colour**	***Total number of overheating events***	**Minimum ambient temperature to achieve an overheating event (ºC)**	
					Black	**Wood colour**
Woodcrete	**1**	102	37	*139*	27,0	33,5
	2	63	23	*86*	-	-
	3	77	25	*102*	-	-
Douglas wood	**1**	157	34	*191*	20,5	33,5
	2	-	-	-	-	-
	3	74	17	*91*	-	-
Plywood	**1**	153	49	*202*	20,5	32,5
	2	74	17	*91*	-	-
	3	68	22	*90*	-	-
Total		*768*	*224*	*992*		

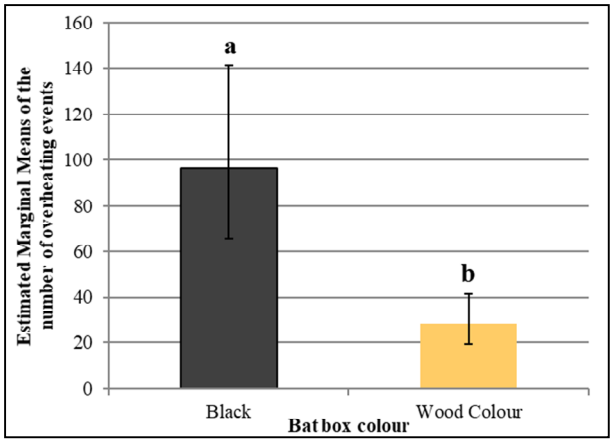

Figure 5 Estimated Marginal Means of the number of overheating events per bat box for each bat box colour. Bars with common letters do not differ significantly, error bars indicate 95% confidence intervals. Means are based on 90 sampling days with n=8 black bat boxes and n=8 wood-coloured bat boxes.

6. Discussion

6.1 Daily maximum, mean and minimum bat box temperature and temperature fluctuation within a bat box

6.1.1 Daily maximum bat box temperature

Daily maximum temperature of black bat boxes was approximately 3 ºC higher than wood-coloured bat boxes. These results were also found in other studies, where dark-coloured bat boxes also experienced highest temperatures (Rueegger, 2019; Weier et al., 2019; Bideguren et al., 2018; Griffiths et al., 2017; Doty et al., 2016; Fukui et al., 2010; Lourenço & Palmeirim, 2004; Kerth et al., 2001). But Van der Wijden et al. (2014) found that external bat box colour had little influence on internal thermal behaviour in bat boxes in forests. Probably because canopy cover prohibited direct sunlight from reaching bat box surface.

Interesting was also that bat boxes in cluster 1 had 3 ºC higher daily maximum temperatures than bat boxes in cluster 2 and 3. Since cluster 1 was located at study site A, and the other two clusters were located at study site B (with no significant differences between them), there must have been a location-effect. Although distance between the two study sites was only 6,4 km (in a beeline), a possible explanation might be that study site A was less influenced by windy conditions because trees were surrounding this study site. Study site B had more open characteristics were wind was more abundant, resulting in lower temperature maxima.

6.1.2 Daily mean bat box temperature

Daily mean bat box temperature was not influenced significantly by bat box colour but when only daytime values were taken into account, colour did have a significant effect. This can be explained by daytime solar exposure and heat absorption of the colour black (Griffiths et al., 2017).

6.1.3 Daily minimum bat box temperature

Daily minimum bat box temperature was not influenced by bat box colour. For bat box colour, this can be explained by the fact that daily minimum bat box temperature values occurred during nighttime, when solar exposure does not affect bat box temperature (Griffiths et al., 2017).

Bat box material did not significantly influence any temperature response variables during this research, including daily minimum temperature. Not even woodcrete bat boxes had higher daily minimum bat box temperatures than Douglas wood and plywood bat boxes. This was not expected because woodcrete bat boxes are thought to retain heat better than wooden bat boxes (Van der Wijden et al., 2014).

Bat boxes in cluster 1 had an almost significantly lower daily minimum bat box temperature than bat boxes in cluster 2 and 3. A possible explanation might be that subsoil around the bat boxes at study site A consisted of long grass. Subsoil of study site B consisted of short grass with a more rocky structure, perhaps causing more heat radiation at nighttime. Some experts confirm the possible influence of heat radiation from subsoil on poles with bat boxes (E. Korsten, personal communication, January 12, 2020).

6.1.4 Daily temperature fluctuation within a bat box

Daily temperature fluctuation within black bat boxes was 2,9 ºC higher than within wood-coloured bat boxes. A slightly higher difference than the difference Griffiths et al. (2017) found between daily temperature fluctuation of dark-green and white bat boxes (2,4 ºC). Maybe this difference can be explained due to dark-green and white bat boxes having different reflectance and absorbance rates than black and wood-coloured bat boxes.

Again an interesting location effect was found where cluster influenced daily temperature fluctuation within a bat box significantly. Bat boxes in cluster 1 had a 2,9 ºC larger daily temperature fluctuation within a bat box than bat boxes in the other two clusters. This is probably explained by the higher maxima and lower (almost significant) minima at study site A. Not surprisingly, bat boxes from cluster 2 and 3, both at the same study site, did not differ from each other.

6.2 Daily maximum, mean and minimum bat box relative humidity and relative humidity fluctuation within a bat box

6.2.1 Daily maximum bat box relative humidity

Although not significantly, interesting was that bat boxes in cluster 1 had a 2% lower daily maximum relative humidity than bat boxes in cluster 2 and 3. An explanation is yet to be found.

6.2.2 Daily mean bat box relative humidity

For daily mean daytime bat box relative humidity an interaction between colour and material was found. Probably due to the effect of daytime solar exposure on bat box colour (Griffiths et al., 2017).

Wood-coloured bat boxes, independent of material, were similar in daily mean daytime relative humidity.

Black woodcrete bat boxes had a 10% higher daily mean daytime relative humidity than black Douglas wood and black plywood bat boxes. Rueegger (2019) found comparable results: bat box material only influenced relative humidity in black bat boxes but not in white bat boxes; black woodcrete bat boxes had a 5,1% higher relative humidity than black plywood bat boxes. Within this colour-material-interaction, remarkable are the higher values in black woodcrete bat boxes compared to wood-coloured woodcrete bat boxes. A difference that was also found in other relative humidity response variables. This was not expected because higher solar radiation absorbance was thought to result in lower bat box relative humidity (Rueegger, 2019).

6.2.3 Daily minimum bat box relative humidity

The hypothesis that black bat boxes were thought to have lower relative humidity than wood-coloured bat boxes as a result of higher solar radiaton absorbance, was supported by the fact that wood-coloured bat boxes had an almost 3,5% higher daily minimum relative humidity than black bat boxes. Rueegger (2019) found an even higher percentage: white bat boxes had a 10% higher relative humidity than black bat boxes. White bat boxes probably reflect solar radiation even more than wood-coloured bat boxes, resulting in higher relative humidity.

As in daily mean daytime relative humidity, the same interaction between colour and material was found for minimum bat box relative humidity. Remarkably, black woodcrete bat boxes had a higher daily minimum relative humidity than wood-coloured woodcrete bat boxes. Perhaps this was due to condensation of water on data loggers. Rueegger (2019) did not find similar results when comparing black and white woodcrete bat boxes.

6.2.4 Daily relative humidity fluctuation within a bat box

Another location effect was found where bat boxes in cluster 1 had an approximately 3% lower daily relative humidity fluctuation than within bat boxes at study site B. This particular effect might be explained due to the lower daily maximum bat box relative humidity at study site A, where cluster 1 was placed.

6.3 Buffer capacity of ambient circumstances

6.3.1 Buffer capacity of ambient temperature

Even though ambient data was not included in the statistical analysis, 24-hour curves still indicated buffer capacity of bat boxes in cluster 1. Based on the 24-hour temperature curves, woodcrete bat boxes came forward as the bat boxes with the highest buffer capacity of ambient temperature: their curve had the least steep incline when ambient temperature rose. Likewise, less extreme values were reached. These differences were particulary visible between the black bat boxes. Very little differences in buffer capacity of ambient temperature were found between wood-coloured bat boxes, as comparable to the little differences Rueegger (2019) found between white woodcrete and plywood bat boxes.

Woodcrete bat boxes also managed to retain heat slightly longer after sunset than the other materials. But temperature in all bat boxes was already comparable just 1,5-2,5 hours after sunset. This indicates that buffer capacity was not as high for woodcrete bat boxes, as was initially thought. The relatively low buffer capacity of bat boxes overall is probably influenced by the choice of poles as a bat box substrate in this study. Andrusiak and Sarell (2019) attached single-chambered, woodcrete bat boxes to rocky surfaces and found that although bat boxes overheated, bat boxes cooled down slowly and temperatures remained higher than ambient. The rocky surface substrate probably had higher thermial inertia than trees or poles. In this way, sudden cooling of bat boxes was prevented.

Nevertheless, placing bat boxes on walls can have other consequences: Flaquer et al. (2014) report that maximum temperatures were 4 ºC higher in bat boxes on walls than bat boxes placed on poles.

6.3.2 Buffer capacity of ambient relative humidity

Based on the 24-hour relative humidity curves from cluster 1, woodcrete bat boxes had as predicted the highest buffer capacity of ambient relative humidity. When ambient relative humidity dropped, relative humidity in the woodcrete bat boxes stayed fairly consistent during daytime. Relative humidity in woodcrete boxes also stayed above ambient for a major part of daytime (10-13 hours). At the same time, relative humidity in the black Douglas wood and plywood bat box experienced a steep drop. Consequently, relative humidity in black Douglas wood and plywood bat boxes dropped below ambient over a long period of time at the hottest part of the day. Rueegger (2019) found comparable results: when ambient temperature rose, black and white woodcrete bat boxes experienced a less steep drop of relative humidity than black plywood bat boxes.

6.4 Overheating events in bat boxes

In hindsight, 2019 was a record-breaking year with an exceptionally warm and dry summer. During this summer an average of 184 mm precipitation and a mean temperature of 18,4 ºC were measured against a ‘‘normal’’ 17,0 ºC and 225 mm precipitation (KNMI, 2019). These extreme weather conditions probably affected the magnitude of overheating events in this study.

In contrary to predictions, every bat box in this study suffered from overheating. Since all bat boxes were placed on poles, this contradicts findings of Flaquer et al. (2014) who reported that overheating events only occurred on bat boxes attached to walls and not on poles.

More bat box overheating events (1,4% of 69.120 measurements) were encountered in this study during 90 days of sampling than the 797 (3,6% of 22.052 measurements) overheating events (when T>40 ºC) Bideguren et al. (2018) encountered during 150 days of sampling in July-September 2014-2015 in Catalonia. Although interesting, comparison is difficult because sampling effort, period, location, latitude, measure interval and overheating threshold differed from this study.

As predicted, black plywood bat boxes encountered the highest total number of overheating events. The highest recorded bat box temperature in this study (51,5 ºC) was encountered in this type of bat box. In contrast, Bideguren et al. (2018) only encountered temperatures above 50 ºC in black woodcrete bat boxes but not in black wooden bat boxes. It was unclear whether these bat boxes were mounted on buildings, trees or poles or all three.
Surprisingly, ambient temperatures at study site A could be as low as 20,5 ºC to achieve bat box overheating in a black plywood and black Douglas wood bat box. This threshold was higher for the black woodcrete bat box (27,0 ºC) and even higher for all wood-coloured bat boxes (32,5-33,5 ºC). Griffiths et al. (2017) found higher thresholds: dark-green bat boxes reached temperatures over 40 ºC when ambient temperatures were in the range of 35-38 ºC. Perhaps these bat boxes received a lesser amount of direct sunlight.
Albeit not tested, bat boxes in cluster 1 encountered more overheating events than bat boxes in cluster 2 and 3. This difference is possibly caused by local microclimate. Although at study site A less windy conditions were present than at study site B, conclusive evidence is lacking.
Additionally, bat box substrate might also influence the number of overheating events. Mol (2019) measured microclimate in a similar-sized, wood-coloured, flat 18 mm plywood bat box with a southern exposition: results indicated that bat box temperatures never exceeded 40 ºC on 25 July, 2019. This is probably because the bat box was hanging in a tree (canopy cover) and received a daily maximum of 4 hours direct sunlight. The rest of the day the bat box was partially shaded, preventing overheating, again indicating that bat boxes placed on poles are more prone to overheating than bat boxes attached to trees.
It is important to highlight that bat boxes in this present study were prevented from being occupied and extreme values could have been even higher: Willis and Brigham (2007) report a 7 ºC temperature increase in occupied bat boxes compared to non-occupied bat boxes. Some commercial plywood bat box models are built with a material thickness even less than what was used in this study. When bat boxes made of thinner materials than used in this study are occupied, temperature extremes are probably even higher.
Bat boxes in this study had only one chamber and microclimate was measured at one location within the bat box. Bideguren et al. (2018) found a significant difference in temperatures recorded at the top and the bottom of bat boxes. Therefore temperatures at the bottom of the bat boxes used in this study might still have offered suitable roosting temperatures during heat waves.

6.5 Management implications

Combined with a large amount of direct sunlight, ambient temperatures as low as 20,5 ºC were able to achieve overheating events in dark-coloured bat boxes; at such locations light-coloured bat boxes are recommended. Dark-coloured, single-chambered bat boxes have shown that they are prone to overheating, show low thermal stability and have lower relative humidity than light-coloured bat boxes when placed at locations with direct sunlight. It is therefore recommended to seriously reconsider the use of dark-coloured, single-chambered bat boxes at sunny expositions. Although all bat boxes in this study were facing a southern exposure, it is expected that overheating events may also occur on other aspects, depending on the interaction of many influencing factors like the amount of direct sunlight reaching bat box surface.
Supported by the results of Flaquer et al. (2014), it is furthermore expected that the effects found in this study are probably even stronger on bat boxes placed on walls of buildings, where wind is less and heat radiation from the wall and subsoil is more of an influencing factor than bat boxes placed on poles.
The risk of fatal overheating events occurring in the Netherlands will likely increase due to climate change and should not be underestimated, therefore overheating should be included as a subject in new guidelines for choosing and placing bat boxes.
The microclimatic response of bat boxes is a result of complicated interactions between factors like bat box exposition, colour reflectance, thermal inertia, substrate, subsoil and insulation. A situation-dependent approach is recommended when choosing and placing bat boxes. Since there was a significant location effect found in this study, it is recommended to take local microclimatic conditions and surrounding environment into account when deciding which model to select and where to place bat boxes.
By experimenting with different bat box constructions, bat box microclimate can be manipulated to fit the desired circumstances. Large, multi-chambered bat boxes offer larger roosting surface, more variety in microclimate and are often more occupied than small bat boxes (Bobeldijk et al., 2019; Hoeh et al., 2018). This does not mean that large, multi-chambered bat boxes never suffer from overheating, as exemplified by the following maternity bat box in the Netherlands: a large, dark-coloured concrete plywood bat box (4-chambers) including a vent also suffers from overheating. When ambient temperatures rose to 32 ºC, all bats were located close to the entrance. The last 3 years

the bats were sometimes even completely absent during heat waves. Although overheating occurs in summer, this particular bat box gets already occupied in March every year by more than 80 common pipistrelles. Thus confirming the need for cold and warm bat boxes (E. Korsten, personal communication, January 12, 2020).
Adding ventilation to small bat boxes might lead to drafty conditions. It would be even better to use larger bat boxes with two (or more) chambers or with a compartment between bat box and substrate (wall). In this way the front chamber can act as insulation for the back chambers, providing more thermal variability and reducing overheating (Rueegger, 2019; Miller, 2018).
Bartonička and Řehák (2007) state that overheating may not be so dangerous if sufficient alternative roosts are available in the vicinity. On the contrary, Flaquer et al. (2014) have directly observed a fatal overheating event in an environment with high relative humidity (wetland) and other roost possibilities within the area. For that reason, placing alternative roosts, especially during the maternity season, may not be the solution.
Woodcrete bat boxes are fabricated from a mix of wood and concrete, making them more durable (25-30 years, Heise & Blohm, 2012) than plywood. Plywood bat boxes seldomly last longer than 5-10 years (Bender & Irvine, 2011) when they are fabricated well. Consequently, replacement is needed less often when placing woodcrete bat boxes (Bat Conservation Trust, s.d). Due to its high specific density, woodcrete also insulates better than plywood and is more rot-resistant (Van der Wijden et al., 2014; Baranauskas, 2009). Implementing polystyrene or styrofoam in bat box material can reduce weight, reduce the magnitude of extremes during heat waves and can provide better insulation (Andrusiak & Sarell, 2019; Larson et al., 2018).
The microclimatic properties of bat boxes fabricated from other materials should also be studied. Other studies have experimented with materials like resin (Mering & Chambers, 2012), bat boxes constructed from a mixture of concrete and recycled polystyrene (Greenwoods Ecohabitats, 2019), vinyl/PVC, rice cement (no overheating events) and clay (Bideguren et al., 2018). New suitable bat box materials will probably arise in the future. Because this study investigated unoccupied bat boxes in the open field, it would be interesting to determine which models bats will prefer when given the option to choose. Also interesting would be to know how bats influence bat box microclimate with their presence. Since most studies only investigated temperature preferences, more research is especially needed to test the relationship between relative humidity and bat presence in bat boxes. Finally, new challenges arise for other types of bat boxes, e.g. on the one hand preventing overheating but also retaining heat at night in maternity bat boxes.

Acknowledgements
Thanks to Erik Korsten for providing useful comments on earlier drafts of the manuscript. Special thanks to Jarno Beijk and Josine de Jongh from NatuurInclusief and Faunus Nature Creations for commissioning and financing the project and Martijn Nijhuis, Hans Klok & Jan-Luc van Eijk for providing and helping to setup the research sites.

Compliance with ethical standards

Conflicts of interest
The authors declare that they have no conflicts of interest.

Ethical approval
This article does not contain any studies with human participants or animals performed by the authors.

Supplementary material available upon reasonable request

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