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RESEARCH ARTICLE

Occupancy of urban roosts by spectacled flying-foxes (*Pteropus conspicillatus*) is not affected by diurnal microclimate

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Abstract

One of the most significant changes to Earth's climate in recent decades has been an increase in the frequency, intensity and duration of heatwaves. During heatwaves, animal's thermal window can be exceeded, and in extreme cases, mass mortality events have been observed. In 2018, a heatwave in north-eastern Australia resulted in the death of approximately one-third of the spectacled flying-fox (*Pteropus conspicillatus*) population at urban roosts in Cairns. The species has now been listed as endangered with future heatwaves considered the greatest threat to its survival. In this study, we investigated long-term climatic trends for Cairns, paying particular attention to the frequency of extreme heat events from 1943 to 2022. We then characterized the microclimate of urban flying-fox roosts during the Austral summers of 2021/2022 and 2022/2023 across Cairns to assess the long-term feasibility of urban spectacled flying-fox roosts. From the long-term climate records, we observed an overall increase in Cairns' average annual temperature of 1.3°C from 1943 to 2022 and an increase in the number of excessively hot days per decade, from 16 in the first decade (1943–1952) to 67 in the last (2013–2022). We regularly detected maximum roost temperatures of 30–35°C during our study, with excessively hot days (>35°C) recorded more frequently than expected compared to Cairns's maximum temperatures from the last decade (2013–2023). We detected only 1 day where roost temperatures exceeded 40°C and no period that replicated the 2018 heatwave conditions. Furthermore, we found a significant negative relationship between roost ambient temperature and humidity, where the hottest days also coincided with those with the lowest humidity. Importantly, we found no difference in microclimate between roosts that were occupied and unoccupied by flying-foxes during our study, suggesting that other environmental or behavioural factors are more influential for roost selection than the roosting microclimate. Ensuring the long-term conservation of spectacled flying-foxes under a changing climate will require the management of urban roosts to increase their thermal resistance to heatwaves, and more research is needed to identify the variables modulating this aspect.

KEYWORDS
bats, climate change, heatwaves, microclimate, roosts, spectacled flying-fox

INTRODUCTION

The warming of the Earth's atmosphere as a result of anthropogenic greenhouse gas emissions has increased the frequency and severity of extreme weather events such as heatwaves (IPCC, 2018). Since 1950, heatwaves have increased in intensity, frequency and duration both globally and regionally (Perkins-Kirkpatrick & Lewis, 2020). Moreover, this trend is expected to worsen as the climate continues to warm (Domeisen et al., 2023; Perkins-Kirkpatrick & Lewis, 2020). Heatwaves are often referred to as periods of excessive heat, but definitions differ between countries (Lee, 2014) and can comprise qualitative and quantitative characteristics.

Qualitative definitions of heatwaves consider its duration and associated humidity, whereas quantitative definitions focus on the duration, frequency and magnitude of the temperature above a threshold, which varies from 2 to 5 days and 25–38°C (Perkins-Kirkpatrick & Lewis, 2020). The Australian Bureau of Meteorology (BOM) uses a qualitative approach, defining a heatwave as three or more consecutive days when daytime and night-time temperatures are 'unusually high' relative to the local long-term climate (Coates et al., 2014). Heatwaves are especially common in dry and temperate climates (defined, respectively, as the area from 15° to 30° N and S of the equator and 30°–65° N and S of the equator) and are rarer in wet tropical regions (defined as the area from 10° N to 10° S of the equator) with highly stable climates relative to environments at higher latitudes (National Research Council, 1995; Seidel & Yang, 2020).

In intact tropical forests, the understorey and canopy are each associated with microclimatic conditions that differ from those outside the forest (Camargo & Kapos, 1995; Murcia, 1995). Both vegetation strata experience gradients in microclimates with air temperature and vapour pressure deficits declining with distance away from the forest edge and relative humidity and soil moisture levels increasing (Camargo & Kapos, 1995). In urban areas, the microclimate within patches of vegetation can be influenced by patch size, the human activities occurring in and around the patch, as well as surrounding water bodies and buildings (businesses, houses, roads and active construction sites) (Li et al., 2020; Yu et al., 2020). Hence, a greater understanding of the factors influencing forest microclimates presents a critical opportunity to enhance the capacity of habitats to buffer the effects of a warming climate (De Frenne et al., 2021).

Canopy microclimates are extremely important for flying-foxes (*Pteropus* spp.) because they roost diurnally within forest canopies in large colonies of hundreds to thousands of individuals (Ratcliffe & Ter Hofstede, 2005; Timmiss et al., 2021). Due to these high population densities, flying-foxes are highly vulnerable to changes in weather, especially heatwaves. For example, Australian heatwaves have now been associated with mass mortality events of black (*P. alecto*), grey-headed (*P. poliocephalus*), little red (*P. scapulatus*) and spectacled (*P. conspicillatus*) flying-foxes (Welbergen et al., 2008). During these events, tens of thousands of bats perished when temperatures exceeded 40°C (Welbergen et al., 2008), with modelling (Australian Community Climate and Earth-System Simulator – Numerical Weather Prediction mode [ACCESS-R NWP-I]) suggesting a temperature threshold of 42°C to predict the occurrence of a die-off (Ratnayake et al., 2019; Welbergen et al., 2008), as this was the cut-off for bats survival.

Mass mortality of Australian flying-foxes associated with heatwaves has been well-documented along the east coast of Australia (Welbergen et al., 2008). Still, the Australian tropics have seen fewer heatwaves when compared with other locations due to their stable climate. A stable climate with low variation in seasonal temperature has allowed tropical species to develop finer specializations and narrower thermal tolerances

(Janzen, 1967; Stevens, 1989), potentially resulting in increased vulnerability to the effects of climate warming and heatwaves (Polato et al., 2018). For example, in 2018, a heatwave killed an estimated third of the population of spectacled flying-foxes (~23 000 individuals) residing in urban roosts in Cairns (Bittel, 2019). Both the extent and rate of population loss during this extreme event have dire implications for the future conservation of the spectacled flying-foxes and have focussed management actions on understanding the thermal resistance of urban roosts.

In this study, we assessed how climate change, and the microclimate preferences of urban spectacled flying-fox colonies may impact roost choice and the long-term success of urban colonies in Cairns. To evaluate this, we: (1) examined long-term temperature trends for Cairns, (2) investigated the temperature and humidity patterns of the 2018 heatwave, (3) described the microclimate conditions of occupied and unoccupied spectacled flying-fox camps in Cairns during the austral summers of 2021/2022 and 2022/2023 and investigated the influence of camp size in roost occupancy. We hypothesized that microclimate conditions influence camp occupancy and can indicate the microclimate preferences of this species.

METHODS

Cairns is a lowland tropical city in north-eastern Australia (16.92° S, 145.78° E) that experiences a mean annual rainfall of ~2000 mm and a pronounced dry season (<100 mm/month) from April to November. The mean monthly maximum temperature ranges from 25.8°C (winter) to 31.5°C (summer) (Australian Bureau of Meteorology [BOM]).

Long-term temperature trends

We retrieved data from BOM to examine climate trends and temperature extremes in Cairns, using the longest and most continuous data record for the region, the Cairns airport (station number 31011), covering a period of 81 years (1943–2023). These data comprise the maximum temperature and humidity recorded at 3 PM daily and are continuously updated and available on the BOM website (Bureau of Meteorology, 2023).

Microclimate characterization

We characterized the microclimate at 20 (nine occupied and 11 unoccupied) spectacled flying-fox roosts in the urban area of Cairns (Appendix S1). The camps ranged from 0.5 to 42.2 ha and supported a diverse range of vegetation communities from remnant primary rainforest to small stands of sclerophyll trees (*Melaleuca and Eucalypt* spp.). We selected roosts that were currently being monitored by Cairns Regional Council and bat carers, in response to the 2018 mortality event. We classified as 'occupied' the camps with bats at any point in time during the fieldwork duration and 'unoccupied' as the camps known as roost sites but were not currently being utilized by bats in the 2.5 years of this study. The roosts selected for this study were spread over a 40 km linear distance from the north to south of Cairns (16.78° S, 145.68° E to 17.09° S,145.78° E) and covered an area of ~160 km^2. The roosts encompassed various vegetation communities, adjacent features and the habitat areas were defined as the extent of the vegetation (0.46–42 ha, Appendix S1). Seven roosts were located in the inner city, surrounded by houses and roads. Where possible, we standardized between occupied and unoccupied sites: roost area, vegetation communities and location, although accessibility was often via private lands which was potentially contentious as flying foxes are not well liked and some landholders disencouraged our access and one landholder withdrew permission during the course of the study.

During two austral summers, November 2021–January 2022, and December 2022–February 2023, microclimate data were collected at spectacled flying-fox roosts on sunny days between 11 AM and 2 PM. Each roost was sampled between 4 and 6 times a year. At each visit, we measured air temperature (°C) and relative humidity (%) across a 25 m transect for large camps (>0.75 ha) and as a 10 min walk throughout the roosts for small camps (<0.75 ha) using a handheld meteorological station (Kestrel 3550). This different approach was necessary due to the variability of roost configuration (as seen in Figure 1b – Map). Our site visits were short and focussed on coinciding with the hottest time of the day in order to determine maximum temperatures; with our study design replicated in space (20 sites) and time (repeated visits during summer/per year).

The Kestrel 3550 measures 13 climate variables including compound ones (such as heat index). The Kestrel collects 12 measurement points per minute, and data collection was for a 10-min visit under the canopy to avoid direct sunlight, resulting in 120 data points per visit. The accuracy of the equipment varied by ±0.5°C for air temperature and ±3% for relative humidity (Kestrel Weather Meters, 2020). We had also installed data-loggers to collect temperature and humidity in the canopy, but the equipment was stolen. Urban roosts are close to neighbourhoods

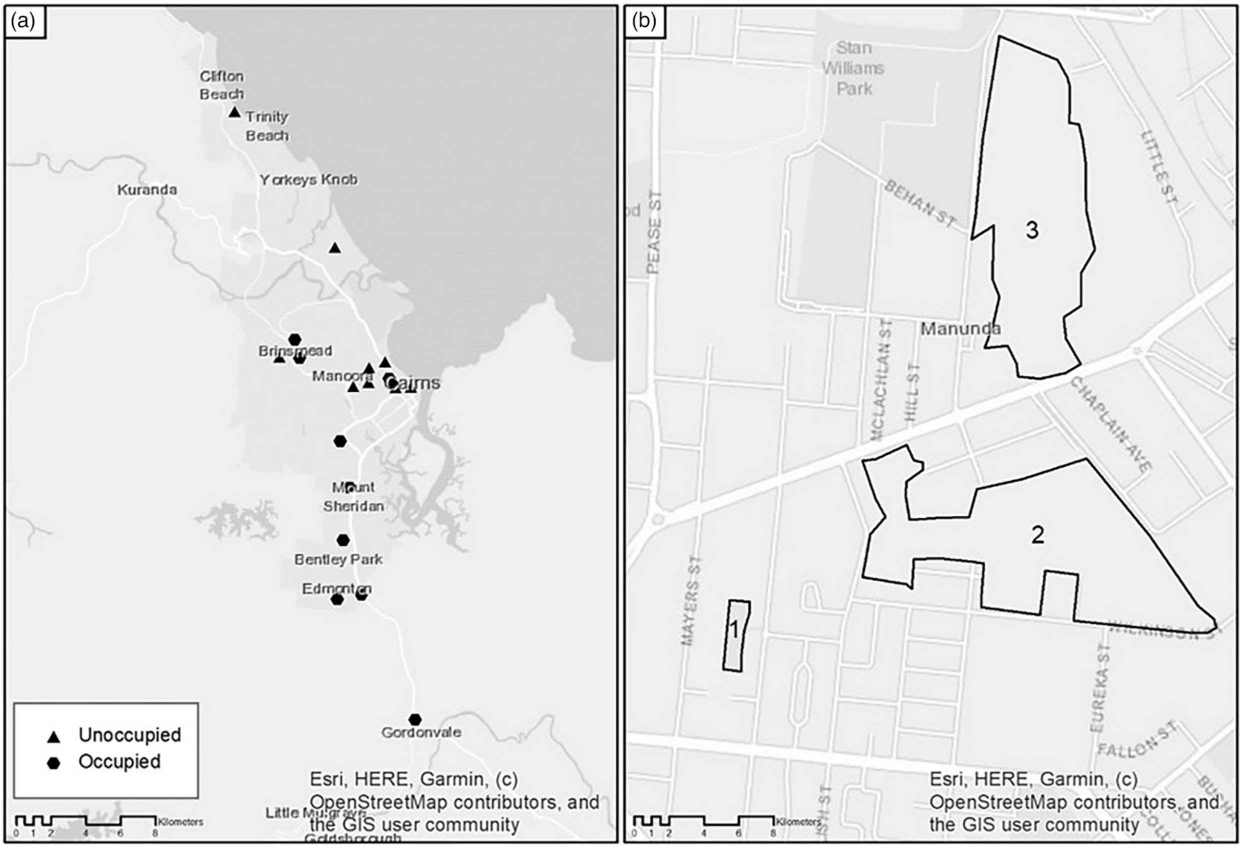

FIGURE 1 The location of spectacled flying-foxes urban roosts (a). The triangles are the unoccupied camps, and the hexagons are the occupied. (b) Illustrates large and small spectacled flying-fox camps. The small camp (1) is Guginy Reserve with a 2.0 ha area, and the large camps represented are Cairns Swamp (2) and Cairns Cemetery (3), with 37 and 24.2 ha of area.

and walking paths, and unfortunately, our research equipment was too accessible.

Data analysis

For long-term climate trends, we calculated standardized anomalies of temperature from the 1980 to 2010 baseline to examine with linear regressions the: (a) annual average maximum temperature, (b) summertime max temp and (c) wintertime max temp. The baseline 30 year period from 1980 to 2010 is the most widely used standard reference period for calculating 'climate normal' (IPCC, 2001). With respect to past extreme weather events, we identified excessive hot days (>35°C) and measured changes in frequency across three ranges (<30, 30–35, >35°C) with Chi-squared tests. To understand the weather conditions of the mass mortality event that occurred during the November 2018 heatwave, we described and compared the temperature and humidity measured during the heatwave with the conditions observed during subsequent years.

We examined the relationships between flying-fox occupancy, roost microclimate and area using binomial generalized linear models and mixed effect models (GLM and GLMM), t-tests and ANOVAs where appropriate. Pearson correlation tests identified which Kestrel climate variables associated significantly with ambient temperature. We compared daily maximum and average temperatures between occupied and unoccupied roosts with Student's *t*-tests. The probability of flying-fox occupancy was examined with binomial models with predictors of maximum temperature, humidity and wind speed modelled both individually and combined as temperature and humidity are often used as a measure of heat stress on animals (Epstein & Moran, 2006). Roost location was included as a random effect. All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022) with the R package *tidyverse* (Wickham et al., 2019) and graphs produced in *ggplot 2* (Wickham, 2016) and *plotly* (Plotly Technologies Inc, 2015).

RESULTS

Maximum temperatures

From 1943 to 2022, the annual maximum temperature in Cairns increased by 1.3°C (from 28.9 to 30.2°C), with the warmest temperatures in our dataset recorded in 2022 (annual $\overline{x} = 30.2$°C). We examined the average maximum temperature per month across the 80 years. For the annual tendency line, we used the average maximum temperature of all the months, while for the Summer, we used December–January and for the Winter, June–August. The fitted linear regression model (*lm(formula = data$std.anom ~ data$Year)*) indicated a significant increase in the long-term average monthly temperature (Figure 2a, $R^2 = 0.02$, $p < 0.01$, df = 958). This analysis was also performed for the summer (December–January) and winter (June to August) seasons separately. We observed a greater increase in annual winter temperatures (0.02°C/y) than in summer (0.009°C) in the dataset, where the overall annual slope for winter indicates an increase in the average temperature of 0.01°C/y. We observed a higher slope in the winter (Figure 2c, $R^2 = 0.06$, $p < 0.01$, slope = 0.01, df = 238), compared to the summer (Figure 2b, $R^2 = 0.01$, $p < 0.01$, slope = 0.0049, df = 238). Since 2022, the summer of 2020 was the warmest on record, followed by the summers of 2016 and 2017 (Figure 2b), whereas 2010 and 2009 were the warmest winters (Figure 2c).

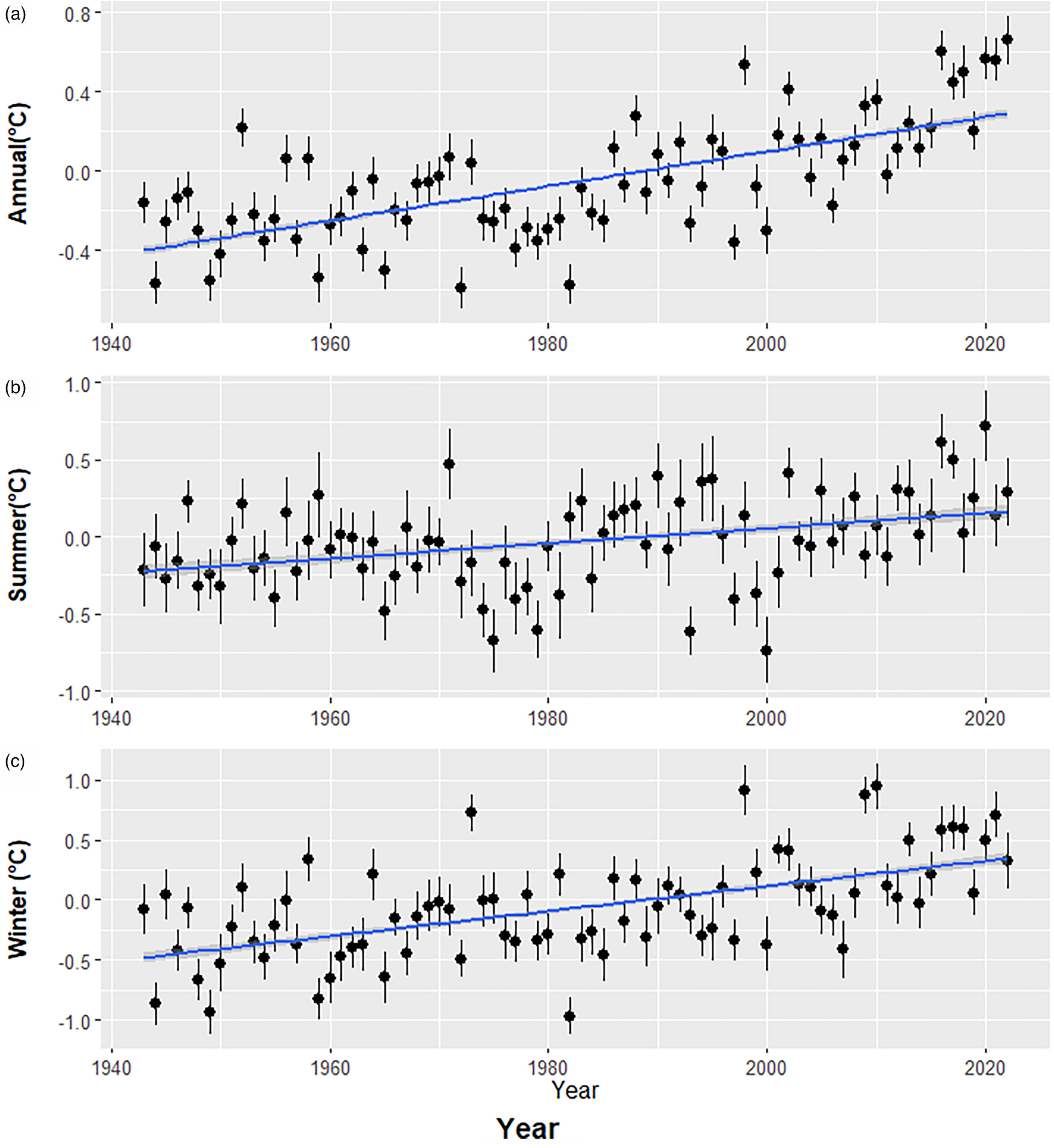

FIGURE 2 The standardized anomaly of the annual average maximum temperature in Cairns (1943–2022), calculated from a 1980–2010 baseline, showing a significant increase in temperature over time for the (a) annual maximum temperature, (b) summer maximum temperature and (c) winter maximum temperature.

Excessively hot days and heatwaves

From 1943 to 2022, Cairns recorded 272 days (0.9%) considered excessively hot (>35°C). There were 32 days with temperatures >38°C and 7 days >40°C. Since 1943, the number of excessively hot days (here stated as days >35°C) per decade increased from 17 in the first decade (1943–1952) to 67 in the last (2013–2022) (Figure 3), which represents an increase of 3.1SD from the mean of hot days. For example, in 2022, the number of days >35°C ($N = 13$) were almost equivalent to the number observed for the decade 1943–1952 ($N = 17$).

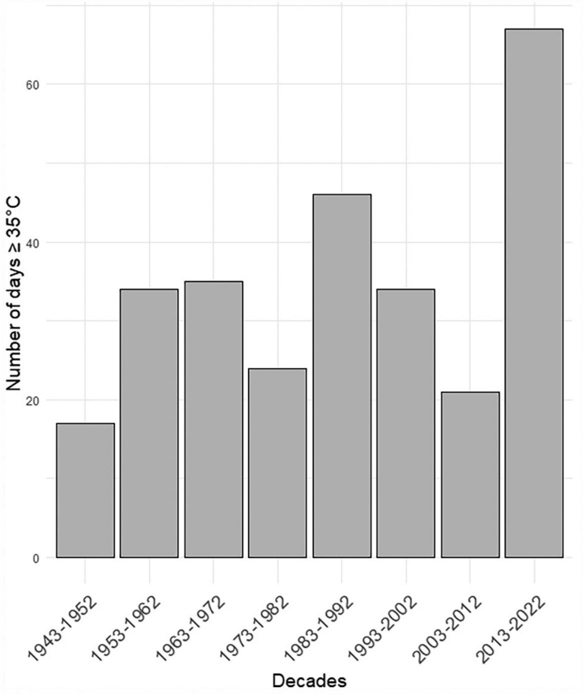

FIGURE 3 The number of days ≥35°C per decade measured at the Cairns airport weather station increased overall over time (3.1 SD).

In November 2018, Cairns had an unusual heatwave with three consecutive days recorded as the hottest on record (41.3, 42.2 and 41.6°C; Figure 4a) and associated with unusually low humidity (Figure 4b). Heatwave temperatures each day were between 10 and 12°C (10.5, 11.4 and 10.8°C) above the monthly average for November, which is >6 standard deviations above the long-term average ($\bar{x}_{\text{November}} \pm$ SD, 30.8°C ± 1.49). The minimum temperatures were also between 2 and 4°C (2.6, 2.3 and 3.9°C) above the monthly average for November ($\bar{x} \pm$ SD, 20.8°C ± 3.1). During this same period, the humidity dropped from 54% to 35% on the first day of the heatwave and remained low (37% and 47%) over the next 2 days. The recorded humidity on all 3 days was 2–3 standard deviations below the average humidity of November (66.9 ± 9.9%).

We compared the daily maximum temperatures and humidity in November over the past 5 years (2018–2022) and found no similar conditions (Figure 4). The temperatures observed in the following years (2019–2022) for the same period were primarily between 32 and 34°C ($\bar{x} \pm$ SD, 32.3°C ± 1.09), with 5 days >34°C and 1 day >36°C. Compared to this average, 2018 had a slightly higher mean and standard deviation for November ($\bar{x} \pm$ SD, 33.7°C ± 3.3), as expected due to the extreme temperatures registered during the heatwave. These characteristics demonstrate how unusual and extreme the weather was during the extreme heatwave. There were 8 days where humidity levels fell below 50% in subsequent years, but they were not associated with excessively hot days.

The microclimate of urban spectacled flying-fox roosts in Cairns

Over the two summer periods (November 2021–January 2022 and December 2022–February 2023), the average maximum temperature among all roosts was 32.9°C (SD = 2.1°C) and the maximum roost

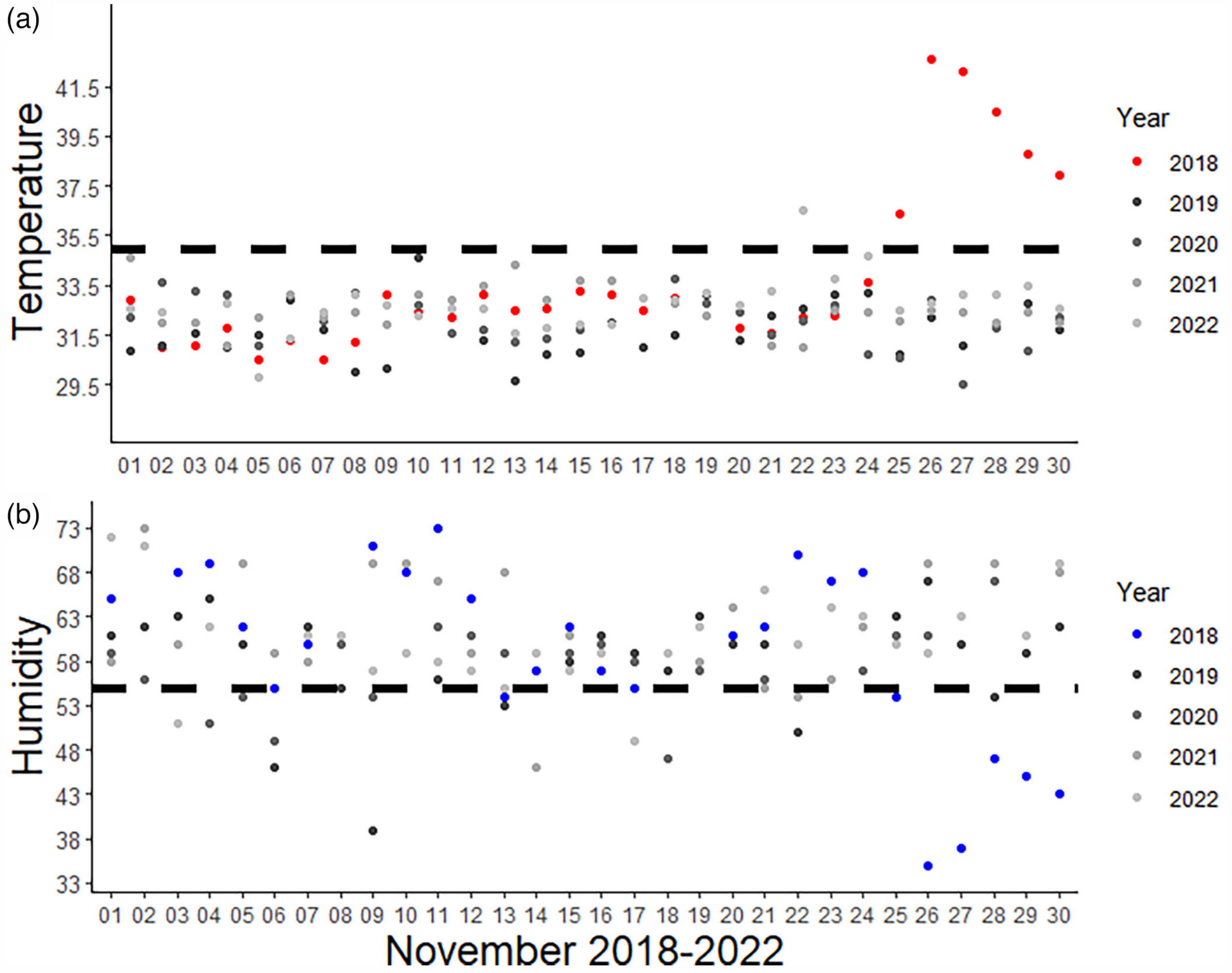

FIGURE 4 Daily maximum temperature (a) and humidity (b) recorded at 3 pm at the Cairns airport weather station from 2018 to 2022. The first graph represents the unusually high temperatures recorded during the heatwave (red dots), and the temperature registered on the same days in the following years (mostly concentrated below 35°C – dashed line) (a). Panel b shows the relative humidity per day, with the majority of the data located above 55% (dashed line) of relative humidity, while the values on the heatwave dropped below 40%, resulting in an unusually hot and dry combination for 4 days.

temperature was 40.1°C. We recorded higher maximum roost temperatures (40.1°C) in the summer of 2021–2022 compared to 2022–23 (35.6°C), with both summers registering daily temperatures >4°C warmer than the long-term average maximum temperature for summer (31.5°C). The roost average maximum temperatures measured by the Kestrel were similar to those recorded from the BOM airport climate station ($\bar{x}_{\text{maxtemp}} \pm \text{SD}$; 32.5°C ± 1.4°C), differing by only 0.4°C. However, the roost standard deviations reveal a greater range in temperature compared to the BOM station during our sampling, with one site recording 3.5°C cooler than the BOM station and another site 7.8°C warmer.

There was no significant difference in maximum temperatures recorded between all 20 roosts (Figure 5, ANOVA, $F(20,131) = 1.152$, $p > 0.05$). With respect to bat occupancy of sites, we observed no significant difference in maximum temperatures recorded between occupied and unoccupied roosts (Figure 5, t-test = 0.50, $p = 0.60$). Further, we also did not find a significant difference in the temperature coefficient of variation between occupied and unoccupied roosts (t-test = −1.39, $p = 0.18$).

We compared the frequency of excessive hot summer days in spectacled flying-fox roosts from 2021 to 2023 with a recent baseline (Cairns airport max temperatures 2012–2023) and found that roosts have experienced a

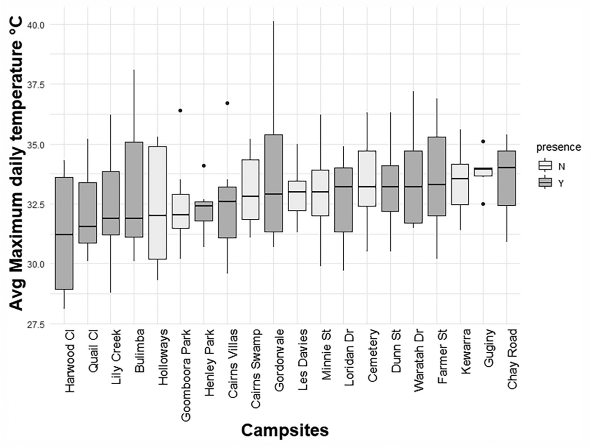

FIGURE 5 The maximum daily temperatures recorded in spectacled flying-foxes roosts during two summers, ordered by the median temperature registered per site. The occupied camps are in light grey, while the unoccupied camps are in dark grey. Boxplots show interquartile ranges (IQR) and are ordered in a crescent order according to the median value.

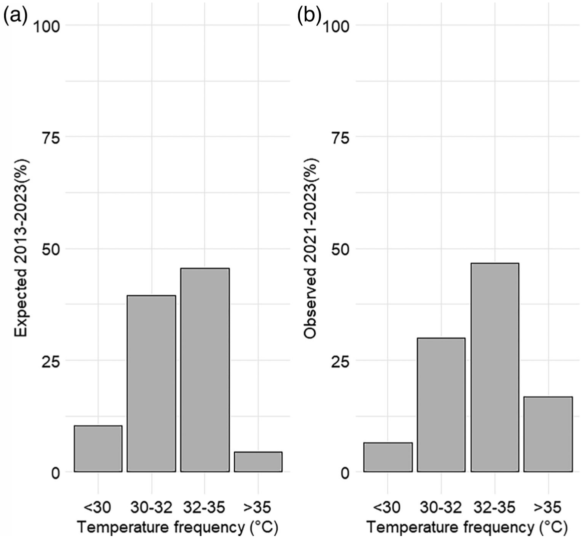

FIGURE 6 The expected frequency, based on 10 years of data (2013–2023) registered at the airport station (a) and the recorded frequency of days in each temperature range in urban spectacled flying-fox roosts (b). There was an increase in the frequency of temperatures above 32°C in the roosts compared to the long-term data.

significantly greater frequency of excessive hot days during the last 2 years of the study (Figure 6, $\chi^2 = 86.1$, df $= 7$, $p < 0.01$, $\alpha = 0.0$) when compared to the excessive hot days registered by BOM. Bat roosts experienced max temperatures of 30–35°C for 76.7% of the time and >35°C 16.9% of the time, whereas airport decadal average was between 30°C and 35°C 48% of the time, and >35°C only 1.7% of the observation period.

We found none of the microclimate variables examined could predict roost occupancy (Table 1, Figure 7), but we did find that roost area was significantly associated (Table 1, $r^2 = 0.39$, $p < 0.01$), whereby smaller camps were more frequently occupied than larger camps. Once roosts were >1 ha in size, the chance of occupancy was reduced by 2% for every additional hectare in the camp size. We also found a significant negative correlation between max temperature and relative humidity over the two summer periods ($\rho_{2021/2022} = -0.61$, $p < 0.01$; $\rho_{2022/2023} = -0.74$, $p < 0.01$).

TABLE 1 Binomial GLMs and GLMEs described the presence of spectacled flying foxes in urban forest camps in Cairns, Australia, over two summer periods from November 2021 to January 2022 and December 2022 to February 2023.

Model	Predictors	z Value	Pr(<|z|)	AIC
	Intercept			
GLM 1	Area	−4.8	<0.01	158.6
	Intercept			
GLM 2	Maximum daily temperature	0.5	0.6	85.7
	Intercept			
GLM 3	Maximum daily humidity	−1.2	0.2	213.9
	Intercept			
GLM 4	Average daily temperature	0.5	0.6	215.2
	Intercept			
GLM 5	Average daily humidity	−1.3	0.6	213.8
	Intercept			
GLM 6	Maximum daily temperature	−0.4	0.7	217.5
	Maximum daily humidity	−1.2	0.2	
	Maximum daily temperature * maximum daily temperature	0.6	0.5	
	Intercept			
GLM 7	Average daily temperature	−0.9	0.4	216.8
	Average daily humidity	−1.5	0.1	
	Average daily temperature * average daily humidity	0.4	0.7	
	Intercept			
GLMM 1	Maximum daily temperature	1.4	0.2	85.7
	Maximum daily humidity	−0.1	0.9	
	Maximum daily temperature * maximum daily humidity + (1|camp)	1.0	0.3	
	Intercept			
GLMM 2	Average daily temperature	−0.9	0.9	87.1
	Average daily humidity	−1.5	0.7	
	Average daily temperature * average daily humidity + (1|camp)	0.4	0.4	

DISCUSSION

We examined the microclimate of urban roosts of the endangered spectacled flying-fox in the tropical lowlands of Cairns in north-eastern Australia and found that roost occupancy was not predicted by maximum daily temperature or relative humidity. During the summers of 2021/2022 and 2022/2023, we observed that maximum roost temperatures were commonly 30–35°C, and included nine times more excessive hot days (>35°C) recorded at urban roosts than expected based on the most recent decade of available temperature data (BOM) for the summer period (2013–2023). We recorded only 1 day where the temperature at urban roosts was greater than 40°C, and no period that replicated the 2018 heatwave, which was characterized by six consecutive excessively hot days and exceptionally low humidity. Notably, we found a significantly negative relationship between ambient temperature and humidity at the roosts, where the hottest days coincided with those of lowest humidity.

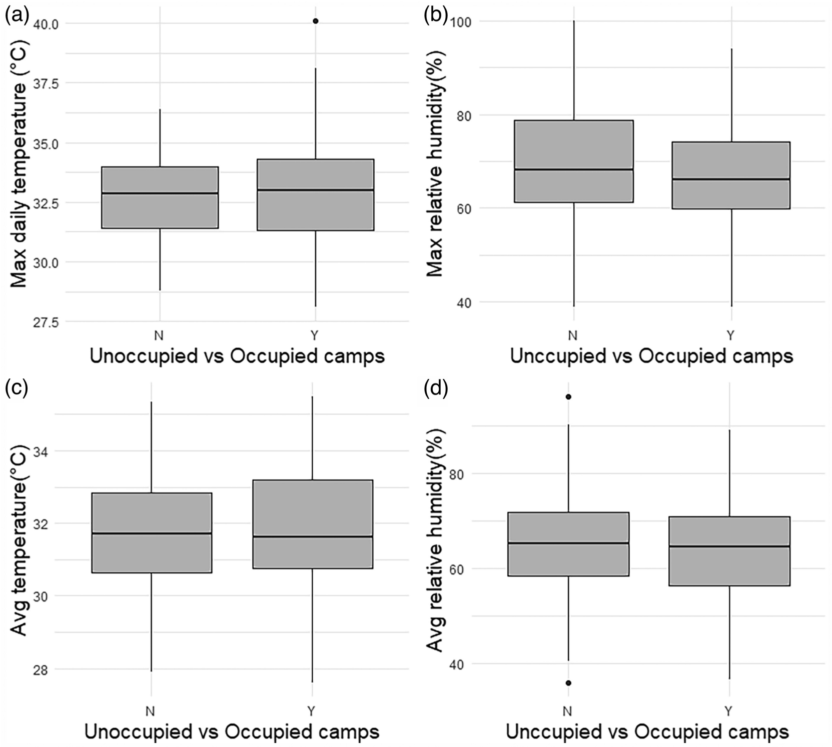

FIGURE 7 The difference between occupied and unoccupied camps in maximum daily temperature (a), maximum humidity (b), average temperature (c) and average relative humidity (d) per visit.

The 2018 Cairns heatwave was caused by warm, dry winds moving eastward from inland Australia and becoming established along the northeast coast (Bureau of Meteorology, 2018). This weather pattern was highly unusual for the region, which is normally influenced by easterly winds that dissipate heat with cooler air and precipitation. Continental climate drivers, such as El Niño and Indian Ocean Dipole conditions, were not a strong influence on the heatwave, but a pulse of Madden-Julian oscillation appears to have contributed to the establishment of westerly winds, along with a low-pressure system in the southeast (Bureau of Meteorology, 2018).

Heatwaves tend to compound, whereby dry areas increase in temperature more quickly, leading to increased rates of drying. Despite occurring at the beginning of the wet season in Cairns, the days prior to the heatwave registered below average rainfall in the northeast (Bureau of Meteorology, 2018). This intensified the conditions that led to the exceptionally low humidity recorded during this period. These regional weather conditions may have been further exacerbated by the effect of urban heat islands, which act to raise the temperature of urban areas with respect to the surrounding areas (Ramsay et al., 2023). This may explain why the urban roost sites were slightly warmer than the airport records overall, over the same timeframe.

However, this trend was not significant, most likely due to the high inter-roost variability in recorded temperatures, which may be a result of the broad range of landscape and vegetation types within the study sites. It is worth noting that the hottest roost temperature we recorded (40.1°C) was 7.8°C higher than the temperature recorded at the airport for the same date, illustrating the importance of direct measurements of roost microclimates for predicting heatwave events at flying-fox roosts.

One of the limitations to this study is the collection of microclimate data from a handheld Kestrel, rather than measuring microclimate conditions in the canopy directly. Although Kestrel use to measure microclimate is a robust approach that has been replicated in other published ecological studies (Magnago et al., 2015; Patten & Smith-Patten, 2012), our expectation is that canopy climates could reach higher temperatures when there is no wind because there is limited shade. The loss of our canopy data loggers was unfortunate as it would have provided an opportunity to compare the understorey and canopy environments and we recommend that this is addressed in future research.

In Australia, flying-fox populations have been ravaged by heatwaves while at roosts (Welbergen, 2012; Welbergen et al., 2008). Between 1994 and 2008, die-offs of at least 19 flying-fox populations were attributed to extreme temperatures (Janzen, 1967; Welbergen, 2012). The microclimate characteristics of flying-fox roosts are an important contributor to the ability of these species to cope with heat stress (Bartholomew et al., 1964), and may also have a significant potential to buffer the effects of heat waves (De Frenne et al., 2021). Roost vegetation features can directly influence the success of thermoregulatory behaviours in flying-foxes. For example, wind permeability can influence the effectiveness of heat dispersion through wing fanning (Bartholomew et al., 1964), vegetation structure provides shade (Rajasegaran et al., 2018), the evapotranspiration of larger trees actively cools the air and plant cover in the understorey reduces latent heat (De Frenne et al., 2021). In a 2002 die-off event, Welbergen et al. (2008) recorded a progression of thermoregulatory behaviours presented by bats during the heatwave, starting with wing fanning, followed by shade-seeking, panting and saliva-spreading (Welbergen et al., 2008).

As flying-foxes have a wide distribution across many different habitats, it is challenging to generalize from this study to roost preferences at a larger scale. We found that although spectacled flying-fox roost sites experienced more excessively hot days during the study period than average over the past decade, maximum temperature and humidity values alone did not predict roost occupancy. However, we found that occupied roosts exhibited greater variation in temperature than unoccupied roosts, although this could be due to differences in vegetation type and the distance between sites, rather than a preference for some inherent habitat quality, as we did not find evidence that temperature and humidity influenced roost occupancy. This is in contrast to a study on grey-headed flying-foxes in Sydney, which found that bats were more likely to permanently occupy roosts with a slightly higher variance in daily temperature and humidity than other camps (Snoyman & Brown, 2010).

As we consider a future where heatwaves are becoming more frequent, supporting flying-fox populations through roost management may be one of the most feasible and effective local options available. Previous suggestions to increase tolerance to heat stress during extreme heat events recommend cooling flying-foxes by vegetation spraying, misting the animals directly and the use of ground-based sprinklers (Mo & Roache, 2021). However, these responses may worsen survival outcomes if spraying and the associated increased human presence leads to bat dispersal, an effect that could be exacerbated by the presence of young pups during the summer months which may be abandoned if roosts are disturbed (Stanvic et al., 2013). Alternatively, a preventive forecast has been developed to predict the occurrence of flying-fox die-offs, with a 24–48 h window of confidence (Ratnayake et al., 2019). This 'flying-fox forecast' uses the gridded temperature from the BOM's Australian Region domain of the 'Australian Community Climate and Earth-System Simulator' (ACCESS-R) Numerical Weather Prediction (NWP) system to evaluate air temperature in a particular area with a 42°C temperature threshold to predict a heat event. However, as the results of this study demonstrate, roost temperatures can be substantially greater than those registered by the BOM, which may result in delayed preventive action or no action. Ultimately, a better understanding of the importance of the microclimate of urban roosts and the interactions between roost occupancy, local environmental features and thermal tolerance will be needed to prevent future flying-fox mass mortality events. Improving thermal resistance to heatwaves through scientifically informed management policies, which may include the identification and monitoring of occupied roosts to reduce the risk of bats dying at these sites during heat waves. Further studies into how the composition and structure of roost vegetation can be managed to buffer the microclimate conditions of roosts would be beneficial in supporting the capacity of flying-foxes to cope with extreme heat events.

AUTHOR CONTRIBUTIONS

Camila Lopes: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (equal); methodology (lead); project administration (lead); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Cadhla Firth:** Conceptualization (equal); methodology (equal); supervision (equal); writing – review and editing (equal). **Susan G. W. Laurance:** Conceptualization (equal); methodology (equal); project administration (supporting); resources (supporting); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Data openly available in a public repository that issues datasets with DOIs. The data that support the findings of this study are openly available in Research Data JCU at https://doi.org/10.25903/vwtb-jh24.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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