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Title

Forecasting wildlife die-offs from extreme heat events

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Abstract

Extreme heat events pose increasing challenges to biodiversity conservation worldwide, yet, our ability to predict the time, place, and magnitude of their impacts on wildlife is limited. Extreme heat events in Australia are known to kill thousands of flying-foxes (*Pteropus* spp.), and such die-offs are expected to become more frequent and widespread in the future under anthropogenic climate change. There is a growing need for predicting when and where such heat-related die-offs would occur, to facilitate short-term wildlife management and conservation actions. In this study, we used gridded hourly air temperature forecasts (ACCESS-R NWP model) from the Australian Bureau of Meteorology to predict flying-fox heat-related mortality based on an empirically-determined threshold of 42.0 °C. We tested the accuracy and precision of this model using a twofold evaluation of the ACCESS-R NWP forecast air temperature during a recorded extreme heat event with *in-situ* air temperature measurements and interpolated weather station data. While our results showed a slight discrepancy between the modelled and measured air temperatures, there was no significant difference in the forecast's accuracy to predict die-offs during an extreme heat event and the overall summer period. We evaluated the accuracy of mortality predictions based on different air temperature thresholds (38.0 °C, 40.0 °C, 42.0 °C, and 44.0 °C). Our results revealed a significant probability of flying-fox mortality occurrence when forecast air temperature was ≥ 42.0 °C, while the 24-hour and 48-hour forecasts accurately predicted 77% and 73% of the die-offs, respectively. Thus, the use of 42.0 °C forecast air temperature from the ACCESS-R NWP model can predict flying-fox mortality reliably at the landscape scale. In principle, the forecaster can be used for any species with known thermal tolerance data, and is therefore a promising new tool for prioritizing adaptation actions that aim to conserve biodiversity in the face of climate change.

Key words

Heat stress, climate change, extreme weather events, heatwaves, Australian flying-foxes, *Pteropus* spp., ACCESS-R

Introduction

Heatwaves are becoming hotter, longer and more frequent under anthropogenic climate change (Meehl & Tebaldi 2004; Climate Council 2014), which poses an unprecedented threat to biodiversity and is likely to cause severe social and economic problems worldwide (Jiguet et al. 2011; IPCC 2012). Yet, our current understanding of biological responses to extreme heat events is limited, warranting an urgent need for multidisciplinary research to quantify the vulnerability of biodiversity to heat extremes (McKechnie et al. 2012; Harris et al. 2018). Moreover, predicting the occurrence, location and magnitude of impacts of extreme heat events on wildlife will become increasingly important for prioritizing adaptation actions that aim to conserve biodiversity in the face of climate change.

There are numerous reports on biodiversity being affected by extreme heat events across the globe, including historic (Johnson 1791) and more recent events (Garrahou et al. 2009; McKechnie et al. 2012). These reports indicate that wildlife mortalities due to extreme heat are becoming increasingly frequent and severe, as expected from current climate models (Parmesan et al. 2000; Meehl & Tebaldi 2004) as well as biophysical models and indices (McKechnie & Wolf 2010; Albright et al. 2011).

There are now several well-documented records of Australian flying-fox (*Pteropus* spp.) die-offs associated with extreme temperature events in excess of 42.0 °C (Welbergen et al. 2008), some dating back to the time of European settlement (Tench 1973). From the late 20th century onwards, flying-fox die-offs have been more systematically recorded along the east coast of Australia, where they are now known to occur during most summers and sometimes multiple times in the same year (Welbergen et al. 2008; personal observations). Flying-fox die-offs are expected to continue to increase over the next decades in Australia as regional climate model projections predict more frequent, longer and hotter summer heatwaves by the end of the 21st century, with increases in frequency and duration expected to be most severe in the north and increases in maximum temperature expected to be most severe in the south (Cowan et al. 2014). Some of the more recently recorded flying-fox die-offs occurred over almost biblical scales; for instance, in 2014, approximately 45,500 flying-foxes died as a result of a heat wave in southeast Queensland in a single day, with mortality rates estimated to be as high as 50% in one of the two species of flying-fox affected (Welbergen et al. 2014; see Fig. 1). Such extreme mortality risks affecting flying-fox

population dynamics (Welbergen et al. 2008) and undermining the key pollination and seed dispersal services afforded by these species (Fujita & Tuttle 1991). It also places enormous demands on wildlife management and conservation agencies and raises important human health concerns. There is therefore an urgent need to predict when and where die-offs are likely to happen, so that such agencies can respond most effectively to these events.

In this study, we cross-reference flying-fox roost locations with gridded forecast surface air temperature, obtained from the Australian Bureau of Meteorology, to develop an automated method to identify flying-fox roosts that may be affected by an extreme heat event. Our aims were to evaluate the use of forecast air temperatures during extreme heat events; test the accuracy of using forecast air temperature to predict flying-fox die-offs using real data from the largest heat-related flying-fox die-off recorded to date; and compare the differences in accuracy of a range of threshold air temperatures to predict flying-fox mortality. We also introduce the “flying-fox heat stress forecaster”, a freely available online tool that can be used to identify flying-fox roosts that may be affected by an extreme heat event, and report briefly on its utility here. We further discuss other biophysical factors that may play a role in causing heat stress in addition to the air temperature, and suggest future work to expand the utility of our approach to wildlife more generally.

Materials and Methods

Study species

Flying-foxes (*Pteropus* spp.) are large bats that form conspicuous daytime roosts in amongst the exposed branches of canopy trees (Churchill 2009). Flying-fox roosts can be located in mangroves, swamps and rainforest often beside water, and increasingly in urban locations (Churchill 2009; Tait et al. 2014). There are four species of flying-fox in mainland Australia: the grey-headed flying-fox (*Pteropus poliocephalus*), the spectacled flying-fox (*P. conspicilatus*), the black flying-fox (*P. alecto*), and the little red flying-fox (*P. scapulatus*). *P. poliocephalus* and *P. conspicilatus* are listed as vulnerable nationally in accordance to the Environment Protection and Biodiversity Conservation ('EPBC') Act 1999 (Threatened Species Scientific Committee 2001) and globally (Lunney et al. 2008). The main threats include habitat destruction, roost disturbance and culling (Eby & Lunney 2002).

Flying-fox heat stress event – case study

We used data from the largest recorded flying-fox heat stress event to test the usefulness of the Australian Bureau of Meteorology forecast weather data to predict flying-fox mortality. This heat stress event occurred on the 4 January 2014 in the southeast Queensland region, where the maximum air temperatures recorded were 38 – 44 °C and the approximate corresponding vapour pressure values were 18 – 28 hPa (data from the Bureau of Meteorology climate database, the Australian Data Archive for Meteorology (ADAM)). The region enveloped 102 flying-fox roosts of which 52 roosts had confirmed presence of mortalities and 50 had confirmed absence of mortalities. Mortality was confirmed *in-situ* for all affected camps during the days following the event. This involved exhaustive searches by wildlife ecologists of occupied camps and surrounding areas for flying-fox corpses (J. A. Welbergen, J. Martin & C. Booth, unpublished). Data from non-affected camps were supplemented by reports from state and local government, wildlife care groups and concerned citizens. We recorded hourly *in-situ* air temperature and relative humidity in one of the affected flying-fox roosts located in Gympie (26°S, 152°E) using a calibrated DS1923 iButton Hygrochron (11-Bit resolution; 0.0625 °C for temperature and 0.5% for relative humidity) deployed in permanent shade and 1.5 m above ground level. The maximum air

temperature recorded on the date was 42.4°C and the corresponding relative humidity was 23.8% (Appendix S4).

Forecast air temperature data

We used gridded forecast air temperature data from the Bureau of Meteorology's Australian Region domain of the "Australian Community Climate and Earth-System Simulator" (ACCESS-R) Numerical Weather Prediction (NWP) system for our simulations (Australian Bureau of Meteorology 2013; Puri et al. 2013). This system has a region-wide resolution of about 12km and runs four times per day (0000, 0600, 1200 & 1800 base times). We acquired and tested the 24-hour and 48-hour forecast air temperature data.

Evaluating the use of forecast air temperature during heat stress events

We defined a "heat stress event" as a day, or series of days, during which flying-fox mortality occurs in association with extreme high temperatures. The skill of the ACCESS-R NWP temperature forecast may be expected to vary with temperature extremes such as heatwaves (Shrestha et al. 2013). In meteorological terms, the forecast skill is the relative accuracy of the forecast against a reference forecast (Murphy 1993). We used *in-situ* measured data and interpolated weather station data to evaluate the skill of the ACCESS-R model forecasts to predict flying-fox die-offs at extreme high temperatures. We extracted interpolated weather station data to obtain daily maximum air temperature for the Gympie roost from historical continent-wide 0.05°grids (c. 5 km) compiled via the Australian Water Availability Project (AWAP) database (Jones et al. 2009; Raupach et al. 2009). We assessed the ACCESS-R forecast separately for the extreme heat event date on the 4 January 2014 and the entire summer period from 2 December 2013 to 18 February 2014. We used three commonly used continuous verification scores to evaluate the ACCESS-R NWP forecast skill during heat stress events: root-mean-square error (RMSE), bias, and correlation coefficient.

Testing the accuracy of using forecast air temperature to predict flying-fox die-offs

We retrieved the longitude and latitude of all 102 roosts located in the case study area from the National Flying-fox Monitoring Program (<http://www.environment.gov.au/node/16393>).

We obtained the forecast maximum air temperature (24-hour and 48-hour) of the 102 roosts from ACCESS-R NWP system on the extreme heat event date. Then we compared the presence or absence of mortality at each roost site with the corresponding forecast maximum air temperature of that site in the 24-hour and 48-hour forecasts. We defined 42.0 °C forecast air temperature as the threshold for occurrence of an extreme heat event (Welbergen et al. 2008).

We used a contingency table to sum up the outcomes of the extreme heat event predictions (Table 1). There were four possible outcomes; an event is forecast and occurs ("Hit"), an event is forecast but does not occur ("False Alarm"), an event was not forecast but does occur ("Miss"), and an event is not forecast and does not occur ("Correct Negative") (Fig. 1).

We calculated the Probability of Detection, False Alarm Ratio, Frequency Bias and Critical Success Index using the contingency table (Table 2). Probability of Detection measures the fraction of deaths that were correctly predicted and is insensitive to false alarms. False Alarm Ratio provides the fraction of instances where the forecast air temperature was ≥ 42.0 °C but no deaths occurred and ignores the misses. Frequency Bias gives the ratio of frequency of deaths to instances where forecast temperature was ≥ 42.0 °C and does not take into account accuracy. Critical Success Index gives the fraction of all predicted and observed events that were correctly diagnosed and considers both false alarms and misses.

Table 1. Contingency table showing the occurrence or non-occurrence of death in flying-fox colonies in the southeast Queensland area on the 4 January 2014 when threshold air temperature is 42.0 °C

Forecast air temperature ≥ 42.0 °C	Occurrence of death in a flying-fox colony	
	Yes	No
24-hour forecast		
Yes	37	8
No	15	42
48-hour forecast		
Yes	44	19
No	8	31

Table 2. Categorical verification scores used to quantify the accuracy of the forecasts in predicting flying-fox die-offs

Score	Formula	Range	Perfect
Probability of Detection	Hits ^a / (Hits + Misses ^b)	[0, 1]	1
False Alarm Ratio	False Alarms ^c / (Hits + False Alarms)	[0, 1]	1
Frequency Bias	(Hits + False Alarm) / (Hits + Misses)	[0, ∞]	1
Critical Success Index	Hits / (Hits + Misses + False Alarms)	[0, 1]	1

^aA “Hit” occurs when an event is forecast and occurs

^bA “Miss” occurs when an event was not forecast but does occur

^cA “False Alarm” occurs when an event is forecast but does not occur

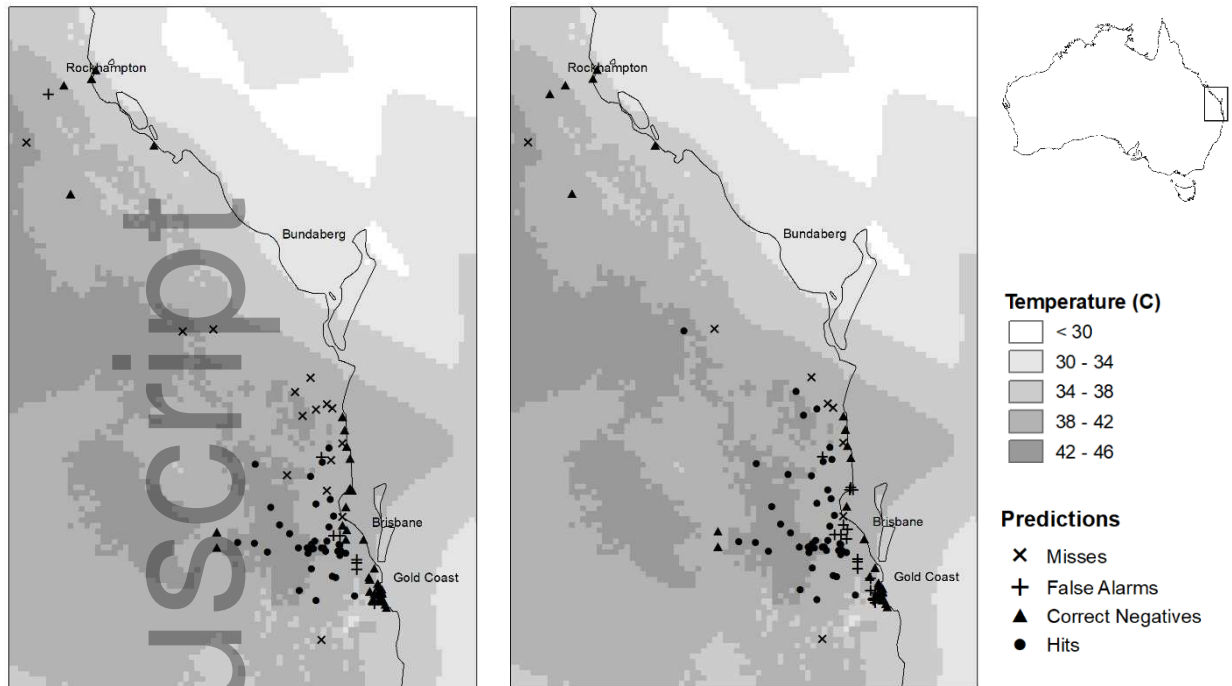


Figure 1. The locations of the flying-fox roosts in the heatwave-affected southeast Queensland area (January 4, 2014). The four possible outcomes of the extreme heat event predictions were: a 'Hit', where an event is predicted and occurred; a 'Correct Negative', where an event is not predicted and did not occur; a 'Miss', where an event was not predicted but did occur; and a 'False Alarm' where an event was predicted but did not occur. The heat map depicts the maximum air temperature observed on the extreme heat event day (data from the Bureau of Meteorology climate database, the Australian Data Archive for Meteorology (ADAM)).

Evaluating the use of different air temperature thresholds to predict flying-fox mortality

We used data from the case study to evaluate the utility of ≥ 42.0 °C as the air temperature threshold value for extreme heat event die-offs. A binomial logistic regression model was fitted to estimate the probability of occurrence of death (outcome variable; 1 or 0 for death occurred or did not occur, respectively) when forecast air temperature is ≥ 42.0 °C (exposure variable; 1 or 0 for forecast air temperature ≥ 42.0 °C or < 42.0 °C, respectively) (Appendix S1). We calculated odds ratios as a measure of association between the occurrence of death and forecast air temperature being ≥ 42.0 °C. The 95% confidence interval (CI) was used to estimate the precision of the odds ratio. We reported odds ratio (OR) values as OR (Standard Error of log (odds)). The above calculations were also made using 38.0 °C, 40.0 °C, and 44.0 °C air temperatures as thresholds. All analyses were conducted in R version 3.3.2 (R Core Team 2016).

We also generated contingency tables using 38.0 °C, 40.0 °C, and 44.0 °C air temperatures as thresholds (Appendix S2) and calculated the above mentioned categorical verification scores to compare with the recommended threshold of 42.0 °C.

Flying-fox heat stress forecaster

We developed the “Flying-fox Heat Stress Forecaster” to assist different stakeholders who are affected and need to respond to the extreme heat events, *e.g.* land managers and wildlife carers. Briefly, the forecaster predicts which flying-fox roosts are most likely exposed to extreme heat up to 72 hours into the future (<http://www.animalecologylab.org/ff-heat-stress-forecaster.html>). Roost data, acquired from the National Flying-fox Monitoring Program, are updated quarterly, and provide georeferenced information on all known flying-fox roosts in Australia, including the estimated population size class of each roost. This enables stakeholders to prioritize management effort depending on the number of bats that may be affected by heat stress. Every six hours we obtained the latest ACCESS-R air temperature forecast, which was queried in the R programming environment to find flying-fox roosts exposed to air temperatures above 38 °C (heat stress threshold) and 42 °C (mortality threshold). Our scripts then generated mapped forecasts of affected areas, hourly temperature profiles of

229 affected roosts, and roost “priority lists” (prioritized according to time, maximum
230 temperature reached and population size).

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Results

Evaluating the use of forecast air temperature during heat stress events

Considering the entire summer period of 2013/2014, the RMSE between the *in-situ* air temperatures and ACCESS-R forecast air temperatures was 2.31 °C. However, more specifically, on the extreme heat event date, the RMSE was 1.41 °C between the measured and forecast air temperatures (Table 3). The bias of the measured and forecast air temperatures for overall summer period was 1.32 °C, and for the extreme heat event date it was 0.91 °C (Table 3). The measured and forecast air temperatures were highly correlated for the summer period (Spearman's $\rho = 0.82$, $p < 0.001$) and for the extreme heat event date (Spearman's $\rho = 0.99$, $p < 0.001$) (Fig. 2 and 3). All three verification scores showed that the error and bias of the ACCESS-R forecast's skill during extreme conditions and the general summer period were similar. The RMSE score between the AWAP maximum air temperatures and ACCESS-R forecast maximum air temperatures in summer was 2.39 °C, while the bias was 1.27 °C. Furthermore, the AWAP maximum air temperatures and ACCESS-R forecast maximum air temperatures throughout the summer were highly correlated (Spearman's $\rho = 0.81$, $p < 0.001$).

The accuracy of using forecast air temperature to predict flying-fox die-offs

When using the threshold as 42.0 °C, predictions of mortality showed an overall percentage correct (considering both Hits and Correct Negatives) of 77.5% for the 24-hour air temperature forecast and 73.5% for the 48-hour air temperature forecast (Table 4). The Probability of Detection of mortality in the 24-hour air temperature forecast was greater than that of the 48-hour air temperature forecast. However, both the False Alarm Ratio and Frequency Bias were greater in the 24-hour air temperature forecast. The Critical Success Indices were similar in both the 24-hour and 48-hour air temperature forecasts, indicating similar success rates of identifying a heat stress event.

Table 3. Verification scores of the ACCESS-R air temperature forecast

Verification score	Extreme heat event date iButton ^a	Summer ^b	
		iButton	AWAP
RMSE ^c	1.41	2.31	2.39
Bias (forecast – observed)	0.91	1.32	1.27
Spearman coefficient (rho, p<0.001)	0.99	0.82	0.81

^aCalculations made considering hourly air temperatures measured using iButtons on 4 January 2014

^bCalculations made considering daily maximum air temperatures on each day of summer (i.e., from 2 December 2013 to 18 February 2014) using iButton measurements and AWAP (Australian Water Availability Project) database

^cRMSE, Root mean square error

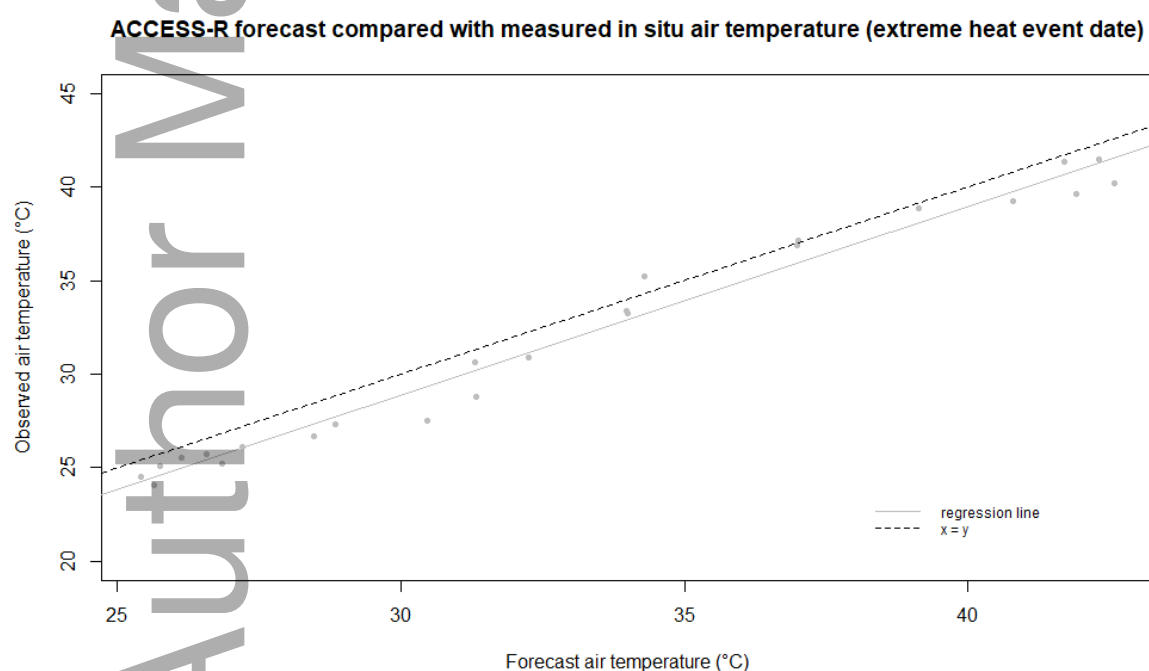
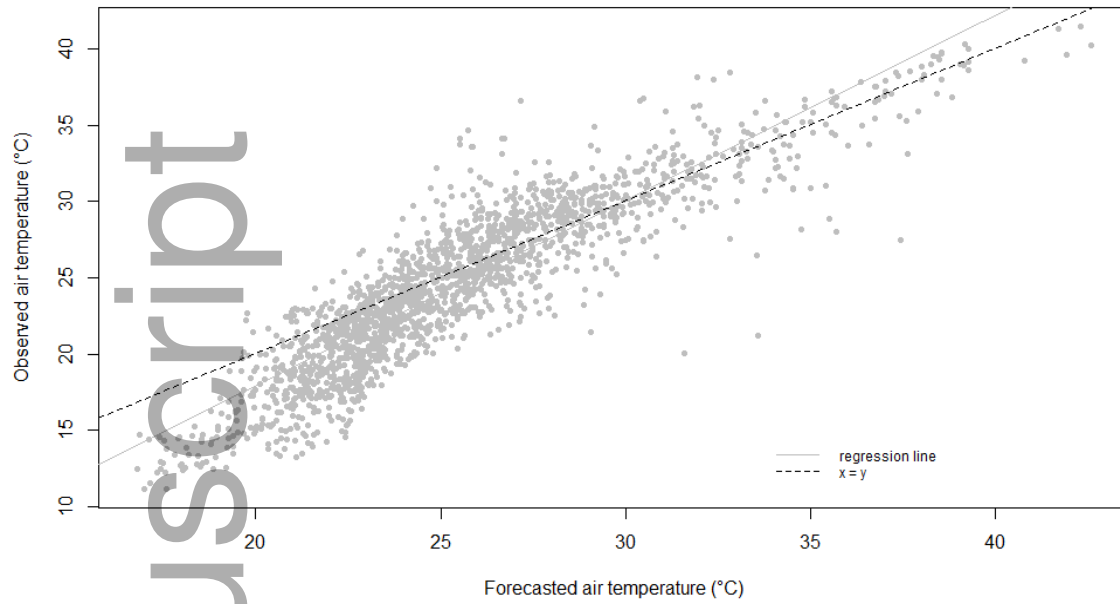


Figure 2. ACCESS-R forecast compared with the measured *in-situ* air temperature on the extreme heat event data (4 January 2014)

ACCESS-R forecast compared with measured in situ air temperatures (summer 2013-2014)



268

269 Figure 3. ACCESS-R forecast compared with the measured *in-situ* air temperature for

270 summer 2013 – 2014.

Table 4. The accuracy and categorical verification scores for the 24-hour and 48-hour forecasts of the flying fox die-off on the 4 January 2014 for different air temperature thresholds

Accuracy / Score	24-hour forecast ^a				48-hour forecast ^b			
	38.0 °C	40.0 °C	42.0 °C	44.0 °C	38.0 °C	40.0 °C	42.0 °C	44.0 °C
Accuracy ^c	76.5%	79.4%	77.5%	52.9%	72.6%	73.5%	73.5%	58.8%
POD ^d	0.96	0.94	0.71	0.11	0.96	0.94	0.85	0.44
FAR ^e	0.31	0.27	0.18	0.25	0.34	0.33	0.30	0.36
FBI ^f	1.38	1.29	0.86	0.15	1.46	1.40	1.21	0.69
CSI ^g	0.68	0.70	0.62	0.11	0.64	0.64	0.62	0.35

^{a,b}Definitions: 38.0 °C, 38.0 °C threshold results; 40.0 °C, 40.0 °C threshold results; 42.0 °C, 42.0 °C threshold results; 44.0 °C, 44.0 °C threshold results

^cAccuracy was calculated considering the sum of “Hits” and “Correct Negatives”. A “Hit” occurs when an event is forecast and occurs. A “Correct Negative” occurs when an event is not forecast and does not occur.

^dProbability of Detection

^eFalse Alarm Ratio

^fFrequency Bias

^gCritical Success Index

Evaluation of different air temperature thresholds to predict flying-fox mortality

In the 24-hour forecast, there was a 12.95 (0.49) fold increase in the odds of death when forecast air temperature is ≥ 42.0 °C compared to when air temperature is < 42.0 °C, whereas in the 48-hour forecast there was a 9.00 (0.48) fold increase in the odds of death in the same conditions (Table 5). Both odds ratios indicate that there was a significant ($p < 0.001$) probability that flying-foxes will die when the forecast air temperature is ≥ 42.0 °C,

irrespective of the forecast used. This implies that either forecast, 24-hour or 48-hour, can be used to make informative predictions of the die-offs.

The odds ratios of the 38.0 °C and 40.0 °C thresholds were greater than that of the 42.0 °C threshold in both 24 and 48-hour air temperature forecasts (Table 5), implying that the use of 38.0 °C and 40.0 °C thresholds would provide a better accuracy for predicting deaths. However, the 95% CI was much larger in both the 38.0 °C and 40.0 °C thresholds compared to the 42.0 °C threshold, which indicates that the precision of the predictions made using a 42.0 °C threshold will be greater compared to the 38.0 °C and 40.0 °C thresholds. The odds ratios of the 44.0 °C threshold for both the 24-hour and 48-hour forecasts were comparatively low and, more importantly, the lower bound of the 95% CI went below 1.0. This indicates that if 44.0 °C is used as a threshold the odds ratio has a possibility of being 1.0, meaning there could be a greater chance of mortality when the air temperature is <44.0 °C compared to ≥44.0 °C. Thus, 44.0 °C is an unsuitable air temperature threshold for forecasting flying-fox heat stress related mortality.

Table 5. Logistic regression model outputs for different forecast air temperature thresholds on the occurrence of flying-fox death

Threshold ^a	Odds Ratio (OR)	Standard error of log(OR)	p-value	95% Confidence interval of OR	
				Lower	Upper
24-hour forecast					
38.0 °C	31.82	0.78	< 0.001	6.96	145.43
40.0 °C	29.05	0.66	< 0.001	7.91	105.34
42.0 °C	12.95	0.49	< 0.001	4.93	34.00
44.0 °C	3.13	0.84	< 0.001	0.60	16.31
48-hour forecast					
38.0 °C	23.08	0.77	< 0.001	5.06	105.34
40.0 °C	17.69	0.66	< 0.001	4.87	64.34
42.0 °C	9.00	0.48	< 0.001	3.49	23.09
44.0 °C	2.26	0.43	< 0.001	0.98	5.21

^aAir temperature threshold used in calculations. Definitions: 38.0 °C, 38.0 °C threshold results; 40.0 °C, 40.0 °C threshold results; 42.0 °C, 42.0 °C threshold results; 44.0 °C, 44.0 °C threshold result

When considering the accuracy of the forecast, the 38.0 °C threshold had a high correctness of 76.5% for the 24-hour forecast and 72.6% for the 48-hour forecast (Table 4). An even higher percentage correctness was shown by the 40.0 °C threshold with 79.4% for the 24-hour forecast and 73.5% for the 48-hour forecast. Both the 42.0 °C and 40.0 °C thresholds thus act as good cut-off points with very high accuracies to predict flying-fox mortality. The 44.0 °C threshold had the lowest percentage correctness in both forecast lead times compared to the other thresholds considered (Table 4).

The Probability of Detection of die-offs when using either air temperature forecast was lowest in the 44.0 °C threshold (Table 4). The Frequency Bias, False Alarm Ratio, and Critical Success Index of die-off predictions showed similar values when using the 38.0 °C, 40.0 °C, and 42.0 °C thresholds. However, the Frequency Bias and the Critical Success Index when

using 44.0 °C as the threshold were comparatively lower. This further reiterates that using 44.0 °C threshold has a lower accuracy compared to the other thresholds.

Flying-fox heat stress forecaster

Our “flying-fox heat stress forecaster” website went live in time for a heat stress event which occurred in February 2017 (Fig. 4). This shared information was shown to be valuable to many stakeholders in South Australia and New South Wales in allocating their limited resources efficiently towards colonies that were likely to be worst affected. For instance, the Singleton flying-fox roost was on the top of our “priority list” during this heat stress event, and in fact was one of the worst affected roosts (ABC North Coast 2017). We currently have 86 subscribers signed up for ‘heat stress alert’ updates. The subscribers include government officials, wildlife rehabilitators, human healthcare professionals, and consultants.

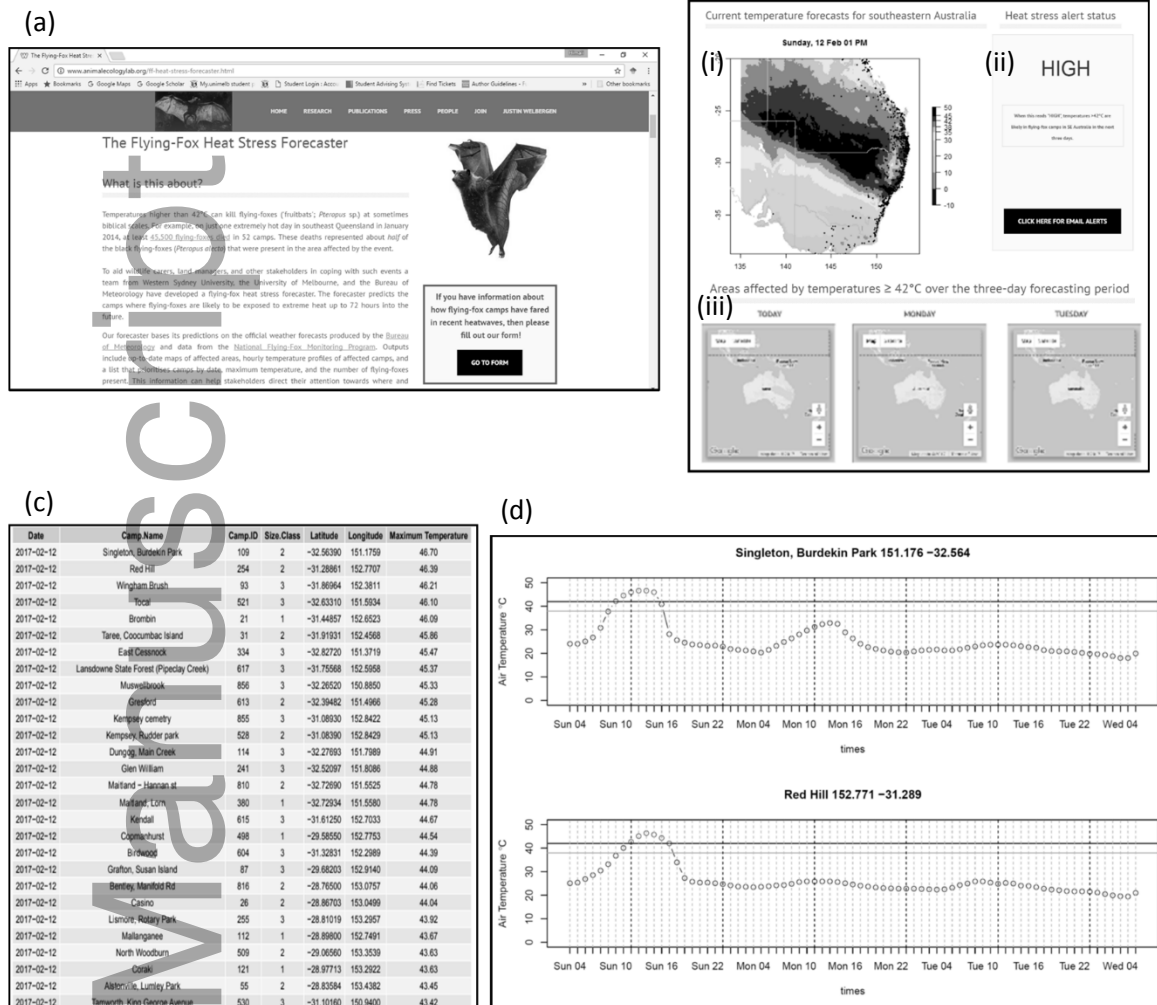


Figure 4. Web interface and auto generated output displayed on the Flying-fox Heat Stress Forecaster website (<http://www.animalecologylab.org/ff-heat-stress-forecaster.html>). (a) Brief description about the forecaster and how it operates. Further details and useful links are provided at the bottom of the webpage. (b) (i) Animated GIF showing temperature forecasts of up to 72 hours in southeastern Australia with black dots representing the flying-fox roost sites; (ii) Heat stress alert status, which is set to 'high' when roosts in Australia are expected to reach and/or exceed 42°C (mortality threshold). The alert status is set to 'moderate' when roosts are expected to be subjected to air temperatures between 38°C – 42°C, and to 'low' when all roosts are expected to be subjected to air temperatures <38°C. Stakeholders (or anyone interested) may also sign up to receive email alerts when the heat stress alert status is high; (iii) Interactive map depicting areas in Australia affected by temperatures ≥42°C. (c) Detailed “priority list” of all known currently occupied roosts that

346 are forecasted to experience temperatures $\geq 42^{\circ}\text{C}$. Roosts are first grouped by date and then
347 ranked by maximum forecast temperature. The population size class as well as the longitude
348 and latitude location of each roost is provided. (d) Hourly temperature profiles of each roost
349 that is forecasted to experience temperatures $\geq 42^{\circ}\text{C}$.

Discussion

Extreme heat events can cause mass scale disasters to biodiversity and our study shows that at least in flying-foxes these impacts can be predicted with great spatiotemporal accuracy and precision. Thus, our forecasting model, which uses gridded forecast air temperatures from the Australian Bureau of Meteorology, can be utilized as an early warning system that increases the preparedness of wildlife management and conservation agencies to such impacts, especially under future climate change scenarios. This allows for the efficient allocation of management resources towards locations that are likely to be most affected.

A concern when using a gridded forecast system is whether the forecast air temperature represents the air temperature experienced by the flying-foxes *in-situ*. Microhabitat conditions experienced by an animal, especially during extreme weather, can vary significantly from the broader weather conditions experienced at the landscape scale (Evans 1939; Johansson 1974). We used the different verification scores to assess such differences in the overall habitat and microhabitat conditions. When comparing the *in-situ* measured air temperature with the ACCESS-R forecast air temperature, the RMSE on the extreme heat event date was 1.41 °C and the bias was 0.91 °C. This reiterates that there is a discrepancy in the air temperature values between the habitat (i.e., ACCESS-R forecast) and microhabitat (i.e., *in-situ* measurement). The bias, which measures the difference between the forecast and measured temperatures, indicates that the forecast overestimates the measured temperatures in general by a small amount, but this overestimation is less in the extreme heat events. This small positive bias in the forecast temperature could be because the forecast (and AWAP) temperatures are for near-surface air temperature in the shade, while the *in-situ* temperatures are in the trees, which are further off the ground. The measured and forecast air temperatures showed a significantly strong correlation during the whole summer period as well as on the extreme heat event date (Spearman's $\rho > 0.9$ and $p < 0.001$). Further testing on a broader range of roosts that flying-foxes may occupy is needed to see if there is a variation in this discrepancy at different locations. Once the discrepancy is well-defined and if it has little variation between sites and times, forecast air temperature can be an excellent indicator of the roost ambient temperature.

Several studies highlight the difficulty in predicting extreme weather events (Barnston & Mason 2011; Hamilton et al. 2012). In our study, the mean RMSE and bias between the

forecast and *in-situ* air temperatures were greater for the summer period compared to the extreme heat event date, and there was a strong correlation between the forecast and *in-situ* air temperatures during both the summer period and extreme heat event date. Importantly, this shows that the ACCESS-R NWP forecast skill to predict an extreme heat event is no less, and possibly higher, than the forecast skill to predict the air temperature on an average summer day.

Our results show that the 24-hour air temperature forecasts have a greater accuracy of predicting flying-fox mortality compared to the 48-hour forecasts. This is expected as forecasts typically have smaller errors with shorter lead time to issue forecasts (Shrestha et al. 2013; Zhang et al. 2014). However, the Critical Success Rates when predicting flying-fox die-offs of both forecasts are similar and thus both forecasts can be considered useful for making die-off predictions.

Our study also demonstrates that the use of 40.0 °C and 42.0 °C air temperatures as thresholds for mortality have accuracies >73% in both the 24-hour and 48-hour lead times. However, comparing the accuracy and each of the categorical verification scores (Table 4), and also considering the empirical findings in Welbergen et al. (2008), where it was found that more than 80% of the roosts that underwent mortality due to extreme heat experienced *in-situ* air temperatures exceeding 42.0 °C, we recommend using 42.0 °C air temperature, as opposed to 40.0 °C, as the cut-off value for flying-fox mortality. From a management perspective, employing such a basic yet accurate guideline is extremely useful, especially when coordinating with a large number of trained and voluntary persons that engage in managing flying-fox roosts across Australia.

Based on the forecaster model that was tested here, we developed the “Flying-fox Heat Stress Forecaster” to aid those involved in managing flying-fox roosts during extreme heat events. Prior to this, predictions were made manually using publicly available resources. This tedious process also had limitations in accuracy due to the lag between the latest weather forecast updates and when the predictions were made. Our Forecaster’s preliminary phase of operation attracted a large number of users and proved useful in managing heat stress events by facilitating a coordinated, cross-stakeholder response (e.g., organize labour to visit roosts, prepare resources to care for casualties and abandoned pups, organize the disposal of dead bats, etc.). The Forecaster website also provides a data submission facility

to document observations from affected and unaffected camps. These citizen science inputs can improve the accuracy of the forecaster and our understanding of the impacts that extreme heat events have for the longer-term persistence of the species.

The accuracy of our 24-hour and 48-hour forecaster models were high (77% and 73%, respectively) despite the intrinsic inaccuracy of weather forecasts at small spatial scales. However, the total heat load on an organism also depends on other environmental factors such as humidity, wind speed, and solar radiation as well as on traits of the animal, for example fur depth and solar reflectance, body mass, and posture (Porter & Gates 1969). In particular, the rate of evaporative heat dissipation is a function of the difference between the absolute humidity of the animal surface and that of the external environment (Lasiewski, Acosta & Bernstein 1966; Webster & King 1987; Powers 1992), and when the air is saturated with moisture (i.e. at high relative humidity) an animal's ability to lose heat through evaporative cooling can be constrained (Adolph 1947). A common strategy adopted when managing flying-fox colonies during heat stress events is to spray water onto the trees where flying-foxes roost or directly on to the bats. This action may influence the water vapour pressure levels of the air surrounding a flying-fox and, in turn, risk constraining the ability of the bat to use evaporative cooling to dump heat when heat stressed (Licht & Leitner 1967). Thus, the influence of relative humidity on evaporative heat dissipation warrants further study on the effect of variation in vapour pressure deficit on the heat budget of flying-foxes.

By considering the effects of air temperature along with other environmental factors and traits of the animal in a biophysical model (Porter et al. 2000; Porter & Mitchell 2006) it should be possible to increase the accuracy of the mortality predictions further. Moreover, using a biophysical model and understanding the mechanistic links between organisms and their environments we can create a robust platform to make projections over much longer timescales, and thereby enable the assessment of the impacts of climate change on a species as a whole (Mathewson & Porter 2013; Briscoe et al. 2016). A biophysical model parameterised for Australian flying-foxes will allow us to identify which variables drive flying-fox heat stress. This will enable us to propose effective solutions to control the heat stress-related mortality by controlling the key elements involved.

With the uncertainty involved with climate change and the expected increase in intensity, duration and frequency of extreme heat events, it is essential that ecologists, conservation biologists and wildlife managers are prepared for unknown challenges that may arise. Likewise, they need to be sufficiently prepared for issues that already occur which may be aggravated in future. The flying-fox die-offs have caught our attention especially because of the high detectability due to their gregarious nature and conspicuous roosting behaviour. Thus, they can be considered a good bioindicator of heat stress on other animals that may be more cryptic or occur in fewer numbers. Consequently, the flying-fox forecaster can be used to gauge the effect of extreme heat events on other affected wildlife, and if thermal tolerance data are known the forecaster can provide heat stress information for any species. Thus, such a simple yet effective forecasting tool can enable the conservation of potentially any species, and would be a valuable asset to possess given global climate change threats.

Supporting Information

Additional information on the binomial logistic regression model (Appendix S1) and contingency tables for the occurrence of death at different forecast air temperature thresholds (Appendix S2) are available online. We have also provided the R code used in the analysis (Appendix S3) and the *in-situ* measured air temperatures and relative humidity at the Gympie roost site (Appendix S4).

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