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Estimating flying-fox mortality associated with abandonments of pups and extreme heat events during the austral summer of 2019–20

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Abstract. Mass mortalities in flying-foxes occur in summers that reach extremely hot temperatures. In this study, we examine the spatiotemporal distributions of mortality from pup abandonments and extreme heat events in Australian flying-fox camps during the 2019–20 summer. We recorded data on flying-fox mortality in known affected camps and applied a standard method to estimate the number of deaths. Pup mortalities from abandonments were recorded in 10 camps in New South Wales. A minimum estimate of 2612 flying-foxes died in pup abandonments, the majority of which occurred in one camp in Bomaderry. Die-offs from extreme heat events were recorded in 40 camps associated with eight separate heat events in south-eastern Australia. A minimum estimate of 72 175 flying-foxes died during these heat events, which all occurred within the range of the threatened grey-headed flying-fox (*Pteropus poliocephalus*). Further, 409 and 2251 live flying-foxes were taken into care from pup abandonments and heat events respectively. The minimum mortality estimated represents the highest recorded mortality of Australian flying-foxes within a single summer. This highlights a need to restore vegetation in flying-fox foraging areas and camps, address anthropogenic climate change and gather more empirical data to inform heat stress interventions to minimise flying-fox mortalities.

Keywords: climate change, extreme weather, heat stress, *Pteropus poliocephalus,* summer, threatened species, wildlife conservation, wildlife rehabilitation.

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Introduction

Mass mortality events in animals provide important triggers for wildlife management and conservation as they may remove a substantial proportion of a population within a short period of time, which, in turn, can affect the dynamics and overall viability of wildlife populations (e.g. Frick *et al.* 2010; Mason-Romo *et al.* 2018), as well as the structure and function of ecosystems (e.g. McDowell *et al.* 2017; Godfree *et al.* 2019). For managers, die-offs highlight the stressors that are potentially important population-level threats for particular species (Kock *et al.* 2018), such as disease (Isidoro-Ayza *et al.* 2019; Gizzia *et al.* 2020), nutritional deficiency (Jones *et al.* 2019), chemical factors such as poisoning (Richards *et al.* 2017), and physical factors such as extreme weather events, including those associated with droughts (Foley *et al.* 2008) and extreme heat (Welbergen *et al.* 2008; Pruvot *et al.* 2019; Till *et al.* 2019). Such extreme weather events are set to escalate under climate change (Easterling *et al.* 2000; Meehl and Tebaldi 2004), and thus understanding how animal populations are affected is key for addressing future challenges for wildlife management and conservation (Maxwell *et al.* 2019).

Flying-foxes (genus *Pteropus*) are phytophagous megachiropteran bats that play an important role in forest ecosystems as long-distance pollinators and seed dispersers (Eby 1991; Fujita and Tuttle 1991; Southerton *et al.* 2004); however, a large proportion of flying-fox taxa are at some risk of extinction (Vincenot *et al.* 2017). Their ecological function is likely encumbered by large reductions in their numbers (McConkey and Drake 2006). In Australia, two of the four mainland flying-fox species, the grey-headed flying-fox (*P. poliocephalus*) and the spectacled flying-fox (*P. conspicillatus*), are federally listed as threatened with extinction (Westcott *et al.* 2015). A highly-mobile species (Welbergen *et al.* 2020), *P. poliocephalus* occurs in eastern and southern Australia as a single interbreeding population (Webb and Tidemann 1996), sharing substantial parts of its range with the black flying-fox (*P. alecto*) and little red flying-fox (*P. scapulatus*) (Roberts *et al.* 2012). Past surveys indicated a population decline of at least 30% between 1989 (Parry-Jones 2000) and 1998 (Eby *et al.* 1999). Recent surveys place population estimates at approximately 680 000 individuals (Westcott *et al.* 2015).

Flying-foxes are seasonal breeders, typically producing one pup per year (Martin *et al.* 1996). In both *P. poliocephalus* and *P. alecto*, males generally establish territories in camps in January prior to nursing females weaning their pups from the previous cycle (Eby 1995; Welbergen 2011). Copulation typically occurs from February to May (Martin and McIlwee 2002; Connell *et al.* 2006). Pups are born mainly in October and November (Eby 1995), and remain with their mothers for at least 3–4 months (Martin *et al.* 1996; Markus and Blackshaw 2002; Welbergen 2011). Nursing females initially carry pups during foraging forays but start to leave them in camps after 3 weeks (Eby 1995). At around 12 weeks of age, juveniles begin venturing out of the camps on their own account (Welbergen 2010). As a consequence of this reproductive phenology, the timing of gestation commonly coincides with seasonal food resource bottlenecks in winter and spring (Eby *et al.* 1999; Parry-Jones and Augee 2001; Law *et al.* 2002). Furthermore, these bottlenecks are exacerbated by large-scale habitat destruction, particularly the removal of winter foraging habitat (Eby *et al.* 1999). Mass die-offs in pups are generally caused by dehydration or starvation following the continued absence of nursing females prior to weaning. This may occur for various reasons, including when pups are abandoned by nursing females suffering nutritional stress or when pups are orphaned when nursing females are killed while foraging (Parry-Jones 2000; Divljan *et al.* 2011). Pups separated from their mothers represent a major component of flying-foxes requiring *ex-situ* rehabilitation by wildlife carers (Mo *et al.* 2021*a*).

Mass die-offs in flying-foxes also occur during extreme heat events (Welbergen *et al.* 2008). This represents an emerging issue, particularly for *P. poliocephalus*, *P. alecto* and *P. conspicillatus* (Welbergen 2012; McKechnie and Wolf 2019), as extreme heat events become increasingly frequent and severe due to anthropogenic climate change (Meehl and Tebaldi 2004; Steffen *et al.* 2014). Furthermore, the hottest months of the year coincide with the time when flying-foxes rear their pups (Snoyman *et al.* 2012). Apart from ambient temperatures, the severity of heat stress in animals is influenced by a range of environmental factors such as humidity, wind speed, solar radiation, roost vegetation condition (affecting availability of shade refuge), and consecutive days of very high temperatures (Bohmanova *et al.* 2007; Ratnayake *et al.* 2021). The internal factors influencing heat stress severity include solar reflectance, fur depth, body mass, posture and pre-existing health status (Porter and Gates 1969; Bohmanova *et al.* 2007; Ratnayake *et al.* 2021). Both megachiropteran and microchiropteran bats deploy a predictable sequence of thermoregulatory behaviours with increasing ambient temperatures (Welbergen *et al.* 2008): wing-fanning to induce forced convection (Laburn and Mitchell 1975); shade-seeking to reduce exposure to solar radiation exposure (Licht and Leitner 1975*a*); and salivation and panting to induce evaporative cooling (Bartholomew *et al.* 1964; Licht and Leitner 1975*b*). However, flying-foxes begin dying from hyperthermia when ambient temperatures exceed 42°C (Welbergen *et al.* 2008), at which stage thermoregulatory behaviours are insufficient to stop body temperatures reaching critical thresholds. Published rescue data for *P. poliocephalus* suggest that extreme heat events are major causes of mortality, alongside powerline electrocutions and fruit-netting and barbed-wire entanglements (Tidemann and Nelson 2011; Scheelings and Frith 2015; Mo *et al.* 2021*a*). Despite frequent representation of this issue in news media, there are few documented estimates of flying-foxes lost in these die-offs in scientific literature (Welbergen *et al.* 2008; Ratnayake *et al.* 2019).

During the austral spring and summer of 2019–20, there were die-offs of *P. poliocephalus* and *P. alecto* in eastern and south-eastern Australia from a sequence of circumstances associated with prolonged drought. Initially, a starvation event across a broad area of northern New South Wales (NSW) and south-eastern Queensland resulted in a large but unquantified number of adult flying-fox deaths (Cox 2019; Heathcote 2019), possibly in the tens of thousands based on anecdotal reports from wildlife carers. There were then die-offs of flying-fox pups in south-eastern NSW, which we assumed resulted from nursing females abandoning or becoming separated from them. These die-offs were followed by further die-offs of both adults and young from extreme heat events across south-eastern Australia. Finally, there were several concurrent megafires, termed the Black Summer bushfires, which burnt more than 10 million hectares of mostly temperate forests (Boer *et al.* 2020; Nolan *et al.* 2020), substantially reducing available foraging habitat for flying-foxes. This was compounded by subsequent heavy rainfall in some areas, which likely induced further starvation from the temporary depletion of pollen and nectar supplies. Although the full extent of the impacts of these events is difficult to establish, the overall impact was likely substantial for flying-foxes, and especially for *P. poliocephalus* as these events occurred over a large proportion of this species' range. Die-offs from abandonments of pups and extreme heat events were localised in camps, which made a collaborative data gathering effort possible so that mortality could be quantified.

In this study, we examined the spatiotemporal distributions of flying-fox mortality in camps known to us from abandonments of pups and extreme heat events during the 2019–20 summer in Australia. We provide conservative estimates of the number of flying-foxes killed in these circumstances, and discuss the implications of such events on flying-fox conservation and management, particularly the need for research to inform heat stress management and building capacity for the wildlife rehabilitation sector.

Materials and methods

Data collection

Die-offs of pups were observed in camps prior to any extreme heat events occurring in those regions during the study period. We assumed these mortalities were due to nursing females abandoning their pups, although we did not gather specific evidence to confirm this. We defined abandonments of pups as events that observers found at least 10 dead pups in a camp within a short period of time (e.g. 1–8 days). This definition excludes circumstances in which fewer carcasses are found in camps, which can be considered normal thresholds during pup-rearing season (M. Mo, J. Hopper, pers. obs.). We became aware of these die-offs from site visits, either as part of routine inspections to monitor camp size, searches for injured flying-foxes, or responsive inspections triggered by reports of injured and dead flying-foxes from the public. Abandonments of pups were distinguished from die-offs caused by extreme heat by (1) the lack of high ambient temperatures at these camps within 5 days prior to observations of carcasses (extreme heat events in flying-fox camps typically involve ambient temperatures exceeding 42°C; Welbergen *et al.* 2008), and (2) carcasses in these camps comprising solely of pups.

We defined die-offs from extreme heat events as a day or series of days during which flying-fox deaths occurred in association with high ambient temperatures, adapted from Ratnayake *et al.* (2019). Wildlife carers and land managers anticipated extreme heat events in their local areas by observing meteorological forecasts for predictions of ambient temperatures above 42°C. This includes monitoring of forecasts made by the Flying-fox Heat Stress Forecaster (Lab of Animal Ecology 2020*a*), which presents spatially-explicit forecasts of which flying-fox camps are likely to experience heat stress up to 3 days into the future (Ratnayake *et al.* 2019). Die-offs from extreme heat events were determined from attending camps during or within 5 days of high ambient temperatures and recording dead flying-foxes. These observations were made by a large number of people including wildlife carers, other volunteers and local and state government staff. Unlike pup abandonments, die-offs from extreme heat events would generally involve deaths in both adult and young flying-foxes (Welbergen *et al.* 2008). All deaths directly associated with high ambient temperatures were attributed to extreme heat events.

We collected information on die-offs from pup abandonments and extreme heat events from persons attending affected camps. Details of camp locations, dates, indicative temperatures from the nearest weather station (Australian Bureau of Meteorology 2020), flying-fox species present at the camp and numbers of flying-foxes that died or were taken into *ex-situ* rehabilitation were collated. The information was collected through formal and informal peer-to-peer networks: these included Wildlife Health Australia's Bat Health Focus Group, which comprises representatives of federal and state government departments of agriculture, public health and environment, research organisations, veterinarians, wildlife carers and other relevant organisations; the NSW Flying-fox Consultative Committee, which comprises representatives of government agencies, not-for-profit organisations and the agricultural sector; and the NSW Flying-fox Land Managers' Network, an email-based network comprising local councils and other public land managers. Information was also collected through an online data form hosted by Western Sydney University's Lab of Animal Ecology (2020*b*). The data captured were therefore dependent on the location of observers available to attend camps and not expected to be evenly distributed throughout the range of *P. poliocephalus*, *P. alecto*, and *P. conspicillatus*.

Numbers of dead flying-foxes were obtained through direct counts where possible. However, in some cases where excessive numbers of carcasses were present, numbers were estimated based on different sampling methods. In these cases, estimates were flagged as 'approximate'. The most common estimation method was the grid method, which involved collecting and laying out carcasses in rows of a set number to obtain estimates by multiplication over the number of rows formed (Fig. 1). A weighing method was also used in which samples of up to 20 carcasses were individually weighed to determine the mean mass of a single carcass. Disposal bags filled with all collected carcasses were then weighed to estimate total number based on the mean individual mass. A density method was also used, which involved counting the number of carcasses within 10–15 quadrats of 1 m^2 to determine an average density that was then applied to the affected area. For some locations, only an eyeball estimation was done, involving the observer making a judgement of the number of carcasses roughly by sight. In these cases, observers assigned a range estimate (e.g. 100–200 carcasses). For cases when complete counts were not possible (if there were carcasses clumped in trees or the core area of the camp was not accessed to minimise disturbance of live flying-foxes), estimates only included carcasses that were visible to observers and were recorded as 'greater than'. Injured flying-foxes that were euthanised *in-situ* were included in the tally of dead animals. Population estimates of affected camps were not recorded at the times mortalities were found, thus it was not possible to scale the numbers of carcasses to population size.

The number of flying-foxes taken into care was obtained from records maintained by wildlife rehabilitation organisations. In some cases, the accuracy of these records was limited due to flying-foxes taken into care being distributed to various carers before a proper inventory was undertaken. In these cases, the minimum number of flying-foxes taken into care was recorded and flagged as 'approximate' or 'greater than' based on the attending wildlife carers' assessment.

Fig. 1. Grey-headed flying-fox (*Pteropus poliocephalus*) carcasses from an extreme heat event in Berry, NSW, laid out in rows to quantify by multiplication. Photo: Michael Smith, Shoalhaven City Council.

Data analysis

To obtain a conservative estimate of flying-fox deaths from the die-offs recorded from pup abandonment and extreme heat, we standardised records of mortality using the following criteria. For mortalities reported as a range estimate, the lower estimate was used (e.g. '100–500 carcasses' was accounted as 100 deaths). Mortalities reported as 'hundreds' or 'thousands' were accounted as 150 and 1500 deaths respectively. Mortalities reported as 'greater than' were only accounted from the known quantity (e.g. '>150 carcasses' was accounted as 150 deaths). Standardised records of mortalities were combined to generate an overall estimate of flying-fox deaths.

Where the numbers of flying-foxes taken into care were estimates, they were standardised as above. Similarly, standardised records of flying-foxes taken into care were combined to generate an overall estimate of flying-foxes transferred to *ex-situ* rehabilitation.

The distribution of recorded die-offs from pup abandonments and extreme heat events were plotted by mapping the locations of affected camps. We used meteorological data collected from Australian Bureau of Meteorology (2020) weather stations nearest to each camp to identify the maximum temperatures occurring within 5 days prior to observations of carcasses.

Results

Abandonments of pups

We recorded die-offs from pup abandonments in 10 camps in south-eastern NSW (Figs. 2, 3). These camps were solely occupied by *P. poliocephalus*, such that we could attribute the total mortality to this species. Meteorological data showed that these events were not associated with extreme heat (Australian Bureau of Meteorology 2020), although extreme heat events were subsequently recorded in three of these camps (Bomaderry, Kangaroo Valley, Picton). Carcasses in one camp (Bega) were first observed on a warmer day (21 November, maximum temperature recorded at the nearest weather station 40.3°C; Supplementary material Table S1); however, carcasses were consistently malnourished and appeared over a 4-week period, mostly between 7 and 14 days after the warmer day. Thus, we deduced that these pups likely died from being separated from their mothers, rather than an extreme heat event. Notably, several *P. poliocephalus* in these camps, both males and females, were in poor condition indicating nutritional stress.

In five camps, die-offs were recorded as early as late November (Table 1, and see Table S2 for specific dates). In one of these camps, mortality was only observed on a single day and the camp was not inspected prior or afterward (Corrimal). Other die-offs that commenced in late November occurred over a period of weeks (Bega, Picton) to months (Batemans Bay, Catalina), though there were notable spikes in mortalities that distinguished these die-offs from normal thresholds of pup mortality (e.g. 73 carcasses found in Bega from 3–6 December). In four other camps, die-offs were identified on single days around mid-December (Booderee Botanic Gardens, Bomaderry, Kangaroo Valley, Shellharbour) but three of these camps were not inspected until subsequent extreme heat events. A die-off in a tenth camp, Yatte Yattah was also recorded at the end of December (meteorological data showed there was no prior extreme heat event; Table S1).

Mortalities from pup abandonments ranged from at least 12 deaths (Shellharbour) to greater than 1600 deaths (Bomaderry) recorded on single days. Our conservative estimate is that at least 2612 pups died from abandonments. The die-off in Bomaderry accounted for approximately 62% of this total estimate. There were also live pups taken into care at three camps, totalling at least 409 pups taken into care from pup abandonments.

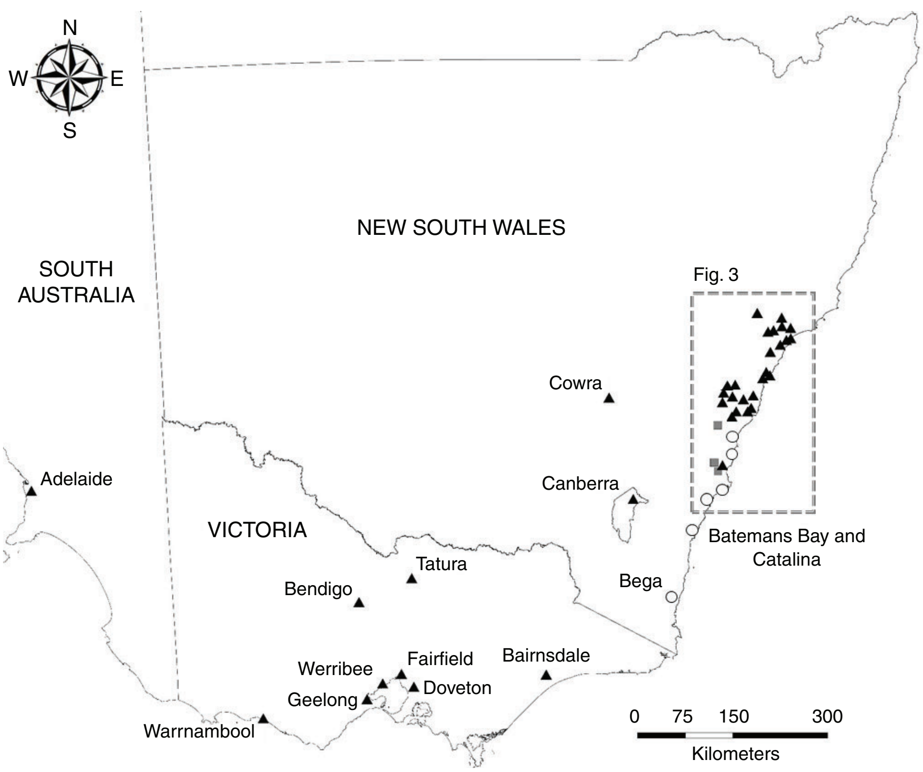

Fig. 2. Flying-fox camps where die-offs were recorded during the 2019–20 summer in Australia. Squares represent camps in which a pup abandonment was followed by die-off from an extreme heat event. Circles represent camps that only pup abandonments were recorded. Triangles represent camps that only die-offs from extreme heat events were recorded. Affected camps from the Hunter to the Shoalhaven region are shown in detail in Fig. 3.

Fig. 3. Flying-fox camps where die-offs were recorded within 150 km of the Sydney metropolitan area during the 2019–20 summer. Squares represent camps in which a pup abandonment was followed by die-off from an extreme heat event. Circles represent camps that only pup abandonment was recorded. Triangles represent camps that only die-offs from extreme heat events were recorded.

Extreme heat events

Die-offs from extreme heat events during the 2019–20 summer were observed in 40 camps: 30 in NSW, 1 in the Australian Capital Territory (ACT), 8 in Victoria, and 1 in South Australia (Table 2). Twenty-three camps were solely occupied by *P. poliocephalus* at the time of mortalities, and the remaining 17 camps were coinhabited by *P. poliocephalus* and *P. alecto* (*P. scapulatus* were also present in some camps but were not recorded as carcasses). All but four affected camps were within 70 km from the coast (Fig. 2). Approximately 65% of affected camps were located within the Sydney metropolitan area and Hunter region (Fig. 3). Of the eight affected camps in Victoria,

Table 1. Records of *Pteropus poliocephalus* pups that died or were taken into care from inferred abandonment based on not being associated with extreme heat events

To the best of our knowledge, there have been no confirmed records of *P. alecto* in these camps

Camp	Date(s) recorded	No. dead	No. taken into care	Source
Bega	21 November–21 December	101	4	H. Pitty
Batemans Bay	28 November–29 January	171		N. Foster
Catalina	12 December–29 January	35		N. Foster
Yatte Yattah	29 December	~100		G. Daly
Booderee Botanic Gardens	12 December	>100		J. Davies
Bomaderry	12 December	>1600	>100	J. Davies, M. Smith
Kangaroo Valley	12 December	>370	>300	J. Davies
Shellharbour	14 December	>12	1	R. Brown
Corrimal	22 November	>20		R. Brown
Picton	21 November–17 December	103	4	S. Taylor
Total estimate		2612	409	

three were located within the Melbourne metropolitan area. There are few known camps in South Australia and its only permanent camp in Adelaide was the only camp in the state from which die-offs from extreme heat events were recorded. No extreme heat events were recorded within the range of *P. conspicillatus*.

Meteorological data show that there were eight discrete heat events from November to February (Table S3), one event over 2 days in November, three events over 1–5 days in December, and four events over 1–4 days in January and early February (Table 3). Heat events were associated with masses of hot air moving from South Australia towards the eastern states in six of these heat events (Australian Bureau of Meteorology 2020). For example, in heat event 1, Adelaide experienced a maximum temperature of 42.2°C on 20 November, preceding Werribee experiencing a maximum temperature of 42.4°C the following day (other die-offs may have occurred in Victoria on 21 November, but were not observed). Similarly, in heat events 3 (17–21 December), 4 (27–31 December) and 8 (29 January–2 February), high temperatures in Adelaide preceded die-offs in the Victorian camps, then camps in Commonwealth Park, Canberra and NSW. The highest numbers of heat-affected camps recorded were in heat events 3 (17–21 December), 4 (27–31 December), and 5 (3–5 January).

In camps where the number of flying-foxes killed was recorded, death rates ranged from only a single individual (Adelaide, 30 January) to approximately 10 000 flying-foxes (Tocal, 10 December) on single days of extreme heat (Table 2). In total, we gathered data to conservatively estimate that at least 72 175 adult and young flying-foxes died in extreme heat events (Table 2). The highest mortalities were recorded in eight camps in which the known number of deaths ranged from 4000 to 10 000. Mortalities from these camps accounted for 76% of our estimate of all extreme heat mortalities. In particular, extreme heat mortalities in Adelaide, Kangaroo Valley, Gordon (Fig. 4) and Tocal each comprised more than 9% of our total estimate of extreme heat mortalities. It was generally observed that a large proportion of mortalities were pups, juveniles and lactating females, though demographic resolution was largely absent in the data to provide any meaningful quantification. From photographs of some carcasses, it also appears some mortalities were of pups that had been born prematurely (Fig. 5).

By observing meteorological data from weather stations close to affected camps, we determined there may have been unrecorded extreme heat-related mortality; using examples of East Cessnock and Yarramundi, there were two and three periods of very high temperatures respectively in which the camps were not monitored (Fig. 6). In contrast, we observed camps during ambient temperatures greater than 42°C that did not result in mortality (e.g. Parramatta on 1 February). In particular, observers monitored the Adelaide camp on any days predicted to exceed 40°C, which showed that mortalities did not result from heat events 4, 5, and 6 despite temperatures exceeding 42°C (Table S3).

We recorded flying-foxes transferred to *ex-situ* rehabilitation from extreme heat events in 19 camps (Table 2). Our records show that the minimum number of flying-foxes taken into care in extreme heat events was 2251.

In at least two camps, heat-related mortalities were likely exacerbated by storms prior to heat events. In Gordon, there were tree falls caused by a windstorm on 26 November, which substantially reduced shade refugia within the camp. This windstorm occurred less than 2 months before heat event 5. Similarly, the camp in Canberra was affected by a hailstorm on 20 January, 11 days before heat event 8 (see also Major 2020). Wildlife carers were recovering flying-foxes with hail-related injuries for 6 weeks following the storm, initially daily for the first 13 days. Most of the flying-foxes that died in this camp during heat event 8 had sustained injuries from the hailstorm (Fig. 7). In other camps, prolonged dry conditions had caused wetlands to dry up (e.g. Raymond Terrace, Oatley), which reduced flying-foxes' access to water during heat events.

Interventions by humans most likely influenced whether heat stress was ameliorated or exacerbated. There was great variation in how affected camps were treated: first, whether there were interventions, and second, which intervention methods (see also Mo and Roache 2021) were implemented and the manner in which they were implemented. As an example, in Cowra, flying-foxes that were observed to have descended within 2 m of the ground were lightly sprayed with water, which potentially

Table 2. Records of flying-foxes that died or taken into care during die-offs from extreme heat events

Where possible, separate count information is provided for separate extreme heat events at each camp. Species present are abbreviated (*P*=*P. poliocephalus*, A=*P. alecto*). Some camps were also occupied by *P. scapulatus*; however, this is not shown due to no recorded mortality of this species

Camp	Date(s)	No. dead	No. taken into care	Species present	Source
South Australia					
Adelaide	20 November	~2000	224	P	L. Collins
	17–20 December	~8000	385	P	L. Collins
	30 December	1		P	J. Van Weenen
Victoria					
Bendigo, Werribee, Geelong, Warrnambool	December–January	~700		P	T. Hogarth
Fairfield	December–January	~4500	~270	P	S. Brend, T. Hogarth
Doveton	December–January	300–500		P	L. Pope
Tatura	31 January	31		P	M. Pethybridge
Bairnsdale	30 December	~300		P	L. Roberts
Australian Capital Territory					
Canberra	21 December	0	5	P	D. Kay, M. Peachey
	30–31 December	0	2	P	D. Kay, M. Peachey
	31 January–1 February	42[A]	9	P	F. Major
New South Wales					
Bomaderry	4 January	~580	1	P	J. Davies, M. Smith
Berry	4 January	>1000	1	P	J. Davies, M. Smith
	23 January	~140		P	M. Smith
	1 February	>300		P	J. Davies
Kangaroo Valley	21 December	>100	>50	P	J. Davies
	1 February	>8300		P	J. Davies
Cowra	21 December	~25		P	L. Colefax
	3–4 January	21		P	L. Colefax
	10 January	13		P	L. Colefax
	1 February	16		P	L. Colefax
Picton	19 December	9	1	P	S. Taylor
	21 December	11	2	P	S. Taylor
	31 December	2		P	S. Taylor
	4 January	29[B]		P	Wollondilly Shire Council, S. Taylor
Campbelltown, Macquarie Fields	31 December	300–400	14	P	C. Simmons
Oatley	4 January	468[B]	20	P, A	G. Francis, M. Wallis
Wolli Creek	4 January	10		P, A	D. Little
Wallacia	10 December	Unknown[C]		P	H. Caulfield
Parramatta	31 December	>696[A]		P, A	R. Hansen
	4 January	2514		P, A	R. Hansen
Colyton	4 January	>65		P	Sydney Metropolitan Wildlife Services
	23 January	>15		P	Sydney Metropolitan Wildlife Services
Emu Plains	10 December	~140		P, A	J. A. Welbergen
	4 January	>1000		P, A	A. Tierney
Gordon	4 January	~7000		P, A	C. Costello
Yarramundi	10 December	247[A]		P, A	S. Judge
	19 December	>5		P, A	J. Stokes, S. Curran
	4 January	110		P, A	S. Judge
Windsor	10 December	~500		P, A	D. Prophet
	19 December	>26[B]		P, A	J. Stokes, S. Curran
	28–31 December	>46[B]		P, A	J. Stokes, S. Curran
	4 January	>27	14	P, A	J. Stokes, S. Curran
Woy Woy	23 January	32	2	P	K. Parry-Jones
North Avoca	23 January	>100[B]	13[D]	P	K. Parry-Jones
Wyoming	4 January	~100	79[D]	P	K. Parry-Jones
Mandalong	19 December	Hundreds		P, A	L. Sweeney
	31 December	Thousands		P, A	L. Sweeney

(*Continued*)

Table 2. (Continued)

Camp	Date(s)	No. dead	No. taken into care	Species present	Source
	4 January	Thousands		P, A	L. Sweeney
Blackalls Park	31 December	~4550	>200	P, A	A. Koosmen
	4 January	>2000	38	P, A	A. Koosmen
	1 February	2	24	P, A	A. Koosmen
New Lambton	31 December, 4 January	Hundreds		P, A	N. Godfrey-Smith
Carrington	10, 31 December, 4 January	~300	34	P, A	J. Hopper
East Cessnock	10 December	100–200	60	P, A	J. Hopper
	21 December	92	40	P, A	J. Hopper
	31 December, 4 January	1200–1400		P, A	J. Hopper
Weston	4 January	40–50		P	J. Hopper
Raymond Terrace	10 December	~1000	150	P, A	D. Coxon, K. Baker, N. Blatchford, K. Kay
	19, 21, 31 December, 4 January	~4000	~500	P, A	D. Coxon, K. Baker, N. Blatchford, K. Kay
Tenambit	10 December	50–100	14	P, A	C. McGarry
	21, 31 December, 4, 23 January	~5500	~110	P, A	C. McGarry
Tocal	10 December	~10 000	20	P, A	J. Hopper
Singleton, Burdekin Park	December–January	>120	18	P, A	J. Kelly
Singleton, Townhead Park	19 December	>200	13	P, A	K. Parry-Jones
Total estimate		72 175	2251		

[A]The number of dead flying-foxes was sometimes underestimated from dead flying-foxes in trees not being counted.
[B]Observers not accessing the core of the camp to avoid disturbing flying-foxes.
[C]In one case, a die-off was known from a report by a member of the public to a wildlife rehabilitation organisation but no count information was provided.
[D]The number of flying-foxes taken into care also included some individuals that were only in care overnight and released the following day. This relates to 62 and 6 pups from Wyoming and North Avoca respectively.

Table 3. Chronology of eight separate extreme heat events, showing the number of camps in which die-offs were recorded in each heat event
The number of camps affected in each heat event is likely to be higher than shown: we report only those camps in which observational evidence is available

Dates	Affected camps recorded	No. camps
Event 1: 20–21 November	Adelaide, Werribee	2
Event 2: 10 December	Wallacia, Emu Plains, Yarramundi, Windsor, Carrington, East Cessnock, Raymond Terrace, Tenambit, Tocal	9
Event 3: 17–21 December	Adelaide, Warrnambool, Bendigo, Werribee, Geelong, Fairfield, Doveton, Tatura, Canberra, Kangaroo Valley, Cowra, Picton, Yarramundi, Windsor, Mandalong, East Cessnock, Raymond Terrace, Tenambit, Singleton (Burdekin Park and Townhead Park)	20
Event 4: 27–31 December	Bendigo, Werribee, Geelong, Fairfield, Doveton, Bairnsdale, Canberra, Picton, Campbelltown, Macquarie Fields, Parramatta, Windsor, Mandalong, Blackalls Park, New Lambton, Carrington, East Cessnock, Raymond Terrace, Tenambit, Singleton (Burdekin Park)	20
Event 5: 3–5 January	Bomaderry, Berry, Cowra, Picton, Oatley, Wolli Creek, Parramatta, Colyton, Emu Plains, Gordon, Yarramundi, Windsor, Wyoming, Mandalong, Blackalls Park, New Lambton, Carrington, East Cessnock, Weston, Raymond Terrace, Tenambit, Singleton (Burdekin Park)	22
Event 6: 9–10 January	Adelaide, Cowra	2
Event 7: 23 January	Berry, Colyton, Woy Woy, North Avoca, Tenambit, Singleton (Burdekin Park)	6
Event 8: 29 January–2 February	Adelaide, Warrnambool, Bendigo, Werribee, Geelong, Fairfield, Doveton, Tatura, Canberra, Berry, Kangaroo Valley, Cowra, Blackalls Park, Singleton (Burdekin Park)	14

reduced the number of mortalities. In these interventions, personnel were limited, which likely contributed to minimising additional distress to flying-foxes. In contrast, there were some instances where interventions were either attempted by unlicensed persons or were inconsistent with existing protocols for intervening during extreme heat events (e.g. Department of Environment and Climate Change 2008; Bishop *et al.* 2019; Collins *et al.* 2019*a*). These situations may have increased the numbers of flying-foxes killed that may have otherwise survived. In addition, one of the authors observed members of the public harassing flying-foxes during heat events, which also potentially exacerbated mortalities.

Fig. 4. Dead grey-headed flying-foxes (*Pteropus poliocephalus*) and black flying-foxes (*P. alecto*) clinging to trees where they died or wedged in tree forks where they fell during heat event 5 in the Ku-ring-gai Flying-fox Reserve, Gordon, NSW (*a*), a juvenile *P. poliocephalus* found alive but later euthanised due to its injuries (*b*), and garbage bags filled with carcasses (*c*). Photos: Chelsea Costello, Ku-ring-gai Council.

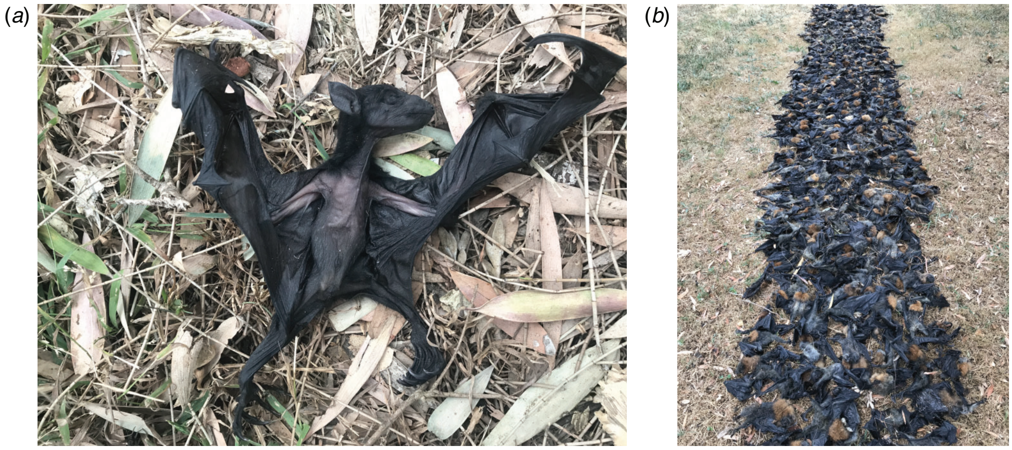

Fig. 5. A slightly premature black flying-fox (*Pteropus alecto*) pup killed during heat event 2 in Raymond Terrace, NSW (*a*), and the mass of other carcasses it was collected with (*b*). Photos: Drew Coxon, Port Stephens Council.

Discussion

As colonial and conspicuous species, flying-foxes represent an important bioindicator of the effects of extreme weather events, raising concern that similar impacts occur in more solitary and cryptic species (Welbergen *et al.* 2014). Our conservative estimates indicated that during the summer of 2019–20 in Australia, at least 72 175 flying-foxes died in 40 camps during eight extreme heat events, and a further 2612 pups died in 10 camps

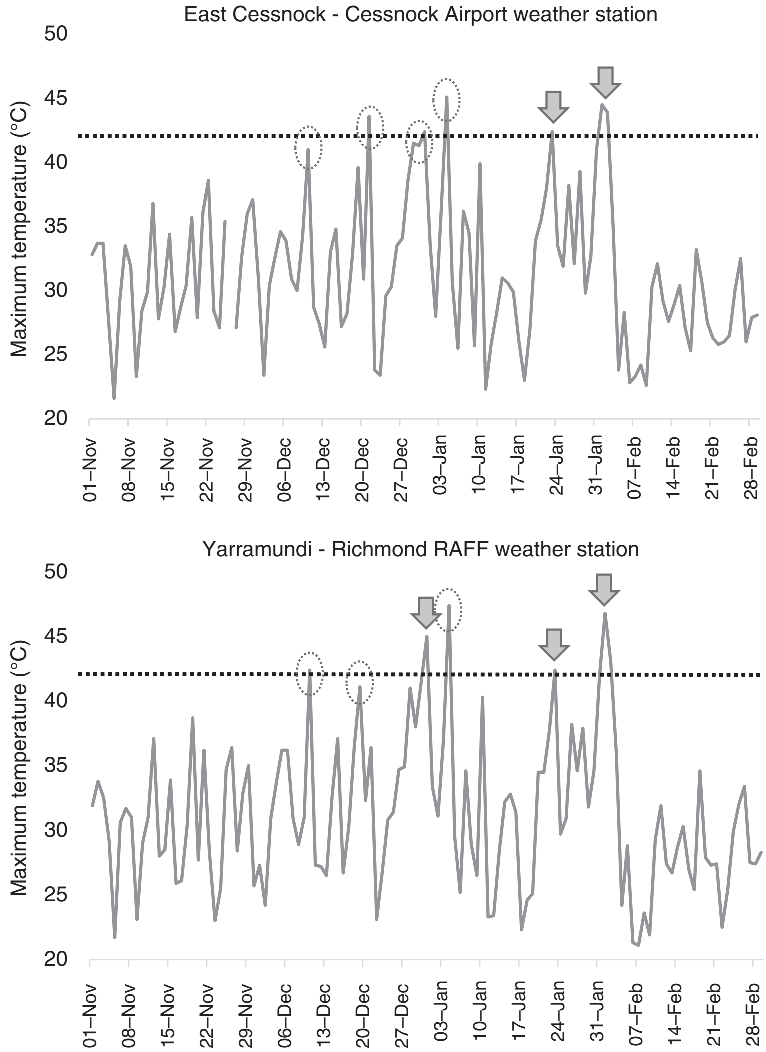

Fig. 6. Daily maximum temperatures recorded near the East Cessnock and Yarramundi camps from the Cessnock Airport and Richmond RAFF weather stations respectively (Australian Bureau of Meteorology 2020). Fieldwork gaps, highlighted by grey arrows, represent potential die-offs from extreme heat events that were not confirmed by observation. Die-offs that were confirmed by observation are circled. Broken line indicates 42°C.

from pup abandonments. This resulted in a total of more than 74 000 deaths of both adult and young flying-foxes. This represents a high level of mortality even though these estimates did not attempt to capture flying-fox deaths from starvation effects from drought and heavy rainfall and possible mortalities directly from the Black Summer bushfires.

A substantial proportion of the reported deaths involved *P. poliocephalus,* a vulnerable species with an estimated population size of around 680 000 individuals (Westcott *et al.* 2015). There were 27 041 mortalities recorded from 23 camps solely occupied by *P. poliocephalus* (Table 2), which alone represents more than one-third of the total estimate of mortalities. The remaining mortality (45 103) was from 17 camps occupied by both *P. poliocephalus* and *P. alecto* (Table 2). Although *P. alecto* is typically worse affected in extreme heat events than *P. poliocephalus* (Welbergen *et al.* 2008), we expect that *P. poliocephalus* comprised the majority of the total estimate based on wildlife carers and land managers noting that there were visually more *P. poliocephalus* carcasses than *P. alecto* carcasses at some shared camps. We also infer this across the affected area from *P. poliocephalus* being considerably more common within this range (McClelland 2009; Roberts *et al.* 2012) and at least seven times more abundant than *P. alecto* at 16 of the shared affected camps from which species composition data are available (Department of Agriculture, Water and the Environment 2020). Although the deaths represent a substantial proportion of the known population, it is unclear whether it represents a true loss to the population or a temporary forward displacement of mortality of already compromised flying-fox individuals that would likely have died from other causes in the short-term anyway ('harvesting effect'; Huynen *et al.* 2001). Nevertheless, what is known is that extreme heat events

Fig. 7. A grey-headed flying-fox (*Pteropus poliocephalus*) killed in heat event 8 in Commonwealth Park, Canberra, ACT, showing injuries likely sustained from the hailstorm 11 days earlier. Photo: Fiona Major, ACT Wildlife.

predominantly affect juveniles and lactating adult females, which is of particular concern for flying-fox conservation as this can have disproportionate impacts on recruitment and the size of the effective breeding population respectively (Welbergen *et al.* 2008). Continued monitoring of population trends is needed to ascertain whether mortality from these series of extreme heat events has had a significant impact on the population of *P. poliocephalus*.

The recorded deaths likely represent underestimates of the true flying-fox mortality associated with extreme heat events of the 2019–20 summer. We expect there was flying-fox mortality in camps affected by extreme heat events, indicated by meteorological data, but not inspected during or following the events (e.g. Fig. 6). However, it is important to note that microclimatic conditions in camps can differ markedly from those recorded at nearby weather stations (Snoyman and Brown 2010), although Ratnayake *et al.* (2019) showed that 24- and 48-h weather forecasts can accurately predict 77 and 73% of die-offs, respectively. Furthermore, in some camps, mortality may have been underestimated due to visually inaccessible carcasses not being counted, carcasses being removed by scavenging animals (N. Foster, pers. obs.) or local residents disposing of them prior to counts. Some of the sampling approaches for estimating the number of carcasses may also have introduced errors. For example, the highest mortality within a camp was recorded in Tocal; here, the number of carcasses within a relatively small representative number of 1 m^2 quadrats (10) was used to infer the mortality across the entire ~3 ha camp. In this case, relatively small initial counting errors and/or inadvertent bias in the selection of quadrats could have led to large over- or underestimates of mortality in that camp. However, the need for such sampling is a reflection of the scale of die-offs encountered at the worst affected camps. The same limitations were relevant to eyeball estimations. On balance, we are confident that our mortality estimates are underestimates, despite the serious practical limitations of estimating mortality at such a vast landscape scale.

Extreme heat events represent an important management issue for flying-fox conservation, reflected in at least two studies as one of the leading causes of debilitation in *P. poliocephalus* and *P. alecto* requiring rescue and rehabilitation (Tidemann and Nelson 2011; Mo *et al.* 2021*a*). Previous researchers have reported die-offs from single summers estimated in the tens of thousands. In the 2013-14 summer, more than 50 000 flying-foxes died in extreme heat events (J. A. Welbergen, unpubl. data), including the 45 500 *P. poliocephalus* and *P. alecto* killed across 52 camps reported by Welbergen *et al.* (2014). More recently, extreme heat events in the 2018-19 summer killed at least 48 000 flying-foxes, including approximately 23 000 *P. conspicillatus* and 20 000 *P. alecto* in north-eastern Queensland (Mao 2019; McKechnie and Wolf 2019), more than 4000 *P. poliocephalus* in Adelaide (Cockburn 2019) and less than 1000 flying-foxes in smaller die-offs (J. A. Welbergen, unpubl. data). In comparison, our conservative estimate of 72 175 deaths from heat events in the 2019-20 summer potentially represents the most severe summer of heat-related mortality in flying-foxes recorded to date. In light of climate change predictions of more frequent, longer and more intense heatwaves in Australia (Steffen *et al.* 2014), similar or potentially worse summers for flying-fox mortalities can be expected in the future (see also Welbergen *et al.* 2008).

Flying-fox camps near residential communities are often a source of human-wildlife conflicts (Kung *et al.* 2015) and there are broad negative public perceptions of bats (Lunney and Moon 2011). Where we observed deliberate disturbance to flying-foxes from humans during heat events, the camp was located on private property and within 20 m of residential dwellings. This suggests that flying-foxes roosting in urban areas may be at greater risk during extreme heat events due to deliberate disturbance if they are perceived by local communities to be a nuisance. During our study, experienced wildlife carers also reported incidents of unlicensed persons spraying flying-foxes in manners contrary to existing protocols (e.g. Department of Environment and Climate Change 2008; Bishop *et al.* 2019; Collins *et al.* 2019*a*). In these situations, there is the risk that these activities could exacerbate flying-fox mortality, rather than ameliorate it.

The severity of heat stress is likely influenced by whether human intervention occurred and the methods used. We were aware that intervention methods aimed at reducing die-offs varied between affected camps, ranging from hand spraying of roost vegetation and ground-based or tree-mounted sprinklers to collecting heat-stressed animals for intensive cooling and rehydration treatments (as described by Bishop *et al.* 2019; Collins *et al.* 2019*a*). Anecdotal observations by experienced wildlife carers suggest that these intervention methods can benefit flying-fox survival during heat events, however carefully controlled studies have not been carried out (Mo and Roache 2021). The absence of empirical evidence for these methods has prompted concerns that some well-meaning actions may cause additional stress for flying-foxes at their thermal limits (Ratnayake *et al.* 2019); for example, human presence may cause already heat-stressed flying-foxes to take flight, or spraying may decrease vapour pressure deficits within camps and interfere with flying-foxes' thermoregulatory responses that rely on evaporative cooling (e.g. Bartholomew *et al.* 1964).

These uncertainties highlight the urgent need for controlled experiments to inform improvements in flying-fox heat stress management.

Our observations allude to some preceding factors that potentially influence the extent of die-offs during extreme heat events. First, the amount of exposure to solar radiation contributes to the total heat load of individual flying-foxes (Snoyman *et al.* 2012; Ratnayake *et al.* 2021). This highlights the importance of intact vegetation strata in camps during extreme heat events. Notably, during heat event 5, flying-foxes in Gordon were affected in areas of the camp that were previously densely vegetated and would have provided adequate shade refuge if not for the prior storm damage. This possibly influenced the numbers of flying-foxes that died, combined with the large numbers of flying-foxes present at the camp around this time (43 000 individuals counted on 20 December, and 35 000 individuals counted on 14 January; Ku-ring-gai Council, unpubl. data). Maintaining vegetation strata in camps could thus potentially provide an effective long-term measure for mitigating the impacts of extreme heat events on flying-fox camps; however, the defoliation of roost trees by flying-foxes in regularly used camps (Eby 1995; Snoyman and Brown 2010) represents an important potential limitation. Furthermore, a key management strategy for managing flying-foxes in urban areas is to remove roost trees to create buffers between camps and homes (Currey *et al.* 2018; Mo *et al.* 2020). These actions may be contrary to vegetation retention objectives, hence the important need for managers to balance efforts to reduce human-wildlife conflict with retaining sufficient roost vegetation. Second, heat-related mortality may possibly be exacerbated when pups are abandoned in the days leading up to extreme heat events. In this study, die-offs were observed from both pup abandonments and subsequent extreme heat events in two camps. It would therefore be possible that pups in other camps were also being abandoned unbeknown to us, especially since some camps were inspected during but not prior to extreme heat events. Knowledge of these preceding influencing factors may assist with anticipating the camps likely to be most affected from future extreme heat events that are forecasted.

At present, the causes of *P. poliocephalus* pups being abandoned in NSW are not clear. Since there was a starvation event confirmed in northern NSW and the south-eastern Queensland during this time, we surmise that abandonments were possibly also related to nutritional stress. We would expect that lactating females in poor body condition would have had low milk production. Although pup abandonments were mostly recorded in December and January, mortality in some camps was recorded as early as November. Nursing females have the highest nutritional demands in the austral spring (Wade and Schneider 1992; Welbergen 2011), which coincide with time of the year food bottlenecks are most likely to occur (Parry-Jones and Augee 1991; Eby 1995), especially with the effects of large-scale habitat destruction (Eby *et al.* 1999). Starving lactating flying-foxes have high levels of physiological stress (Parry-Jones *et al.* 2016). It is therefore possible that nursing females could not maintain lactation as the drought continued (Sadleir 1969) or were unable to reunite with pups at camps if exhaustion occurred during foraging forays. At the time, the Black Summer bushfires had already been burning vast areas of northern NSW (Boer *et al.* 2020; Nolan *et al.* 2020) that represent important foraging habitat (Eby *et al.* 1999). In Batemans Bay and Catalina, there is the additional possibility that bushfire smoke presented obstacles for nursing females trying to return to their pups. Both the starvation event and bushfires are associated with drought and climate change (Sherwin *et al.* 2012; Collins *et al.* 2019*b*), which form broader management issues. However, the exacerbating effect of the destruction of foraging habitat on food shortages likely represents a major factor in nutritional stress in flying-foxes. Thus, a reasonable intervention would be to restore vegetation communities identified as important foraging habitat, especially in winter foraging sites (Eby and Law 2008; Eby *et al.* 2019).

During seasons of die-offs, wildlife carers may suffer stress from encountering large numbers of deaths and injuries, as well as exhaustion from personal burdens on time and finances when large numbers of animals require rehabilitation (Yeung *et al.* 2017; Englefield *et al.* 2018). During this study, large numbers of flying-foxes coming into care created overwhelming workloads for carers, such that many carers did not have capacity to accept further animals. This resulted in some flying-foxes that would normally have been considered viable being euthanised. This issue highlights the need to continue to build capacity in the wildlife rehabilitation sector to withstand such circumstances. Capacity building may involve improved state and national coordination between stakeholders, development of training resources, and partnerships that facilitate the provision or subsidising of resources such as food (e.g. Mo *et al.* 2021*b*), equipment and rabies vaccinations. The numbers of flying-foxes taken into care during the 2019–20 summer demonstrate the value of both the collective voluntary efforts of wildlife carers and ongoing research into heat stress management to minimise flying-fox mortality in the first instance (e.g. Ratnayake *et al.* 2019).

Mass die-offs of flying-foxes also have serious implications for a broader range of stakeholders. For instance, large numbers of decaying carcasses represent both an amenity and public health issue for communities living close to camps (Merone *et al.* 2020). Heat-stressed flying-foxes on or near the ground also increase opportunities for human-bat contact, which represent an increased risk of transmission of zoonotic diseases such as Australian bat lyssavirus (Francis *et al.* 2014; Field 2018). Despite public messaging from state government authorities and wildlife rehabilitation organisations advising against directly handling of injured bats, there are numerous cases of members of the public doing so (S. Guy, pers. obs.) and putting themselves at risk. Wildlife carers attending camps during extreme heat events therefore provide barrier measures for the community at these times by facilitating separation between members of the public and flying-foxes. However, the broad social implications associated with mass flying-fox die-offs highlight the importance of collaborative mitigation and assistance from a broader range of stakeholders such as land managers, veterinarians, researchers, health authorities, community groups and corporate partners.

Conflicts of interest

The authors declare no conflicts of interest.

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