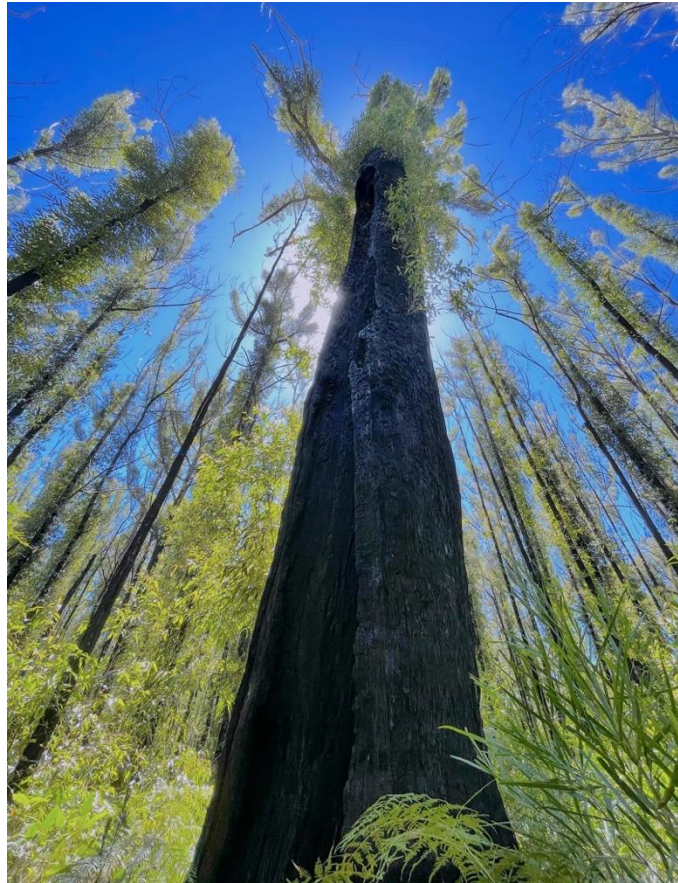


Fauna conservation in the age of megafire



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A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy



THE UNIVERSITY OF
SYDNEY

School of Life and Environmental Sciences

Faculty of Science

The University of Sydney

December 2023

“The rapidity of change and the speed with which new situations are created follow the impetuous and heedless pace of man rather than the deliberate pace of nature.”

—Rachel Carson, 1962

Declaration

I, Vivianna Miritis, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Life & Environmental Sciences, The University of Sydney, is wholly my own work unless otherwise referenced or acknowledged. This document has not been submitted for qualifications at any other academic institution.

Vivianna Miritis

20/12/2023

Acknowledgements

First and foremost, I acknowledge the Murramarang, Ngarigo and Walbunja peoples, the Traditional Custodians of the land on which I carried out my research. I extend my respects to their Elders past and present.

This thesis and achievement really go out to my mum, **Adamantia Miritis**, who has been my biggest support. Without a word of English, she moved to Australia knowing it would provide a brighter future for me. She didn't have a formal education, worked multiple jobs, and, with our family on the other side of the world she raised me on her own. She taught me resilience and strength, and all the life skills that have made me who I am today. I am so lucky to know and have such an incredible woman in my life; this would not have been possible without her.

I thank my supervisors, **Chris Dickman**, **Tim Doherty**, and **Dale Nimmo**. There are few people that come to mind who are as eloquently spoken as Chris. Always reassuring and supportive. Thank you for sharing your passion for ecology, knowledge, and stories. Thank you for calmly listening to my ideas, as wild as some were, and attentively listening to me talk about concepts that I later found you had written a book on. It has been such a pleasure to have one of the most brilliant ecologists as a supervisor. Tim has been there from the very start, stuck with me since honours, and has been pushing me to do better every step of the way. I would not have achieved as much as I have without him. He has been with me in the field, working through project dramas, encouraging me to collaborate, attend conferences, apply for grants, helping me with analyses, improving my writing, and generally keeping me on track. An incredibly talented scientist so early in his career, I have learnt so much from him. Finally, Dale brought his little gems of knowledge and wisdom. Always so approachable and encouraging. Helping me work through ideas and listening to my analysis dramas. Thank you.

This research would not have been possible without the help of research assistants, particularly **Matt Sleeth**, and countless volunteers, who helped me catch little creatures in leech-infested forest, and who endured early wake ups and long hours in the field and history making rains. Special mention to my partner **Mark** who joined me on some of these field trips, helped me load and unload the field vehicle countless times, and who has been an endless support while I have gone through the ups and downs of a PhD.

A special thank you to **Bobby Tamayo**, who helped with field logistics, car bookings, car breakdowns, and things constantly going missing in the field storeroom (which I had taken). A massive thank you for the team from WWF, in particular **Kita Ashman** and **Patrick Giumelli**. Kita is an incredible friend that I have worked with on various projects. She is a constant inspiration and a powerhouse early career ecologist. I cannot wait for many more field trips—filled with laughs, zig zagging wombats, and conversations about whether humans have eyeshine on our third hour of being lost in some dark forest.

Also, a massive thank you to the staff at the NSW National Parks and Wildlife Service, in particular **Michael Phelan** and **David Cunningham**, who provided park access, local knowledge and assistance for the last three years of this project. A special thank you also to **Kai Wild** and **Sam Hardingham**, my incredibly talented team of climbers.

Funding was provided by the NSW Environmental Trust, Holsworth Wildlife Research Endowment fund, and the World Wide Fund for Nature Australia.

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Thesis context and authorship attribution

This research tracked the recovery of forests from three months to three years following Australia's most unprecedented wildfire season. Over the duration of my PhD (2020–2023) Australia experienced an international pandemic and flooding rains, which impacted my field sites and resulted in multiple setbacks to fieldwork and data collection. Despite this, the datasets collected during my study were extensive. Reviewers of the submitted chapters commended the data collection, describing it as 'an impressive feat'. The value of the datasets I have collected extend beyond this thesis and have been included in collaborative international studies that will inform a global audience.

This thesis is set out as a series of papers, which is an option available at The University of Sydney. Each chapter has been written for publication and has either been published, submitted or is being prepared for submission to a journal. This means that there may be some journal specific-formatting and repetition within and between chapters. Furthermore, in some chapters the term “we” has been used to reflect the contribution of the co-authors for that chapter. However, I am first author on all the published and submitted chapters and made substantial contributions to the conception, planning, fieldwork, data analyses and interpretation, and writing of all of them. Chapters that have been accepted or submitted for publication are indicated at the beginning of each chapter. Each of those chapters also includes a contribution statement outlining my specific contributions. Reference lists appear after each chapter to match the published work and follow a consistent referencing style throughout the thesis. Prof. Chris Dickman (lead supervisor), Dr Tim Doherty and A/Prof. Dale Nimmo provided supervision of the project, including planning and discussions on the project's design, analyses and interpretation of the data, and suggestions and improvements to the earlier versions of the chapters. In addition to the statements above, in cases where I am not the corresponding author of a published item, permission to include the published material as appendices has been granted by the corresponding author.

Vivianna Miritis

19/12/2023

As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statements above are correct.

Prof. Chris Dickman

21/12/2023

Thesis structure

This thesis comprises six chapters, including an introduction, four data chapters, and a summary. It explores the recovery, response, and management interventions for vertebrate species in relation to contemporary fire regimes, using the 2019–20 Australian megafires as a case study.

Data chapters:

Chapter 2: Post-fire recovery

In Chapter 2, I assessed the general recovery of forest vertebrates following the megafires. In this chapter, I used data I collected through traditional live trapping surveys to investigate small mammal abundance post-fire, and provided a foundation for further exploration of vertebrate succession in the aftermath of extreme wildfires.

Chapter 3: Fire variables influencing recovery

In Chapter 3, I used extensive data collected from camera trap surveys to expand on my analysis of post-fire succession. I assessed how nuanced fire variables, such as proportion of an area burnt, and vegetation type influence the recovery of vertebrate species. In this chapter, I demonstrated that animal species' responses to fire are better captured using broader landscape scale fire variables, and that detailed fire variables and vegetation type provide a better understanding of post-fire succession compared to simpler contrasts between burnt and unburnt.

Chapter 4: Fire-driven animal adaptations

In Chapter 4, I explored fire-driven animal adaptation. I examined the movement patterns and habitat use of the southern greater glider (*Petauroides volans*) post-fire, offering insights into this species' response to extreme wildfire events and the challenges faced by fire-sensitive species in adapting to rapidly shifting fire regimes.

Chapter 5: Aiding post-fire recovery

In my final data chapter, Chapter 5, I assessed the efficacy of nest boxes for facilitating the post-fire recovery of hollow-using mammals. I evaluated the occupancy rates of nest boxes and the activity rates of arboreal mammals in both burnt and unburnt areas, and contributed to the discussion on effective post-fire remedial management tools.

Approvals and funding

This research was approved by The University of Sydney Animal Ethics Committee (2020/1821), the Department of Planning, Water and Industry (SL102361), and Forestry Corporation of NSW (RES100157). Funding was provided by the NSW Environmental Trust, Holsworth Wildlife Research Endowment, and the World Wide Fund for Nature.

Publications

Thesis publications:

Chapter 3

Miritis V, Dickman CR, Nimmo DG & Doherty TS (2023). After the 'Black Summer' fires: faunal responses to megafire depend on fire severity, proportional area burnt, and vegetation type. *Journal of Applied Ecology*. 1365-2664.14545

Chapter 4 – Under review

Miritis V, Ashman, KR, Dickman CR, Nimmo DG & Doherty TS (2023). Adapting to novel fire regimes: Using movement to inform conservation of a threatened arboreal mammal. *Biological Conservation*.

Conferences:

Miritis V, Dickman CR, Nimmo DG & Doherty TS (2023). Gliders out on a limb: using movement to inform conservation. Ecological Society of Australia.

Miritis V, Dickman CR, Nimmo DG & Doherty TS (2022). Surviving in a black forest: two years of predator and prey responses to the 'Black Summer' bushfires. Ecological Society of Australia.

Additional peer-reviewed publications:

Additional (non-first author) peer reviewed publications completed during PhD candidature.

Doherty TS, Geary WL, **Miritis V** & Watchorn DJ (2023). Multiple Threats Affecting the Marsupials of Australasia: Impacts and Management. In NC Cáceres & CR Dickman (Eds.), *American and Australasian Marsupials* (pp. 1531–1554). Springer International Publishing.

Doherty TS, Watchorn DJ, **Miritis V**, Pestell AJL & Geary WL (2023). Cats, foxes and fire: Quantitative review reveals that invasive predator activity is most likely to increase shortly after fire. *Fire Ecology*, 19(1), 22.

Doherty TS, Geary WL, Jolly CJ, Macdonald KJ, **Miritis V**, Watchorn DJ, Cherry MJ, Conner LM, González TM, Legge SM, Ritchie EG, Stawski C & Dickman CR (2022). Fire as a driver and mediator of predator–prey interactions. *Biological Reviews*, 97(4), 1539–1558

Jolly CJ, Moore HA, Cowan MA, Cremona T, Dunlop JA, Legge SM, Linley GD, **Miritis V**, Woinarski JCZ & Nimmo DG (2022). Taxonomic revision reveals potential impacts of Black Summer megafires on a cryptic species. *Pacific Conservation Biology*, 29(1), 17–25.

Publications from data collected during PhD (under review):

Non-first author manuscripts currently under review.

Devarajan K, Fidino M, Farris ZJ, [et al., including **Miritis V**] (2023). When the wild things are: Defining mammalian diel activity and plasticity. *Science*.

Driscoll DA, [et al., including **Miritis V**] (2023). Megafire impacts are mediated by protected areas, rainfall, and fire regime. *Nature*.

Abstract

Record-breaking wildfires have become more common globally and are increasingly affecting areas where fire was previously rare or absent. While many vertebrate species are adapted to particular fire regimes, changes in fire activity are having complex and far-reaching implications, especially for species that have not typically encountered fires. Despite extensive research on fires, empirical data on population loss and recovery post-fire, especially megafire is limited. The Australian 2019–20 megafires were unprecedented in scale, severity, and duration, and highlighted the paucity in key information that allow practitioners to assess the impacts of such fires on animal species. As such, priority management recommendations were proposed that would guide a better understanding of the impacts of these megafires and future ones to come. These recommendations included rapid fauna assessments, long-term monitoring, analysis of fire impacts on different species' persistence, and evaluating the effectiveness of post-fire remedial management strategies. In this thesis I investigate how species are responding to novel fire regimes by using the 2019–20 Australian megafires as a case study. Specifically, my research aims were: (1) assess the recovery of vertebrate species, primarily mammals, over time, (2) assess if recovery is influenced by specific fire variables, such as fire severity and proportion burnt, (3) assess how some species are adapting to novel fire regimes and whether these adaptations are sufficient in aiding population persistence, and (4) investigate the efficacy of artificial shelters, specifically nest boxes as a tool for facilitating recovery following fire events.

In **Chapter 1**, I provide a brief introduction on novel fire regimes and the 2019–20 Australian megafires, I then discuss the impacts of contemporary fire regimes on Australian mammals and key knowledge gaps. In **Chapter 2** and **Chapter 3**, I assess the post-fire recovery of vertebrate species following the 2019–20 Australian fires over two years. **Chapter 2** focused on small mammals, and revealed increased species diversity over time, particularly in burnt areas. However, this included the prevalence of invasive and generalist rodent species. Conversely, species with specific habitat and dietary needs were less abundant in fire-impacted areas throughout the study.

In **Chapter 3**, I extend the analysis to consider the impact of detailed fire metrics and vegetation type on vertebrate recovery. Using extensive camera trap data, I studied the varied responses of 14 animal species/groups, encompassing predators, mammals, herbivores, and birds. The results indicated that the response of co-occurring vertebrate species to fire are variable, and vegetation type and nuanced fire

metrics including severity and proportion burnt, were better at capturing the complexity of post-fire successional changes, in comparison to simple contrasts between burnt and unburnt.

In **Chapter 4**, I assess how an endangered arboreal mammal is responding and adapting to altered fire regimes. Using fine-scale data collected from GPS collars, I assessed the effect of the fires on the space use and movement behaviour of the southern greater glider (*Petauroides volans*). The data I collected provided empirical evidence on how a fire-sensitive species is persisting in heavily burnt areas, potentially by altering its movement to access necessary resources. However, the data also showed that these gliders maintain home range fidelity, a behaviour shaped by historical fire regimes, suggesting that frequent and severe environmental disturbances could pose considerable challenges for its persistence.

Finally, in **Chapter 5**, I investigate the efficacy of nest boxes, a recommended management tool, in facilitating mammal recovery post-fire. I deployed 54 nest boxes across burnt and unburnt sites and monitored them over two years through physical checks and camera monitoring. I also conducted camera surveys monitoring arboreal mammal activity at sites with and without nest boxes. Two years after deployment, over half the nest boxes in burnt forests were occupied. Camera surveys showed increased arboreal mammal activity in burnt forests regardless of nest box presence, contrasting with higher activity at nest box sites in unburnt forest. The results suggest that while nest boxes offer some benefit to fire-affected arboreal mammals, they could potentially be more effective in increasing the carrying capacity of unburnt areas, which could aid future recolonisation of burnt forest.

Collectively, the results of this thesis have covered a broad scope of aims relevant to contemporary fire regimes and enhance our understanding of the responses of vertebrate species to a megafire event. Further, this research sets the foundation for future studies which will be required to continue understanding the long-term impacts of past and future megafires.



Burnt Banksia sp. pod. Vivianna Miritis.

Chapter 1 – Introduction

Fire is a natural and integral part of many terrestrial ecosystems. It is a major ecological and evolutionary force that promotes and maintains biodiversity at local, regional and global scales (Bowman et al., 2009; He et al., 2019). This has manifested through relatively stable and predictable fire regimes over millions of years (He et al., 2019). However, fire regimes are shifting from historical norms due to climate change, human-induced habitat change, fire suppression, prescribed burning, and displacement of Indigenous Peoples (Bowman et al., 2020; Fletcher et al., 2021; Jones et al., 2022; Penman et al., 2011; Taylor et al., 2016). While the specific type, frequency, severity, and extent of fire events varies considerably between different ecosystems and vegetation types, a common theme is a relative increase in these factors globally (Bowman et al., 2020).

Record-breaking fires have occurred on almost every continent (Attiwill and Binkley, 2013; Duane et al., 2021). Many have been termed ‘megafires’ due to their unprecedented scale (often >10,000 ha in size), severity, duration, and resistance to control (Linley et al., 2022; Stephens et al., 2014). Megafires can have disastrous impacts on biodiversity (Ward et al., 2020), people, and infrastructure (Jolly et al., 2015). While many species have co-evolved with fire, megafires often create environments with detrimental consequences that outweigh the benefits that fire typically brings to fire-adapted landscapes and the animals that inhabit them (Stephens et al., 2014). Further, recent megafires have impacted ecosystems where fire has historically been rare or absent (Bowman et al., 2020; Kelly et al., 2020; Ward et al., 2020; Wintle et al., 2020), introducing new challenges for species lacking an eco-evolutionary history with fire, as they may be naive to fire cues as warning signs of impending danger (Nimmo et al., 2021).

The ongoing shifts in fire activity are threatening biodiversity in habitat types and biogeographic realms worldwide (Kelly et al., 2020). Based on records from the International Union for the Conservation of Nature (IUCN), Kelly et al. (2020) reported that over 4,300 threatened species are being adversely impacted by novel fire regimes and this is likely an underestimation, as recent unprecedented fires such as the 2019–20 Australian megafires, mean that the conservation status of many species has likely changed (Ward et al., 2020; Wintle et al., 2020). These changes increase the necessity to better predict and reduce the risk of occurrence of extreme fires, and develop strategies to manage the consequences most effectively when they do occur (Dickman, 2021).

The 2019–20 Australian megafires

For much of 2019 and into 2020, Australia experienced its worst fire season on record (Khan, 2021). Megafires have burned intermittently in Australia over the past 150 years, however, the 2019–20 megafires were unprecedented in geographical scale, intensity, and duration and had major impacts on species and their ecosystems (Wintle et al., 2020). The fires burned millions of hectares of native vegetation, predominantly along eastern Australia (Fig. 1). Over 21% of Australia's eucalypt forests were burned, 10 times higher than the annual average (Boer et al., 2020). Further, the megafires extensively burnt through regions that rarely experience fire including globally significant biodiversity hotspots with high richness and endemism, including Gondwanan and subtropical rainforests (Godfree et al., 2021; Nolan et al., 2021).

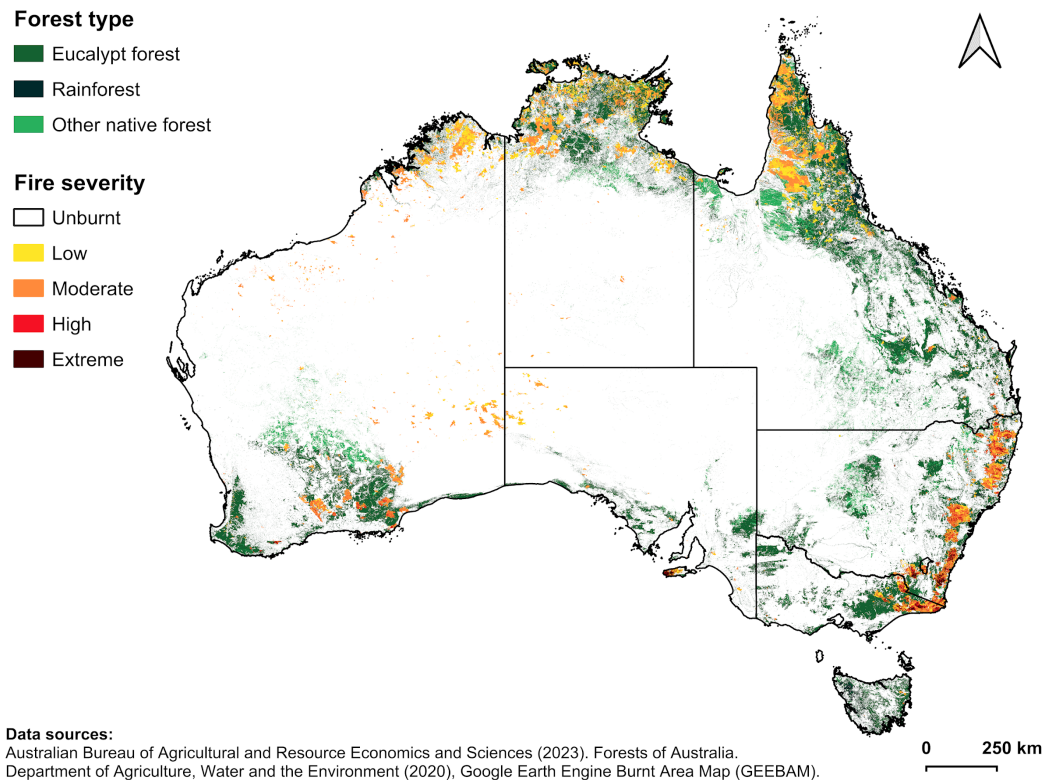


Fig. 1. Extent and burn severity of the 2019–20 megafires. Fire severity is categorised according to the GEEBAM classification system: 'Low' indicating some impact to vegetation, 'Moderate' indicating moderate impact, 'High' where vegetation was mostly scorched, and 'Extreme' where vegetation was mostly consumed.

The impact of the megafires on vertebrate species was considerable; estimates suggest that the fire footprint overlapped with the ranges of over 832 vertebrate species, 107 of which were already classified as threatened (Ward et al., 2020). The fires led to mass animal mortality (van Eeden et al., 2020), and removed access to vital post-fire resources such as food and shelter across large areas, including in patches that would normally serve as refuges (Geary et al., 2022; Wintle et al., 2020). The fires also consumed the entire geographic ranges of some species (Ward et al., 2020), and likely reduced the ability of animals to recolonise burned habitats as they become more suitable (Wintle et al., 2020). This presented considerable challenges not only for species adapted to fire-prone environments but especially to those that have evolved within ecosystems that rarely burn (Nimmo et al., 2021).

Knowledge gaps and significance

Despite extensive research on fires, information on the post-fire responses of most species to fires, especially to megafires, remains limited (Dickman, 2021; Jolly et al., 2022; Legge et al., 2022b; Pausas and Parr, 2018). Prior to the 2019–20 megafires, numerous authors highlighted the need for monitoring ecological communities and threatened species, and the scarcity of such empirical data in Australia (Legge et al., 2018; Lindenmayer, 2018). The responses of animal species to fires vary widely and are influenced by factors such as habitat and resource requirements, fecundity, and dispersal abilities (Dickman, 2021; Legge et al., 2022a). Therefore, understanding the impacts of fires on vertebrate species responses is crucial for determining recovery timeframes, prioritising conservation management for vulnerable fauna, and reassessing the conservation status of various species (Ensbeay et al., 2023; Godfree et al., 2021; Wintle et al., 2020). Furthermore, information on species responses to megafires will be instrumental in understanding the long-term ecological consequences of changes in fire regimes (Dickman, 2021).

In response to the 2019–20 megafires, various conservation recommendations were proposed to improve post-fire biodiversity management and better prepare for future fire crises. These recommendations included conducting rapid assessments of fire-affected fauna, ongoing long-term monitoring, evaluating the variable impacts of fires on species' survival, and experimentally assessing the effectiveness of various post-fire remedial management strategies (Dickman, 2021; Dickman et al., 2020; van Eeden et al., 2020; Ward et al., 2020; Wintle et al., 2020). Further, there is

emerging evidence that novel fire regimes are driving rapid animal adaptations, and a better understanding of these mechanisms may be critical in prioritising and managing post-fire recovery efforts (Jones et al., 2023; Wong and Candolin, 2015). More broadly, investigating these research questions will enhance the understanding of the recovery processes and future management strategies for Australian fauna, and may also help address the wider threats that are driving population declines globally under changing fire regimes.

Thesis aims and structure

The primary objective of this thesis was to assess how species are responding to novel fire regimes, specifically megafire (>10,000 ha), by using the 2019–20 Australian megafires as a case study.

Specifically, my research aims were:

1. Assess the recovery of vertebrate species, primarily mammals, over time (Chapters 2 and 3);
2. Investigate if recovery is influenced by specific fire variables, such as fire severity and extent (Chapter 3);
3. Assess how some species are adapting to novel fire regimes and whether these adaptations are sufficient in aiding population persistence, and;
4. Investigate the efficacy of nest boxes as a management tool for facilitating mammal recovery following fire events.

I address each of these aims sequentially in the data chapters of this thesis (Chapters 2–5). I address the first aim (‘assess the recovery of vertebrate species over time’) by collecting continuous data 3 to 27 months following the 2019–20 megafires, using live trapping (Chapter 2) and motion-sensing camera surveys (Chapter 3). This was one of the few studies that collected data in the initial months post-fire and continued to do so continuously for two years. To address the second research aim, (‘assess how specific fire variables may be influencing recovery’) I used the data collected from the camera surveys to statistically assess the responses of 14 animal species/groups to nuanced fire variables including fire severity, extent, and proportion burnt (Chapter 3). To address the third aim, (‘assess fire-driven adaptations and their ability to aid persistence’), I used GPS telemetry to assess the space use and movement patterns of the endangered southern greater glider (*Petauroides volans*) in severely burnt forest (Chapter 4). This research was novel in that GPS

collars that enable collection of very fine-scale movement data were not previously accessible for this species. In Chapter 5, I address my final aim ('investigate the effectiveness of nest boxes as a recovery tool for fire-impacted mammals') by conducting a field experiment assessing arboreal mammal recovery over two years post-fire in sites with and without nest boxes. Lastly, in Chapter 6 I provide general conclusions that I have drawn from my work. I outline how my research findings have contributed new knowledge on species responses to novel fire regimes and discuss key management implications.

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Chapter 2 – Two-year assessment of small mammal responses to megafire

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Manuscript in preparation for submission.

My contribution to this data chapter was substantial. I conceptualised ideas and led the fieldwork, collected and analysed the data, and wrote and edited all drafts, in consultation with my co-authors.



*White-footed dunnart (*Sminthopsis leucopus*) caught during small mammal surveys. Vivianna Miritis.*

Abstract

Rapid environmental change has increased the frequency of extensive, high-severity megafires in recent decades, with novel consequences for forest ecosystems. In particular, small mammals that are vital to forest health are vulnerable to shifting fire regimes that alter resource availability. This study focuses on the post-fire recovery of small mammals following the 2019–20 Australian megafires, examining their abundance, diversity, and species-specific responses over 3 to 27 months after the fires. Specifically, using live-trapping data collected from 12 burnt sites and 4 unburnt sites, we compared small mammal abundance and diversity over time in response to burn status and severity. Species diversity increased with time since the fires and was higher in burnt sites by the end of the study. However, this included the occurrence of invasive house mice (*Mus musculus*) which had a strong preference for burned forest, especially sites burned at high/extreme severity. Native bush rats (*Rattus fuscipes*) and antechinuses (*Antechinus agilis* and *A. stuartii*) showed contrasting responses to the fires, with bush rat abundance increasing and becoming higher in burnt sites over time, in comparison to antechinuses which had higher abundance in unburnt sites throughout the study period. By the end of the study the most commonly captured species in burnt sites were the bush rat and house mouse, while species including the mainland dusky antechinus (*A. mimetes*) that have more specialised diets and require specific habitat resources to persist were infrequently captured. Our results provide important data for understanding the recovery of small mammal species in response to megafire, but also highlight the need for sustained management for the recovery of species with habitat and dietary specialisations, as well as pre-existing declines and threatened conservation status.

Introduction

Fire is a natural phenomenon and an integral part of the landscape, to which many ecosystems and their organisms have adapted (He et al., 2019). However, fire regimes are changing, and the intensity, severity and duration of recent wildfires are reducing the capacity for ecosystems and their fauna to respond and recover (Nimmo et al., 2021). Many of these wildfires have been termed “megafires” due to their unprecedented scale, intensity and impact (Linley et al., 2022; Stephens et al., 2014). Models of climate change predict that the occurrence of megafires will continue to increase in many parts of the world over the next century (Jones et al., 2022). In Australia, the 2019–20 megafires that burned at an unprecedented scale are a prime example (Boer et al., 2020). These megafires were a significant move from historical fire regimes and caused a devastating loss of habitat across millions of hectares including through areas that do not typically burn (Khan, 2021; Ward et al., 2020).

Understanding how fires affect animal populations is critical for assessing the conservation status of species and developing targeted management interventions in the aftermath (Wintle et al., 2020). However, despite a large breadth of research on fires, empirical data on animal population responses to wildfires, especially megafires, is limited (Ensbeys et al., 2023; Jolly et al., 2022; Pausas and Parr, 2018). Animal species’ responses to fire are varied and often complex. The capacity for species to survive the immediate impact and aftermath of fire is often dependent on different variables including animal traits (e.g., surviving by seeking shelter; Ensbeys et al., 2023; Nimmo et al., 2021) and fire characteristics (e.g., species responses to fire severity; Culhane et al., 2022; Jones et al., 2021; Lewis et al., 2022). Further, fires can influence animal community structure by changing the availability of key resources (Brehme et al., 2011).

Small mammals are particularly sensitive to changes in fire regimes and have been pivotal in understanding how biodiversity responds to fire (Fox, 1982; Kelly et al., 2011; Monamy and Fox, 2000). One commonly adopted theory is that the responses of small mammal species to fire are associated with changes in vegetation, as small mammals are often reliant on ground vegetation for food and shelter (Fox, 1982). Consequently, small mammal species are likely to establish in an ecosystem when the vegetation first meets their habitat requirements and may decline or be outcompeted when vegetation changes render the habitat unsuitable (Fox 1982; Fox et al., 2003). However, these patterns of mammalian succession are not always consistent and can be highly context-dependent (Kelly et al., 2011). Further, wildfires may lead to reduced diversity, often favouring more adaptable generalist species over specialist ones (Brehme et al.,

2011; Dickman and Happold, 2022). Even so, reduced diversity post-fire is also not a universal occurrence (Roberts et al., 2015). Indeed, the abundance and distribution of small mammals following fires can vary greatly across different environments (González et al., 2021; Horn et al., 2012; Torre et al., 2023).

While fires are commonplace in Australia, to which many species have co-evolved, megafires often outweigh the benefits that fires typically bring (Stephens et al., 2014). Most fires leave a mosaic of unburnt patches in topographical features within the fire footprint, however, the Australian megafires burnt extensively through landscape features such as rainforest edges, gullies, and rocky outcrops that would normally act as refuges during fire events (Wintle et al., 2020). This can be particularly problematic for small mammals, as previous research suggests that small mammal population recovery is driven by local-scale processes through in situ survivors or local recolonisation from refuges (nucleated recovery; Banks et al., 2017).

In Australia, terrestrial mammals have suffered rapid declines and extinctions in the last 250 years, with altered fire regimes a major driver (Woinarski et al., 2015). Small mammals are important components of functioning ecosystems. They consume and spread seeds (Briggs et al., 2009), pollinate plants (Goldingay et al., 1991), regulate insect populations (Baker and Dickman, 2018; Kollberg et al., 2014), and spread mycorrhizal spores (Pyare and Longland, 2001; Tory et al., 1997), all of which have considerable influence on forest health. Small mammals are also prey for various predators, including vulnerable forest owls like the sooty owl (*Tyto tenebricosa*; Bilney et al., 2010). Therefore, understanding the impacts of fire on small mammal species is crucial for the long-term sustainability of their populations and the overall health of forest ecosystems.

The primary objective of this study was to assess the impact the 2019–20 Australian megafires on small mammal communities. While the ecological consequences of the megafires were profound, they remain largely unquantified (Dickman, 2021; Jolly et al., 2022; Legge et al., 2022; Wintle et al., 2020). Common knowledge gaps include: the subsequent effect of fire on animal survival and recovery (Jolly et al., 2022; Ward et al., 2020), and how the severity of the burns affected ecosystems and their species (Dickman, 2021). To address these knowledge gaps, we conducted small mammal live-trapping and habitat surveys three to 24-months following the 2019–20 megafires. The principal aims were to: 1) assess small mammal

species abundance and richness over time, and 2) assess how small mammal abundance is influenced by low/moderate versus high/extreme severity burns.

Materials and methods

Study area

Our study sites were in Murramarang National Park (35.61° S, 150.30° E) which is located on the south-eastern coast of Australia. The park occupies approximately 1,970 ha and consists of diverse vegetation communities dominated by temperate eucalypt forest. Mean maximum temperatures across the study area are 17°C in winter and 26°C in summer (Bureau of Meteorology, 2023). The 2019–20 Australian wildfires, primarily the Currowan fire which spanned over 300,000 ha, burnt more than 80% of the park in December 2020. The fire burned the park at variable severity and only the southernmost area remained unburned (Fig. 1).

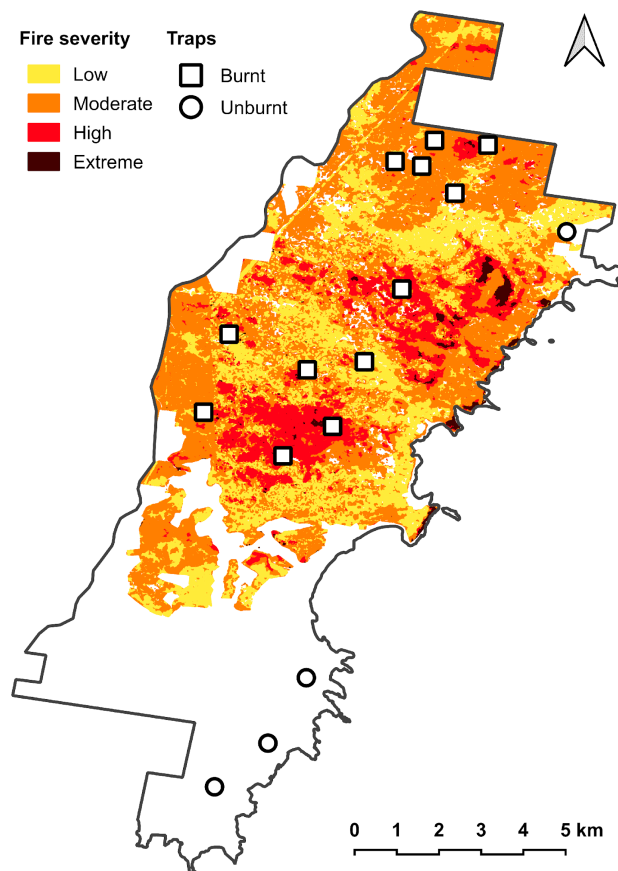


Fig. 1. Survey sites in Murramarang National Park across fire severity gradient, derived from Fire Extent and Severity Mapping layer (Department of Planning, Industry and Environment, 2020).

Site selection

We selected a total of 16 sites, both burnt and unburnt, within Murramarang National Park. We used QGIS (QGIS Development Team, 2023) to create a grid of sites, spaced roughly 1.5 km apart and overlaid them with the Fire Extent and Severity Mapping (FESM) layer (Department of Planning, Industry and Environment, 2020) layer. This layer allowed us to assess burn status and fire severity derived from Sentinel 2 satellite imagery. Final site selection occurred in the field where we assessed the mapped sites against visual observations of burn status and severity. The fire severity classes were unburnt, low severity (<10% burnt understorey with >90% green canopy), moderate severity (20–90% canopy scorch), high severity (>90% canopy scorched with <50% canopy consumption), and extreme severity (>50% canopy consumption) as outlined by (Gibson et al., 2020). We pooled low and moderate, and high and extreme burn severities due to their visual similarities in the amount of burnt vegetation (Fig. 2). Our final sites included four in unburned forest and 12 in burned forest—of which seven were in low/moderate, and five were in high/extreme burned forest.



Fig. 2. Example of small mammal survey sites for each fire severity class.

Live trapping surveys

Trapping took place over four sessions ranging from ~3 months to 27 months after the fires. The sessions were March 2020 (session 1), September 2020 (session 2), March 2021 (session 3) and March 2022 (session 4). Thirty aluminium Elliott traps (330 mm x 90 mm x 100 mm; Elliott Scientific Equipment, Upwey, Victoria, Australia) were used to target small terrestrial mammals at each site. Traps were placed along a 10 x 3 m transect at approximately 10 m intervals. Traps were baited with peanut butter, oats and honey rolled into 30 mm balls. Each trap was insulated with a plastic protective sleeve, and coconut fibre was used as bedding. Trapping took place over four consecutive nights, and traps were checked in the

mornings and evenings. Upon capture, animals were identified, weighed, sexed, marked, and released. Animals <50 g were marked using a 2 mm ear notch, and animals >50 g were marked using numbered ear tags. Upon recapture animals were reweighed, their mark recorded, and released.

Analysis

We investigated the relationship between small mammal richness and abundance, with time since the fires (session as a factor), burn status (burned or not during the 2019–20 fires) and fire severity. We tested these relationships using generalised linear mixed models (GLMMs). Modelling was undertaken in R v.4.3.1 (R Core Team, 2023) using the package glmmTMB (Brooks et al., 2017). Bush rats (*Rattus fuscipes*), *Antechinus* (*Antechinus agilis* and *A. stuartii* combined), and all small mammal species combined had sufficient records across sessions for the GLMM modelling. We estimated species abundance at each site using trap success, calculated by dividing the number of individuals of each species captured by the total number of trap nights minus total captures of other species (Hale et al., 2016). Total trap nights were the sum of all nights each trap was active, multiplied by the number of traps set at each site. In each model we included site as a random effect to account for repeated sampling (Zuur, 2009). Species richness models were fitted using a Poisson distribution, and abundance models were fitted using a Gamma distribution with a log link function, fitted with zero inflation. We used Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson, 2004) to select the best supported models for each species. All models with a delta AICc value <2 were considered to have substantial support, and were plotted to make inferences.

Results

We captured 485 individual animals comprising six species/groups (five native and one introduced), over 6,417 trap nights. The most frequently captured species was the bush rat which occurred predominantly in burnt forest (*R. fuscipes*; Fig. 3). Antechinuses (*A. agilis* and *A. stuartii*) were also frequently captured but occurred predominantly in unburnt forest (Fig. 3). Mainland dusky antechinuses (*A. mimetes*) were captured in session 1 only (~3 months post-fire) in forest that was unburnt (Fig. 3), while eastern pygmy possums (*Cercartetus nanus*) were captured in sessions 3 and 4 (~15- and 27-months post-fire) in forest that was burned at low/moderate severity (Fig. 3). Similarly, white-footed dunnarts (*Sminthopsis leucopus*) were caught predominantly in low/moderate severity burned forest but in sessions 1 and 2 (~3- and 9-

months post-fire). Introduced house mice (*Mus musculus*) were caught in sessions 3 and 4, predominantly in burnt forest, and had a slightly higher occurrence in sites burned at high/extreme severity (Fig. 3).

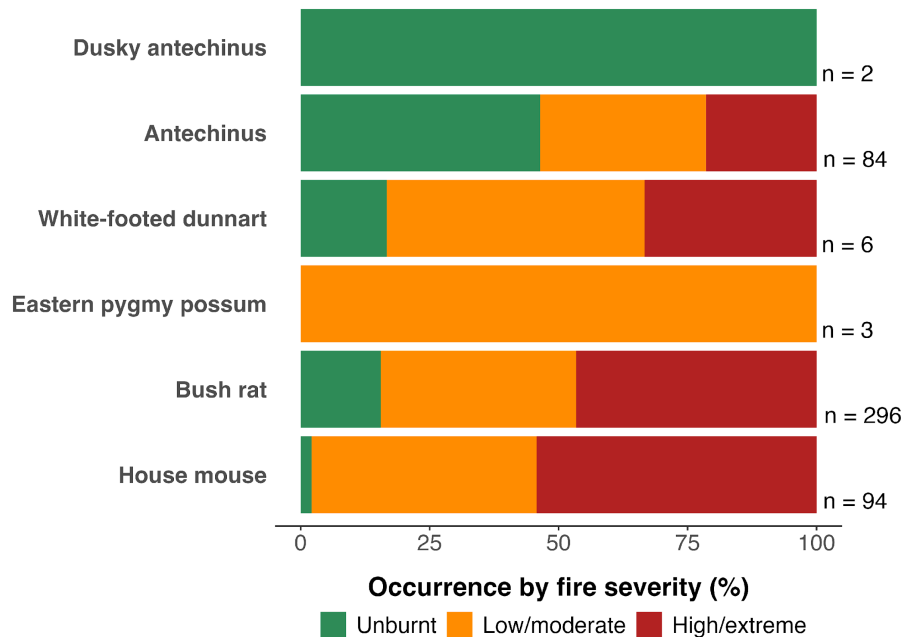


Fig. 3. Percentage occurrence of species within each fire severity class across all sessions, ‘n’ denotes total captures of unique individuals. Antechinus denotes *Antechinus agilis* and *A. stuartii* combined.

Burn status was a better predictor of species richness than fire severity (Table S1 in Supporting Information) and richness was significantly higher in burnt sites than unburnt by sessions 3 and 4 (Fig. 4b). Burn status was also well supported for the bush rat and antechinuses; however, these species showed opposing responses to fire. Bush rats had low abundance initially following the fires, with no animals recorded in session 2, but by session 4 their abundance increased substantially and was significantly higher in burnt than unburnt sites (Fig. 4a; Table S1). Conversely, antechinus abundance was higher in unburnt sites than burnt across all sessions, despite gradually increasing in burnt sites over time (Fig. 4c). Abundance of all small mammal species captured was higher in unburnt sites than burnt sites in the first two sessions but was significantly higher in sites burned at a high/extreme severity by session 4 (Fig. 4d; Table S1).

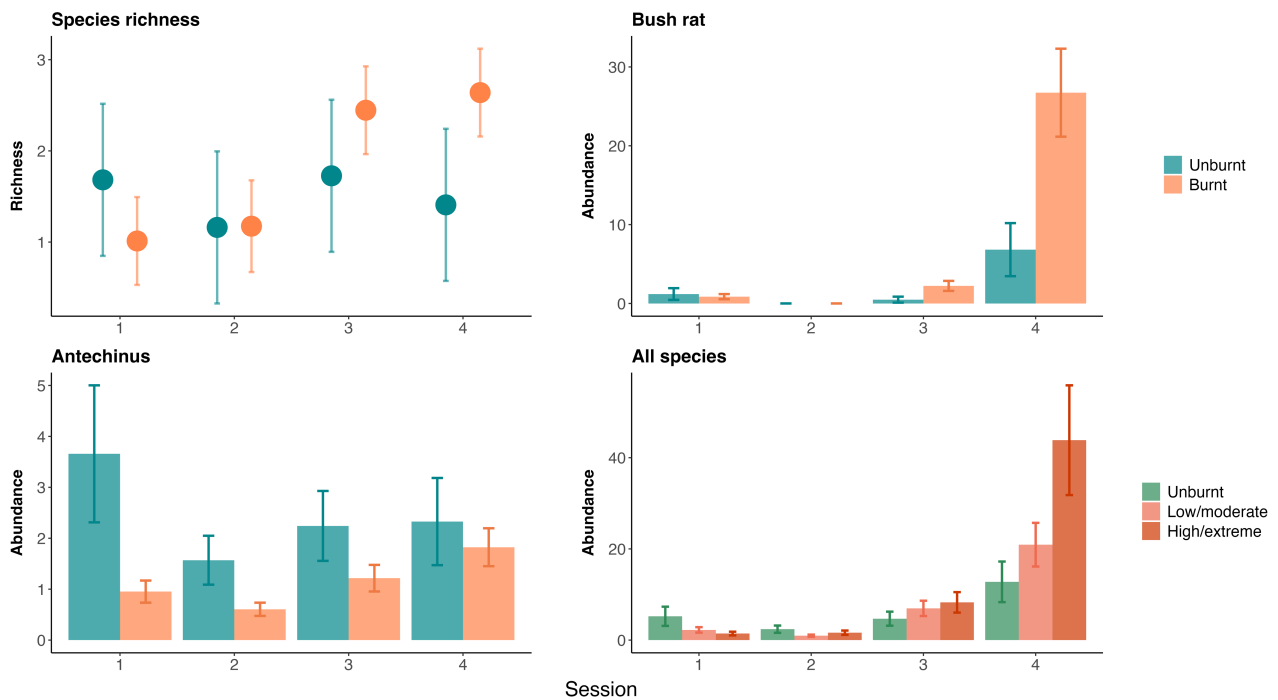


Fig. 4. Predicted relationships of species richness (b) and estimated abundance (a, c-d) from well supported burn status and fire severity models, derived from GLMMs. Each plot presents mean predictions with associated standard errors.

Discussion

With the threat of extensive, high-severity wildfires increasing globally, the 2019–20 Australian fires presented an important opportunity to examine wildlife responses to megafire. We assessed the response of various small mammals to the megafires 3–27 months post-fire. Native bush rats and antechinuses had contrasting responses to the fires, with bush rat abundance increasing and becoming higher in burnt sites over time, in comparison to antechinuses which had higher abundance in unburnt sites throughout the study period. Further, invasive house mice had a strong preference for burned forest, especially sites burned at high/extreme severity.

In line with previous studies (Banks et al., 2017, 2011; Fordyce et al., 2016), we found that the fire reduced bush rat abundance for over a year after the fires which is likely due to the species' requirements for dense vegetation. These findings are consistent with those on other small mammal species which share a similar dependency on dense vegetation for food and shelter (Horn et al., 2012; Plavsic, 2014). Bush rats rely on

understorey vegetation for diurnal shelter, and access to foraging resources such as green plant foods, fruits, fungi, and invertebrates (Dickman and Steeves, 2004). Preference for dense vegetation may also reduce predation risk (Doherty et al., 2022) and may be related to predator avoidance, which has been noted in bush rats (Strauß et al., 2008) as well as other rodent species (Jacob and Brown, 2000). Conversely to other studies (Fordyce et al., 2016), we did not find strong support for fire severity influencing bush rat abundance. Bush rat abundance was very low until over a year after the fires in all burnt sites. Previous evidence suggests that many small mammals survive fires in situ by seeking refuge in gullies, rocks, large trees or other habitat components that provide shelter (Banks et al., 2017; Hale et al., 2022). While the 2019–20 fires burned through natural fire refuges that were once considered less flammable or unlikely to burn, including rainforest gullies and south-facing slopes (Wintle et al., 2020), the succession of bush rats in burnt forest observed in our study, and their relatively poor dispersal ability (Banks et al., 2017), suggests that individuals did persist within fine-scale refuges and recolonised once understorey regeneration occurred.

The initial abundance of antechinuses was also impacted by 2019–20 fires, but in comparison to bush rats their recovery was slower and remained lower in burnt sites than unburnt throughout the study irrespective of fire severity. The initial low abundance observed for the antechinus species may be partly due to torpor which is an energy saving strategy used during periods of resource scarcity (Dickman and Happold, 2022; Stawski et al., 2015). In post-fire environments this strategy can reduce foraging requirements and exposure to predators (Stawski et al., 2015). Apart from torpor, another plausible explanation for the reduced antechinus abundance in burnt sites is reduced food resources. Antechinuses are not as strongly influenced by vegetation cover so their reduced abundance likely is the result of their more specialised carnivorous diets dominated by invertebrates (Baker and Dickman, 2018). Dietary flexibility is an important but commonly overlooked mechanism enabling species' persistence in post-fire environments (Dickman and Happold, 2022). Fire has been shown to decrease the abundance of terrestrial invertebrates (York, 1999) preyed upon by the antechinus species (Dickman and Happold, 2022). Furthermore, invertebrate recovery is slow (Henry et al., 2022), and this likely explains the observed difference in recovery rates between bush rats and antechinuses in burnt forest. Lastly, conversely to bush rats, the key shelter resources for antechinuses are hollow-bearing trees (Banks et al., 2011) which can be lost in major wildfires (Lindenmayer et al., 2012) and take decades to recover (Gibbons and Lindenmayer, 2002).

The abundance of all small mammals captured in our study was influenced by fire severity. Abundance was highest in unburnt forest and lower in high/extreme severity burnt forest initially following the fires. However, one-year post-fire introduced house mice started to occur in burnt sites, especially at sites burned at high/extreme severity. By two years post-fire, much of the native small mammal response to high/extreme severity fire was driven by the generalist rodent species, bush rats and house mice, which accounted for 80% of total captures. This pattern 2 years after the fires matches that of other rodents such as the deer mouse (*Peromyscus maniculatus*), which has been shown to increase in abundance in burnt landscapes 2–3 years post-fire (Brehme et al., 2011).

Existing research suggests that high severity fires can promote the prevalence of invasive species like house mice (Stevens et al., 2012), and this may be partly due to their generalist diet, fast reproduction, and opportunistic ability to exploit disturbed areas (Sutherland and Dickman, 1999), especially in the absence of intraguild competitors and potentially predators such as antechinuses (Baker and Dickman, 2018). More broadly, the ability of generalist species to exploit severely burnt areas post-fire has been documented in studies globally (Brehme et al., 2011; Culhane et al., 2022; Morandini et al., 2023). In contrast, dietary specialists white-footed dunnarts and mainland dusky antechinuses were caught in very low numbers (less than 2% of total species captures) and only during the first two sessions (3–9 months post-fire). Furthermore, while our observations indicated a marginal increase in small mammal diversity in burnt forest relative to unburnt approximately 1–2 years after a fire, this included a minimal number of records (less than 1%) of eastern pygmy possums in sites affected by low/moderate severity burns, along with the surge in house mice. Therefore, we suspect that frequent and severe fires will favour generalist rodent species and potentially exclude more specialised species whose preferred resources are depleted after fire.

Conservation and management

While our study species encompass a small proportion of Australian vertebrates, they are representative of the threats to small mammals that are typically driving population declines elsewhere in the world (Woinarski et al., 2015). Our results suggest that fire and burn severity had a limited negative effect on species like the bush rat. However, species' responses to fire are driven by the availability and spatial distribution of critical resources, which are also influenced by fire. Therefore, species that are relatively insensitive to a single fire may be challenged under potential future scenarios of increasing fire frequency.

For example, short inter-fire intervals can influence plant recruitment (Plumanns-Pouton et al., 2023) or formation of hollow-bearing trees (Gibbons and Lindenmayer, 2002). Furthermore, species that are poor at dispersing and that use shelter sites to survive and recolonise are at threat of suffering greater population losses during future extreme fires (Ensbeys et al., 2023). For species with more specialised dietary or shelter requirements, such as diets featuring invertebrates that take time to recover, or hollows that are slow to re-establish, are likely to suffer greater mortality risks post-fire (Ensbeys et al., 2023). Therefore, under expected changes in the occurrence, intensity and extent of wildfires, active management of refuges to safeguard sensitive species from displacement or local extinction will become more important. Reducing pressures from invasive predators may become especially valuable as vegetative cover re-establishes. Finally, protection of unburned forest and unburned refuges from major disturbances such as logging will support healthy habitats for fire sensitive species, and support the recolonisation of recovering burnt areas (Fitzsimons, 2020; Von Takach et al., 2022).

While most of the native species in our study are considered common, we emphasise that this is not an immutable attribute and that even abundant taxa may decline quickly and become locally extinct if habitat is degraded or conditions generally become unsuitable (e.g., Lindenmayer et al., 2011). Additionally, identifying initial stages of decline can provide more cost-effective management outcomes (Possingham et al., 2002). Notably, some species in our study were already in a state of decline. The broadscale population loss of the mainland dusky antechinus due to the 2019–20 fires was severe enough to propose this species for listing as threatened under the EPBC Act 1999 (Legge et al., 2022). Meanwhile, white-footed dunnarts are listed as Vulnerable in NSW under the Biodiversity Conservation Act 2016 and are part of the NSW Saving our Species strategy (NSW Department of Planning and the Environment, 2023). Key actions under this strategy include focusing on protecting and maintaining habitat, revegetation to enhance habitat quality and connectivity, and retaining dead timber and preventing firewood collection in critical habitat.

Author contributions

The study's conception and design were a collaborative effort between VM, TD, and CD. VM collected and analysed the data and led the writing of the manuscript. TD and DN gave valuable feedback on the data analysis. CD made important contributions to the final draft.

Acknowledgements

We acknowledge the Murramarang peoples, the Traditional Owners of the lands and waters on which this work was conducted, and extend that respect to their Elders past and present. We thank the NSW National Parks and Wildlife Service staff, Michael Phelan and David Cunningham, for providing local knowledge, assistance, and equipment during the course of this project. We also thank the volunteers that assisted with fieldwork. Funding for this research was provided by the NSW Environmental Trust.

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*Supporting information***Table S1.** Relationships between fire variables and species richness and abundance, derived from GLMMs.

Only top-ranked models (<2 AIC units) are shown.

Model	Estimate	SE	z	P	AIC
Richness					
<i>Burn status</i>					176.46
Session 2 (Burnt)	0.68	0.70	0.98	0.33	
Session 3 (Burnt)	1.39	0.69	2.00	0.05	
Session 4 (Burnt)	1.90	0.69	2.73	0.01	
All species					
<i>Fire severity</i>					347.44
Session 2 (Low/Mod)	-0.06	0.52	-0.11	0.91	
Session 2 (High/Extreme)	0.89	0.52	1.71	0.09	
Session 3 (Low/Mod)	1.24	0.54	2.30	0.02	
Session 3 (High/Extreme)	1.85	0.53	3.51	<0.01	
Session 4 (Low/Mod)	1.34	0.50	2.66	0.01	
Session 4 (High/Extreme)	2.52	0.51	4.99	<0.01	
Bush rat					
<i>Burn status</i>					253.81
Session 2 (Burnt)	-0.67	0.00	0.00	1.00	
Session 3 (Burnt)	1.85	0.86	2.17	0.03	
Session 4 (Burnt)	1.69	0.56	3.00	0.01	
Antechinus					
<i>Burn status</i>					214.28
Session 2 (Burnt)	0.39	0.53	0.74	0.46	
Session 3 (Burnt)	0.73	0.53	1.37	0.17	
Session 4 (Burnt)	1.10	0.57	1.94	0.05	

Reference levels: Session 1 and Unburnt.

Chapter 3 – After the ‘Black Summer’ fires: faunal responses to megafire depend on fire severity, proportional area burnt, and vegetation type

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Manuscript accepted:

Miritis, V., Dickman, C.R., Nimmo, D.G., Doherty, T.S., 2023. After the ‘Black Summer’ fires: Faunal responses to megafire depend on fire severity, proportional area burnt and vegetation type.

Journal of Applied Ecology. 1365-2664.14545. <https://doi.org/10.1111/1365-2664.14545>

My contribution to this data chapter was substantial. I conceptualised ideas and led the fieldwork, collected and analysed the data, and wrote and edited all drafts, in consultation with my co-authors.



Red fox (Vulpes vulpes) captured by motion-sensing camera. Vivianna Miritis.

Abstract

1. Climate change and human activities have disrupted historical fire regimes, leading to complex and far-reaching impacts on global ecosystems. Despite extensive research in fire ecology, studies exploring vertebrate responses to megafires, and to nuanced fire characteristics, remain limited.
2. We collected camera trap data 3–27 months following Australia’s 2019–20 ‘Black Summer’ megafires from 30 burnt sites and 10 unburnt sites. Our data included 14 animal species/groups, encompassing mammalian predators, small and medium-sized mammals, large herbivores, and birds. We used generalised additive mixed models to assess the influence of time-since-the-fires, burn status, fire severity, proportional area burnt, and vegetation type on species’ activity.
3. Models that included fire variables were well-supported for all species. The proportional cover of low-moderate or high-extreme severity fire had substantial support for five species, particularly herbivores, which generally showed a preference for burnt sites but at differing fire severities. The proportional area burnt, disregarding severity, was well supported for four species. At highly burned sites fox activity peaked shortly after the fires while small to medium-sized mammal activity increased more gradually. Vegetation type strongly influenced the response of four species to fire; in particular, wet forest birds preferred unburnt areas.
4. *Policy implications.* We document variable short- to medium-term responses of a range of species to fire which could help guide management interventions. We demonstrate that animal species’ responses to fire are diverse and better captured using broader landscape scale fire variables. We found that species were strongly influenced by proportional area burnt, fire severity, and vegetation type. Introduced foxes were attracted to recently burnt areas, so timely predator control may benefit vulnerable prey species. Wet forest species were sensitive to fires and could benefit from preservation and restoration of these habitats. Some species exploited low-moderate severity burnt areas, while others preferred high-severity burns. This suggests that species will face diverse challenges and opportunities in future extreme fire events. We emphasise the importance of using multi-faceted approaches to account for the complex responses of co-occurring species to fire events.

Introduction

Fire is a significant natural disturbance that has shaped ecosystems worldwide (He et al., 2019). These ecosystems have evolved under dynamic environmental conditions, with species often relying on disturbances such as fire for crucial aspects of their life histories (Pausas & Parr, 2018). However, a combination of climate change and human-induced suppression of natural fires has resulted in “mega-disturbances” that diverge from historical disturbance regimes (Jones et al., 2022; Stephens et al., 2013). These changes have led to increases in fire size, severity, and frequency in many regions (Jones et al., 2022). Record-breaking wildfires have become more common on nearly every continent (Attiwill & Binkley, 2013; Duane et al., 2021) and are increasingly affecting areas previously considered less flammable or unlikely to burn (Bowman et al., 2020). While many species are adapted to regular disturbances, these unprecedented disruptions to historical fire regimes can have complex and far-reaching implications, especially for species that do not typically encounter fires (Nimmo et al., 2021).

Understanding the impact of fires on populations is vital not only for broader habitat management, but also for prioritising species and conservation actions. Despite a significant body of research on fires, empirical data on the response of animal populations to wildfires, especially megafires, remains limited (Ensbey et al., 2023; Pausas & Parr, 2018; Tingley et al., 2018). This is in part due to studies rarely coinciding with megafires, and the differing susceptibility of animal species to fire. Some species require long-unburnt habitat (Von Takach et al., 2022), some benefit or are challenged by specific burn severities (e.g., Jones et al., 2021; Tingley et al., 2018), and some rely on fire heterogeneity (Lewis et al., 2022). Therefore, a key priority is understanding how specific fire characteristics influence the response of species within burned areas, and how these processes manifest over spatial and temporal scales (Tingley et al., 2018).

Studies on time since fire and fire return intervals have provided valuable insights on vertebrate responses to fires (Nimmo et al., 2012; Watson et al., 2012). Time since fire can act as an indirect indicator of habitat suitability and can be used to generate temporal fire response curves for different species. However, the importance of fire characteristics such as fire severity and area burnt, remain poorly understood (Kelly & Brotons, 2017; Lindenmayer et al., 2014). Fire severity is a measure of post-fire organic matter loss, above and below ground (Keeley, 2009). Fire severity impacts animal survival and forest structure, affecting post-fire availability of shelter and forage (Smucker et al., 2005; Tingley et al., 2018), and animal occurrence and activity (Chia et al., 2016; Lindenmayer et al., 2014). The impacts of spatial variation in fire severity and the

proportion of area burnt are complex, and can benefit some animal species (Lewis et al., 2022) and disadvantage others (Taylor et al., 2012). Additionally, it remains unclear to what extent the response of species to fire is influenced by spatial scales. Burn area and severity may impact animals at very fine spatial scales (e.g., <10 m) or at broader landscape scales (e.g., hundreds to thousands of meters; Tingley et al., 2018; Blakey et al., 2021).

In addition to fire characteristics, vegetation can influence how disturbance impacts a landscape and how species respond to disturbance. Different species rely on specific vegetation types for food and shelter (Culhane et al., 2022), but vegetation itself can influence the immediate and ongoing impact of fire due to its differing characteristics (Clarke et al., 2014). For instance, during fire, some vegetation types may exhibit pyrogenic traits (e.g., flammable leaf oils) that encourage fire propagation, while others may have pyrophobic traits (e.g., higher soil moisture) that suppress fire spread (Clarke et al., 2014). Beyond these immediate effects, differing vegetation types may also show varied regeneration patterns as a result of both the fire behaviours they have influenced and inherent functional traits (e.g., variation in resprouting) that affect their post-fire response (Clarke et al., 2013); these may further impact vertebrate species.

To further understand the post-fire responses of vertebrate species to fire and vegetation variables, we collected data 3–27 months after the 2019–20 Australian megafires, known as the 'Black Summer' fires. The Black Summer marked Australia's most severe wildfire season on record (Bowman et al., 2020) and our study was one of the few that collected data in the initial months post-fire. Our objectives were to examine how fire characteristics and vegetation type shape species' responses to fire and how these responses change over time. Specifically, we statistically assessed the responses of 14 animal species/groups to, time-since-the-fires, burn status (burned or not during the 2019–20 fires), proportional area burnt (within a buffer), fire severity (at point and buffer scales), and vegetation type.

Materials and methods

Study area

Our research was conducted in Murramarang National Park (35.61° S, 150.30° E), on the south-eastern coast of Australia (Fig. 1). Field methods were approved by the University of Sydney Animal Ethics Committee (2020/1821), and the NSW Department of Environment and Planning granted permission for these methods to be carried out in the National Park (SL102361). The park is approximately 1,970 ha and

has a temperate climate with mean maximum temperatures around 17°C in winter and 26°C in summer (Bureau of Meteorology, 2023). The Black Summer fires, primarily the Currowan fire which was ~315,000 ha in size, burnt over 80% of the park at variable severity, leaving only the southernmost area unburnt (Fig. 1).

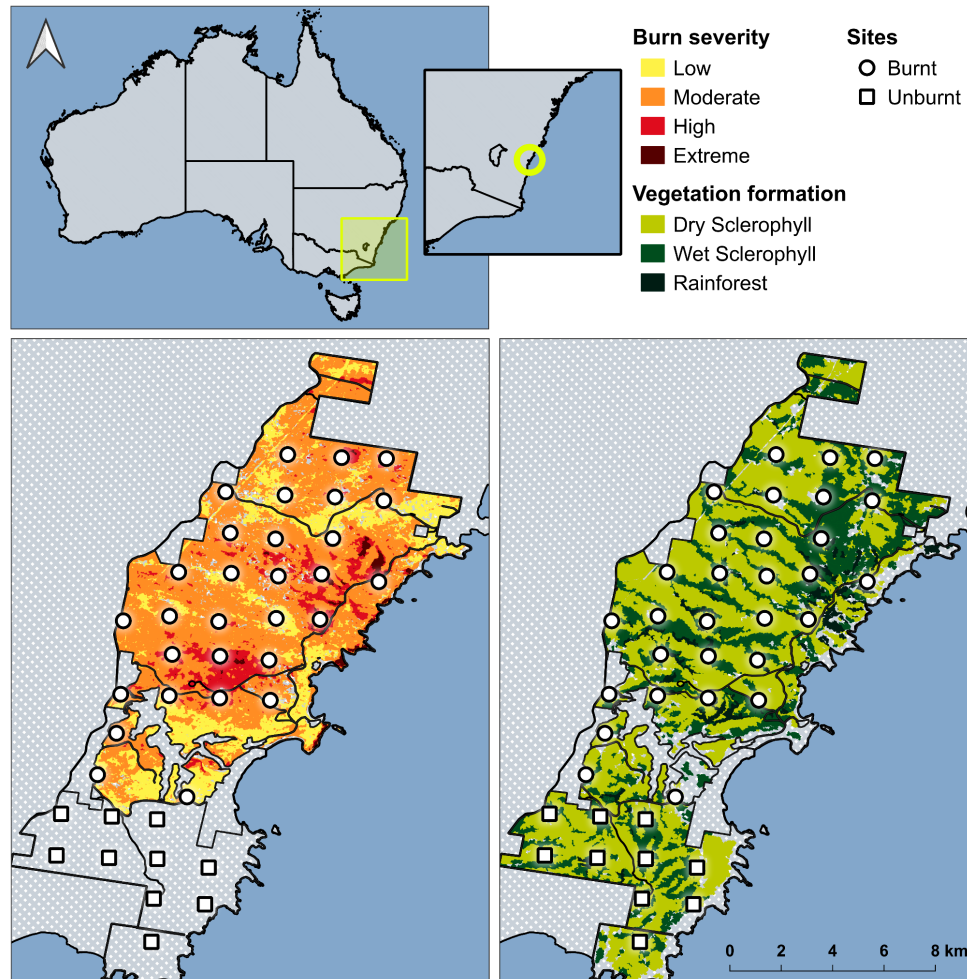


Fig. 1. Location of Murramarang National Park in south-eastern Australia (top-left) and locations of camera traps relative to burn severity (bottom-left; DPIE, 2020) and vegetation formations (bottom-right; DPIE, 2022) within the park.

Study design

We used QGIS (QGIS Development Team, 2023) to create a grid of sites, spaced roughly 1.5 km apart. We overlaid the resulting 40 sites with the Fire Extent and Severity Mapping (FESM) layer (Department of

Planning, Industry and Environment [DPIE], 2020). This showed that 30 sites were in burnt forest and 10 in unburnt forest (Fig. 1), which we confirmed through visual observation during field deployment. Motion-sensing cameras (HF2X, Reconyx, Holmen, WI, USA) were deployed in mid-March 2020, three months post-fire, which was the earliest we could gain access to the study area. Due to inaccessibility, three camera positions were placed 200–300 m from their intended position, but the final positions were in a grid formation (Fig. 1). All cameras were positioned facing south to minimise sun glare, fastened to a tree at a height of ~50 cm and angled slightly down. A PVC pipe bait canister containing tuna oil-soaked fabric was pegged to the ground 2 m in front of each camera. We cleared understorey vegetation between the camera and bait to minimise false triggers and ensure animals were clearly visible. Cameras were set to motion trigger on a continuous schedule, on ‘high’ sensitivity, and ‘fast shutter’ night mode, and took five consecutive photos per trigger with no delay between triggers. Cameras were serviced and re-baited every three to six months and stayed in continuous operation until March 2022.

Vegetation type

The cameras were positioned within two vegetation formations, wet sclerophyll forest (grassy sub-formation) and dry sclerophyll forest (shrubby sub-formation). These vegetation formations are classified by Keith (2004) and represent broad groupings of plant community types that share similar ecological characteristics. One site fell within rainforest, which we reclassified as wet sclerophyll forest for the analysis. Wet sclerophyll forest is a tall (>30 m) to extremely tall (>60 m) eucalypt forest with a mid-storey of mesophyll and sclerophyll shrubs, and a ground layer of grasses, climbers, and cycads (DPIE, 2022). Wet sclerophyll forests often grow near rainforests and contain some rainforest species. They are relatively fire sensitive, highly combustible, and can produce harsh crown fires. Dry sclerophyll forest is a widespread tall (>30 m) to very tall (>40 m) dry shrubby open eucalypt forest with a sparse ground cover of grasses, graminoids and bracken (DPIE, 2022). The structure and composition of dry sclerophyll forests is strongly affected by the frequency and severity of fires, and fires are vital to their regeneration.

Proportion burnt

For the ‘proportion burnt’ model, we created a series of circular buffers with radii of 50 m, 200 m, and 500 m from each camera. These buffers were used to extract data on proportional area burnt from the FESM layer irrespective of fire severity. This fire metric was highly correlated between the three buffer sizes ($r = 0.95\text{--}0.99$), thus we selected the 200 m buffer to capture the fine scale responses of smaller less mobile

species, such as small dasyurids, while still accommodating the broader spatial requirements of more mobile species.

Fire severity and proportion of fire severity

We assessed burn severity in two ways—within the immediate vicinity of each camera (point scale), and as proportional area burnt using the 200 m buffers. The resulting models were ‘fire severity’ and ‘proportion of fire severity’ (Fig. 2). We derived burn severities from the FESM layer, which followed the classification system outlined in Gibson et al. (2020). This classification categorises burn severity as ‘Unburnt’ (0% understorey and canopy burnt), ‘Low’ (<10% burnt understorey with >90% green canopy), ‘Moderate’ (20–90% canopy scorch), ‘High’ (>90% canopy scorched with <50% canopy consumption), and ‘Extreme’ (>50% canopy consumption). For ‘fire severity’ we verified burn severities on the FESM map with visual observations in the field, using the classification categories. We pooled the low and moderate, and high and extreme burn severities so that the final variables were unburnt, low-moderate, and high-extreme.

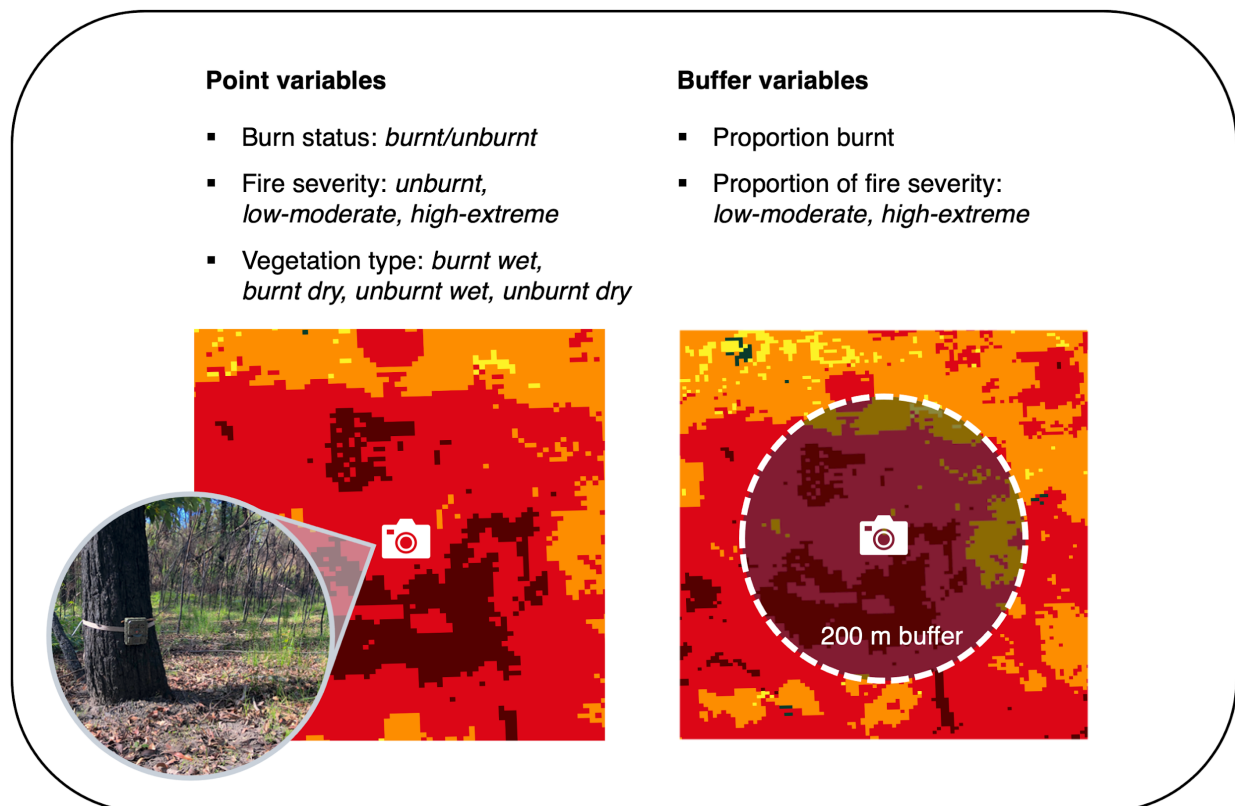


Fig. 2. Models and their predictor variables at point and buffer scales.

Analysis

We established 24 one-month survey periods, based on the number of months the cameras were operating post-fire. These periods ranged from three months (mid-March 2020) to 27 months (early-March 2022) post-fire. For each period, we identified the presence of animal species in the camera images and counted the number of independent detections per species per camera. An independent detection was defined as images of the same species captured on the same camera, separated by at least 60 minutes. We excluded 90 survey periods across 40 cameras (from a total of 960) where the number of survey days was less than 14 (e.g., due to camera failure) to ensure that the sampling period was representative of species activity, as shorter sampling periods may not provide robust estimates for species' occurrences (Kays et al., 2020).

Twelve species, plus two groups representing multiple species, were detected in sufficient numbers for modelling. The two groups were brushtail possums (genus *Trichosurus*) and small dasyurids (genera *Antechinus* and *Sminthopsis*). Small dasyurids included common and white-footed dunnarts (*Sminthopsis murina* and *S. leucopus*), and brown and agile antechinuses (*Antechinus stuartii* and *A. agilis*), which were difficult to accurately identify to a species level in the images. Brushtail possums included common brushtail possums (*Trichosurus vulpecula*) and mountain brushtail possums (*T. cunninghami*). These were combined because preliminary analysis showed similar trends and the same best supported models for both species, and combining them provided a more robust modelling dataset.

We used generalised additive mixed models (GAMMs) fitted with the 'mgcv' package (Wood, 2017) in R v.4.3.1 (R Core Team, 2023) to model species' activity in relation to time since the fire (months), burn status (burned or not during the 2019–20 fires), proportion burnt, fire severity, and vegetation type (Table 1). The 'time-since-the-fires' model did not incorporate any fire-related variables; it solely focused on changes in species activity over time to account for seasonal variation (Table 1). The 'burn status' model used a binary variable to indicate whether a site was burnt or unburnt. In all models, we included a variable for the months elapsed since the fire, aiming to capture changes related to post-fire succession (Table 1). The response variable was the number of independent animal species detections per survey period. We also included an offset term to account for the varying number of days in each period, along with a random effect for each site to adjust for repeated sampling. Models were fitted using maximum likelihood estimation and assumed a negative binomial distribution. Residual plots indicated that data for the swamp

wallaby were under-dispersed, so we instead fitted those models using the Gaussian distribution, which was deemed appropriate based on diagnostic tests (see Figure S1 in Supporting Information).

Table 1. Explanatory variables in the GAMM analysis for each model (+ denotes inclusion of the variable in the model).

Model	months post- fire	burnt, unburnt	low-mod, high-extreme	% burnt (200m)	% low- mod(200m)	% high- extreme(200m)	wet forest, dry forest
Time since the fires	+						
Burn status	+	+					
Fire severity	+		+				
Proportion burnt	+			+			
Proportion of fire severity	+				+	+	
Vegetation type	+	+					+

We used Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson, 2004) to select the best supported models for each species. All models with a delta AICc value <2 were considered to have substantial support, and were plotted with 95% confidence intervals to make inferences.

During our study, lethal fox (*Vulpes vulpes*) control was undertaken near our sites. We accounted for the potential effect of baiting on fox activity by including bait uptake as a covariate in our models. We specifically examined how fox activity varied by time-since-the-fires, and our results indicated that baiting did not affect fox activity.

Results

The camera surveys collected 830,725 images over 751 days. Of these, 573,133 were of animals, and 16,325 were considered to be 'independent'. In total, we identified 65 vertebrate species, comprising 18 mammals, 43 birds, three reptiles, and one amphibian. We statistically assessed the activity of 14 animal species/groups.

The 'time-since-the-fires' model was well supported for the short-beaked echidna (*Tachyglossus aculeatus*) and swamp wallaby (*Wallabia bicolor*). However, models that included fire variables were well supported

for all species (see Table S1 in Supporting Information). The ‘proportion of fire severity’ model had substantial support for five species. The ‘proportion burnt’ and ‘vegetation type’ models had substantial support for four species each, and the ‘fire severity’ model was well supported for two species. The ‘burn status’ model had substantial support for five species but other models containing more detailed fire characteristics were also well supported for these species (see see Table S1).

Effects of burn status

The ‘burn status’ model was supported for the fox, cat (*Felis catus*), short-beaked echidna, bush rat (*Rattus fuscipes*), and swamp wallaby. However, plotting the relationships for all species revealed temporal fluctuations (Fig. 3). The large herbivores—eastern grey kangaroo (*Macropus giganteus*), swamp wallaby, and bare-nosed wombat (*Vombatus ursinus*)—had higher activity in burnt sites throughout the study. Fox activity in burnt sites was initially high but decreased over time, whereas cat activity was initially similar between burnt and unburnt sites but decreased in burnt sites over time. Southern long-nosed bandicoots (*Perameles nasuta*) became more common at burnt sites over time, whereas brushtail possums became less common. The activity of small mammals (bush rats and small dasyurids) was initially low in burnt sites but increased over time. Superb lyrebirds (*Menura novaehollandiae*) and painted-button quails (*Turnix varius*) had lower and higher activity in burnt sites, respectively, throughout the study. While the activity of satin bowerbirds (*Ptilonorhynchus violaceus*) and wonga pigeons (*Leucosarcia melanoleuca*) decreased in burnt sites and increased in unburnt sites over time.

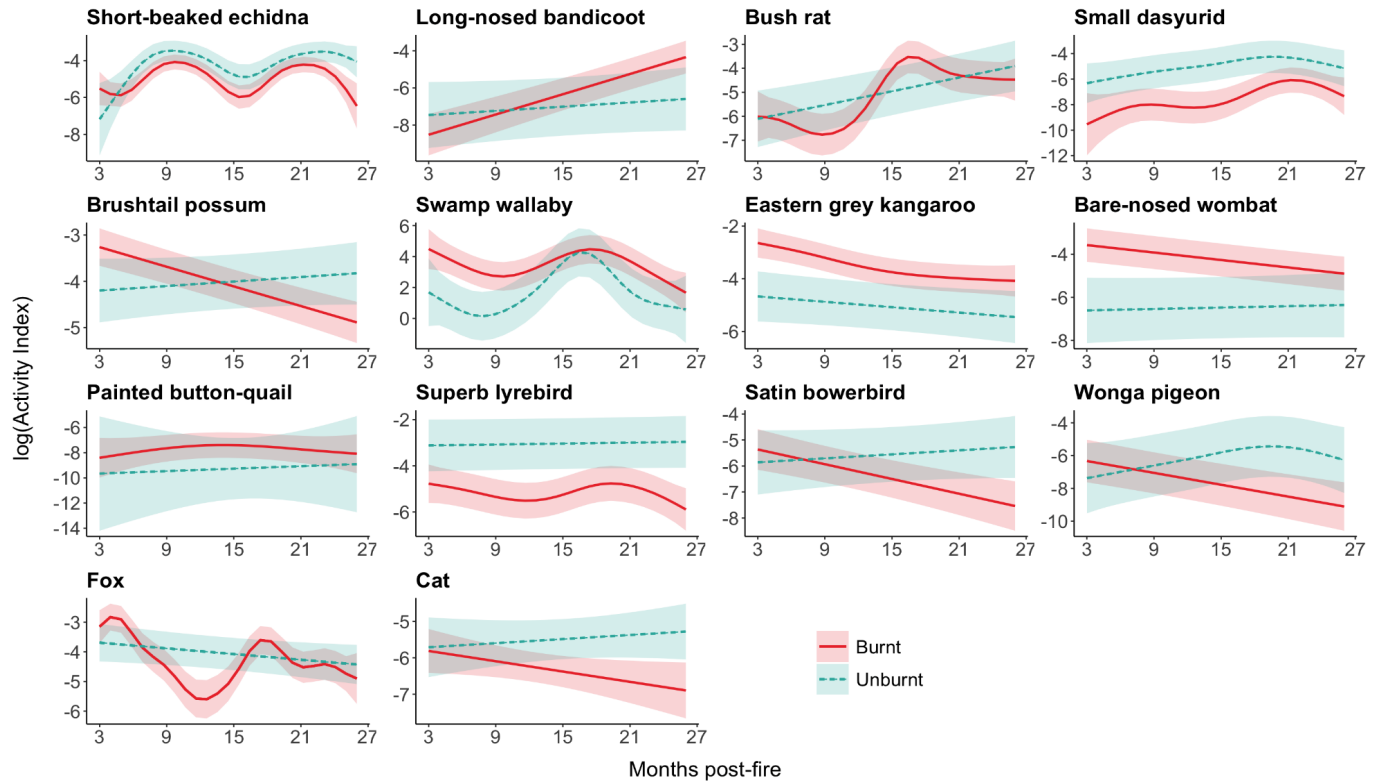


Fig. 3. Species' activity in burnt and unburnt sites, 3–27 months following the Black Summer fires. Lines indicate means, shading indicates 95% CI.

Effects of proportion burnt

Peak fox activity was observed ~3–5 months post-fire at sites where >50% was burnt, and 18 months post-fire where >90% was burnt (Fig 4). Bush rat activity was lowest ~8 months post-fire in burnt sites (Fig. 3) and peaked ~18 months post-fire at sites where >90% was burnt (Fig. 4). Similarly, southern long-nosed bandicoot activity was lowest ~3–9 months post-fire in burnt sites but peaked ~26 months post-fire at sites that were >75% burnt (Fig. 4). Conversely, brushtail possum activity was highest ~3–8 months post-fire at sites with a high proportion of burnt forest (~75–80%; Fig. 4).

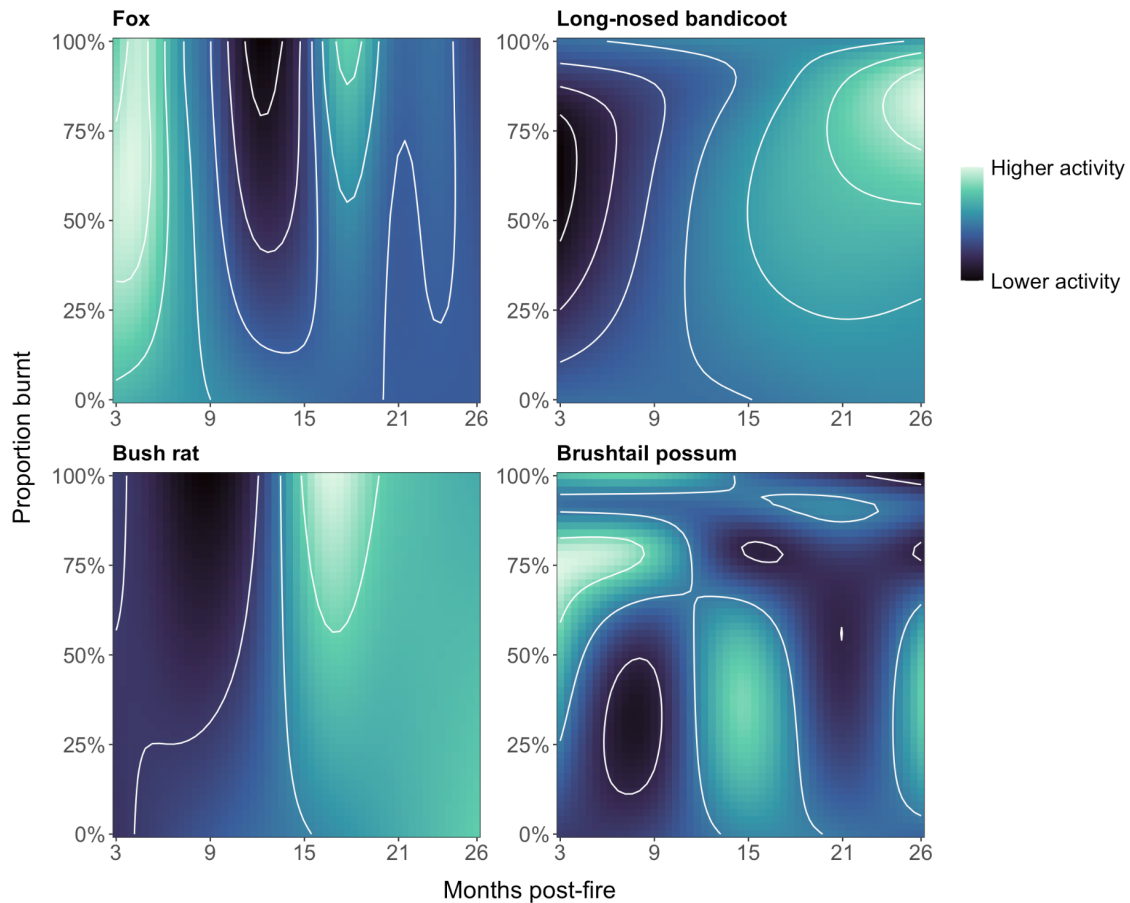


Fig. 4. Predicted relationships from well supported ‘proportion burnt’ models.

Effects of fire severity and proportion of fire severity

Wombat activity was higher in burnt than unburnt forest throughout the study (Fig. 3), but peak activity was observed ~3–9 months post-fire at sites with >60% burnt at low-moderate severity (Fig. 5). Kangaroo activity peaked ~3–6 months post-fire, at sites with ~20% burned at high-extreme severity (Fig. 5). In contrast, swamp wallaby activity peaked three- and 17-months post-fire, at sites with ~50% and >90% burnt at low-moderate severity, respectively (Fig. 5). Short-beaked echidna activity was similar in burnt and unburnt sites (Fig. 3), but within burnt sites, higher activity was observed at low-moderate severity (Fig. 5).

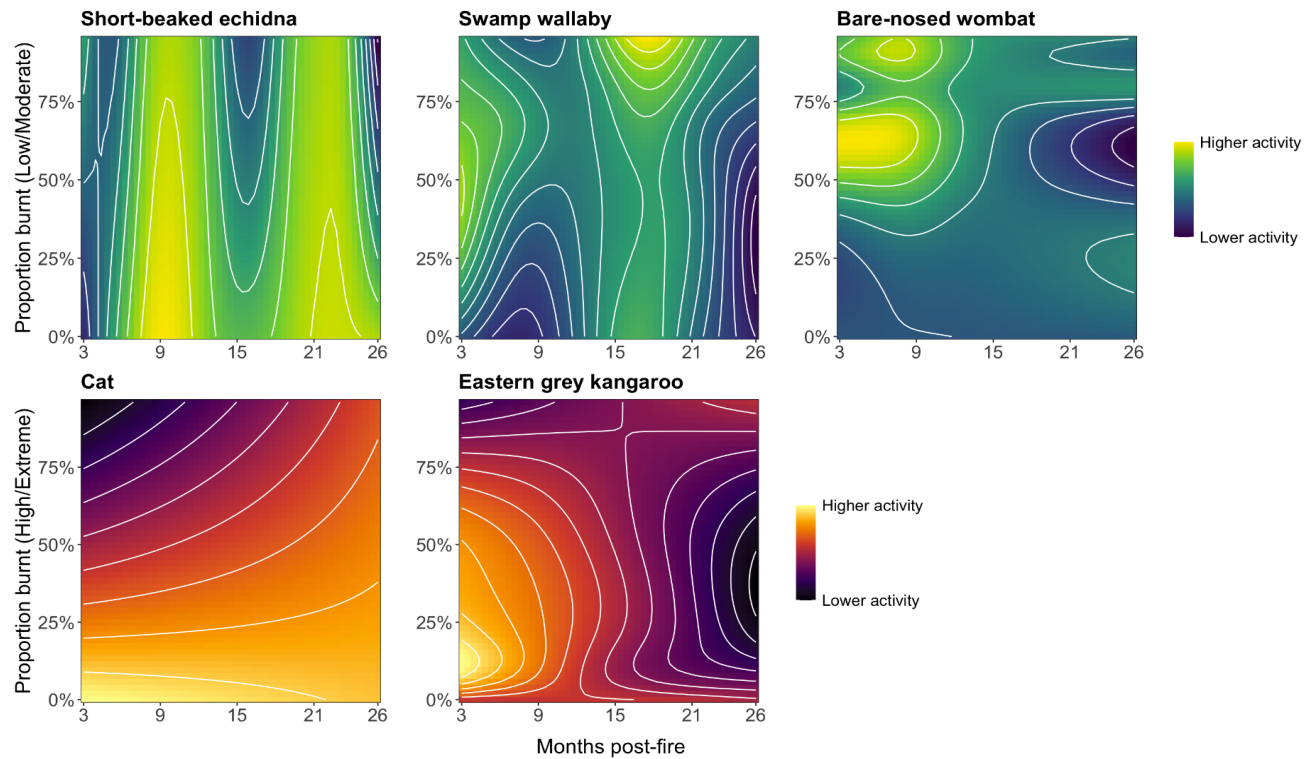


Fig. 5. Predicted relationships from well supported ‘proportion of fire severity’ models for low-moderate and high-extreme burn severities.

Cat activity was highest 3–9 months post-fire at sites burnt at low-moderate severity (Fig. 6) and at sites with minimal surrounding high-extreme burns (Fig. 5), although the interactions were not significant (see Table S1). Painted button-quail activity was highest 12–18 months post-fire at sites burnt at high-extreme severity (Fig. 6).

Effects of vegetation type

Small dasyurids had higher activity in unburnt than burnt sites (Fig. 3), especially in dry forest (Fig. 6). Superb lyrebird activity was lowest in burnt dry forest throughout the study and was generally higher in wet forest in comparison to dry forest, irrespective of burn status (Fig. 6). Satin bowerbird and wonga pigeon activity was initially similar between burnt and unburnt sites, but declined over time, especially in dry forest (Fig. 6).

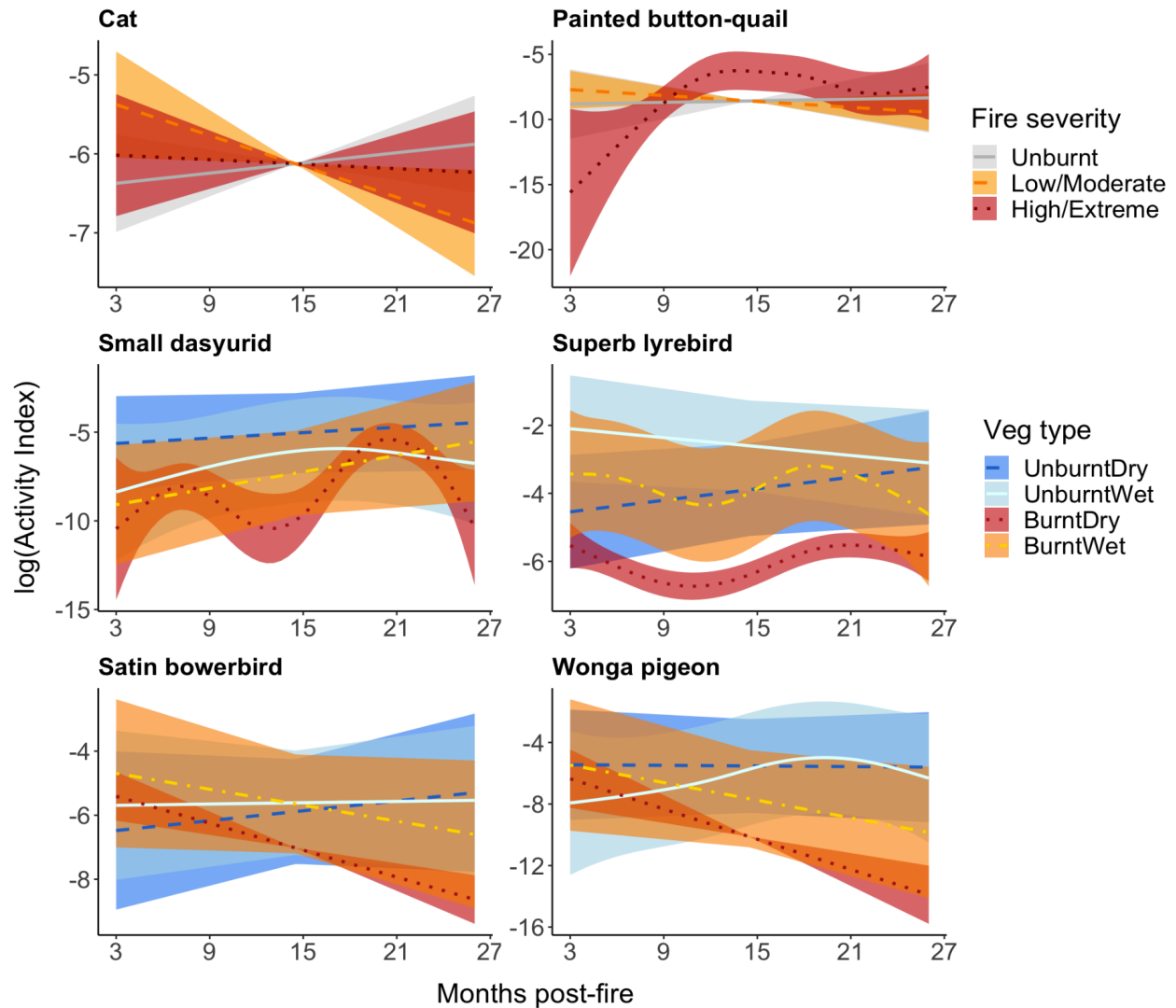


Fig. 6. Predicted relationships from well supported ‘fire severity’, and ‘vegetation type’ models, with 95% confidence intervals.

Discussion

With the risk of megafires increasing globally, Australia’s Black Summer fires presented an important opportunity to examine wildlife responses to record-breaking disturbance. These megafires impacted many forest-dependent vertebrates, but their effects manifested differently between species, suggesting that several mechanisms drive faunal responses to fire.

Effects of time-since-the-fires and burn status

The burn status model had strong support for the fox, cat, short-beaked echidna, bush rat, and swamp wallaby. However, models incorporating specific fire characteristics were also well supported for these species. One species that was strongly influenced by time-since-the-fires and burn status was the short-beaked echidna. The support for time-since-the-fires likely reflects seasonal variation in echidna activity, which decreases during the summer and increases during the spring according to food availability and energy requirements (Clemente et al., 2016). Furthermore, echidnas use torpor during periods of environmental stress; allowing them to reduce activity, maintain lower body temperatures, and decrease energy demands (Nowack et al., 2016). This adaptation may account for the lower overall activity observed in burnt sites and support for the burn status model.

Effects of proportion burnt

Foxes were strongly influenced by burn status and responded positively to recently burnt areas with a higher proportion burnt. Fires favour some predators by removing vegetation and simplifying the landscape (Hradsky et al., 2017; McGregor et al., 2015), which in-turn can expose prey species to enhanced predation risk (Banks & Dickman, 2007; Leahy et al., 2015). The initial peak and then subsequent decline of foxes in burnt areas, observed five months post-fire, suggests that any hunting advantage in burnt areas may diminish over time, particularly if food availability declines or vegetation recovery hampers hunting efficiency (Doherty et al., 2022). Other research found no discernible difference in fox occurrence between burnt and unburnt sites around one year after the Black Summer fires (Spencer et al., 2022). This further suggests that these responses driven by hunting opportunities are time-sensitive and more likely to occur shortly after the fires, supporting existing findings on this topic (Doherty et al., 2023).

The bush rat and southern long-nosed bandicoot increased in burnt sites over time, especially in areas with a higher proportion burnt. This response likely reflects habitat requirements, as they depend on dense vegetation for shelter, and often select habitats with high understorey cover even when food resources are greater, or competition is lower, elsewhere (Dexter et al., 2011; Spencer et al., 2005). Brushtail possum activity was higher at sites with a large proportion of burnt forest up to eight months post-fire, but strongly declined at burnt sites thereafter. This elevated activity in sites with extensive fire damage may reflect more frequent ground movements by possums. Such behaviour is similar to that of Bornean orangutans (*Pongo pygmaeus*), which can modify their terrestriality based on understorey and canopy structure

following disturbance (Ancrenaz et al., 2014). Further to this, dry sclerophyll forests which were dominant in our study, have tree species that rapidly recover their canopies through epicormic bud growth on trunks and branches (Clarke et al., 2014). Therefore, the decline in activity of brushtail possums may reflect a reduction in ground-level activity due to improved canopy connectivity and reduced need or increased difficulty in navigating the understorey as vegetation recovered post-fire.

Effects of fire severity and proportion of fire severity

Eastern grey kangaroos, swamp wallabies and bare-nosed wombats had higher activity in burnt sites throughout the study. Large herbivores (>2 kg) are commonly attracted to recently burnt areas to feed on the flush of regrowth, as shown in studies from North America (Lewis et al., 2022), Asia (Moe & Wegge, 1997) and Africa (Archibald & Bond, 2004). However, the fire severity models revealed that kangaroo activity peaked shortly after the fires at sites with a low proportion of high-extreme severity burns, whereas swamp wallaby activity peaked more than one year post-fire at sites predominantly burned at low-moderate severity. This may reflect different habitat preferences—kangaroos seek open habitats for foraging (Moore et al., 2002), while smaller macropods like swamp wallabies favour lateral vegetation cover for concealment from predators (Di Stefano et al., 2009). White-tailed deer (*Odocoileus virginianus*) in North America similarly increased their activity in burnt areas as vegetation cover recovered to minimise predation risk (Cherry et al., 2017). Notably, the strong effect of time-since-the-fires on swamp wallaby activity suggests that other factors, such as seasonal variation in forage availability, could also influence their activity.

Bare-nosed wombats were more active shortly after the fires at sites predominantly burned at low-moderate severity, consistent with prior findings of reduced activity in areas burned at high severity (Chia et al., 2016). Wombats typically take refuge in their burrows, which may be effective during low-moderate severity fires, but less effective in high-extreme severity burns (Nimmo et al., 2021). As such, in areas with low-moderate burn severity, wombats' ability to survive in-situ and rapidly take advantage of newly burnt patches could explain the observed peak in their activity shortly after the fires at these sites. Conversely, painted button-quails responded positively to high-extreme severity burns, similar to mountain quails (*Oreortyx pictus*) in North America (Brunk et al., 2023). The painted button-quails' preference for high-severity fires in our study likely reflects their preference for dry open forests with sparse understories

(Menkhorst et al., 2017), as well as their opportunistic foraging behaviour that attracts them to burns that promote canopy-released seeds (Newman et al., 2020).

Feral cats had lower activity at sites dominated by high-extreme severity burns and moderate activity in sites burnt at a low-moderate severity, however, these patterns were weak. Although cats target severe fires in tropical northern Australia to take advantage of vulnerable prey (McGregor et al., 2016), there is little evidence of cats increasing their activity after severe fires in temperate Australia (Doherty et al., 2023). Cats have generalist diets and occupy a broad variety of habitats, and often have large home ranges (Santos et al., 2014). This makes them highly adaptable to changing environmental conditions but may also explain why they show contrasting responses to fire across different ecosystems.

Effects of vegetation type

In our study, wet forest birds—specifically, the superb lyrebird, satin bowerbird, and wonga pigeon—exhibited the strongest responses to vegetation type. These species predominantly favour rainforests and wet sclerophyll forests (Menkhorst et al., 2017), which was evident in our results. In particular, we observed higher superb lyrebird activity in wet forest than in dry forest, irrespective of burn status. However, all three bird species were generally more active in unburnt sites throughout the study. This is in contrast to painted-button quails which are a dry forest species (Menkhorst et al., 2017) and generally preferred burnt sites. These observations align with another study on the Black Summer fires, which found that rainforest birds were vulnerable to fires, showing reduced diversity and abundance, compared to birds in dry sclerophyll forest which favoured burnt sites (Lee et al., 2022). Suggesting that species in wet forests are likely more susceptible to fires than those in dry forests where fire is more common (Lee et al., 2022).

These contrasting responses partly reflect variations in how different vegetation types respond to fire (Clarke et al., 2014), and also the co-evolution of vertebrate species within these habitats that influence their foraging and shelter requirements. For instance, wonga pigeons and satin bowerbirds primarily feed on fruit (Menkhorst et al., 2017). Frugivores are highly impacted by fires due to the loss and slow recovery of mature fruiting plants (Willis, 2003), but are also pivotal in these forests, aiding regeneration through seed dispersal (Lee et al., 2022). Further to this, lyrebirds, bowerbirds, and wonga pigeons share terrestrial behaviours that likely make them sensitive to changes to ground-level vegetation (e.g., Maisey et al., 2019). Our findings indicate that changes in foraging resources and emergence of dense regenerating understorey

vegetation likely contributed to the reduced activity of these wet forest species in burnt areas. This aligns with global research emphasising the important role of habitat type in mediating fire impacts on vertebrate species (Brehme et al., 2011; Chergui et al., 2019).

Conservation and management implications

Our study demonstrates that the responses of co-occurring vertebrate species to fire are variable and influenced by differing fire metrics. In the face of altered fire regimes, our results suggest that some species will benefit while others will be disadvantaged. Our findings show that variables including fire severity, proportional area burnt, and vegetation type, with time-since-fire, can better capture the complexity of post-fire successional changes, rather than simple contrasts between burnt and unburnt.

In our study, introduced foxes showed a temporary association with sites with a higher proportional area burnt. Therefore, forest systems where invasive predator activity increases in the months preceding fires should be considered for targeted predator control, especially in heavily burnt areas. Small and medium-sized mammals showed a gradual increase in activity over time at burnt sites, indicating a need for sustained conservation management as vegetation recovers. These species may benefit from preserving unburnt refuges and from targeted post-fire interventions such as the provision of artificial shelters (Watchorn et al., 2022).

Our study also demonstrates that spatial variation in fire severity, associated with major wildfires, is an important factor influencing post-fire animal responses and that fire variables measured at broader landscape scales can better capture these responses. This warrants consideration in studies assessing the effects of fire on vertebrates. Further, the variable responses to fire severity indicate that even fire-adapted species will face challenges as fires become more extreme, while others may benefit. Conversely, species within wet forests showed limited tolerance to fire, suggesting that species such as lyrebirds, wonga pigeons, and satin bowerbirds, require unburnt habitat, and given their functional importance to forest health and recovery, this should be prioritised. Protecting unburnt refuges and maintaining large, intact areas of forest, as well as restoring habitat where needed, will be crucial for species that are fire sensitive.

Author contributions

The study's conception and design were a collaborative effort of all authors. Vivianna Miritis conducted the data collection, GIS work, and analysis. Tim Doherty made substantial contributions to the data analysis, and Dale Nimmo provided valuable feedback. Vivianna Miritis interpreted the results with assistance from Tim Doherty, Dale Nimmo and Chris Dickman. Vivianna Miritis led the writing of the manuscript. All authors contributed critically to the final draft and gave final approval for publication.

Acknowledgements

We acknowledge the Murramarang peoples, the Traditional Owners of the lands and waters on which this work was conducted, and extend that respect to their Elders past and present. We thank the NSW National Parks and Wildlife Service staff, Michael Phelan and David Cunningham, for providing local knowledge, assistance, and equipment during the course of this project. We also thank the volunteers that assisted with fieldwork. Funding for this research was provided by the NSW Environmental Trust. TSD was supported by the Australian Research Council (DE200100157).

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Supporting information

Table S1. Relationships between fire variables and vertebrate species' activity, derived from GAMMs. Only top-ranked models ($\Delta < 2$) are shown. The table shows estimated degrees of freedom (edf), log-likelihood (logLik), Akaike weight (w), percentage deviance (D), and statistical significance of the smooth terms (P).

Models	df	logLik	AICc	delta	weight	D (%)	Predictor variable	edf	P
Null									
Cat	22	-252.86	552.9	1.49	0.13	20	null	19.93	0.00
Time-since-the-fires									
Short-beaked echidna	40	-644.44	1374.1	0.00	0.37	31	months post-fire	7.77	0.00
Swamp wallaby	40	-2743.64	5571.5	0.04	0.30	23	months post-fire	5.09	0.00
Burn status									
Cat	22	-252.61	551.4	0.00	0.28	20	unburnt	1.00	0.46
							burnt	1.00	0.05
Short-beaked echidna	44	-640.85	1375.2	1.14	0.21	32	unburnt	5.85	0.00
							burnt	7.19	0.00
Fox	45	-913.87	1923.2	0.00	0.67	37	unburnt	1.00	0.00
							burnt	8.85	0.04
Bush rat	44	-713.83	1520.6	0.00	0.42	63	unburnt	1.00	0.00
							burnt	6.23	0.00
Swamp wallaby	44	-2739.09	5571.6	0.11	0.29	24	unburnt	4.82	0.00
							burnt	4.18	0.00
Proportion burnt									
Long-nosed bandicoot	41	-334.42	755.6	0.00	0.96	63	% burnt 200m	5.81	0.00
Brushtail possums	51	-968.35	2045.7	0.00	1.00	39	% burnt 200m	12.77	0.00
Fox	50	-909.39	1925.0	1.73	0.28	37	% burnt 200m	3.59	0.01
Bush rat	44	-713.90	1520.6	0.02	0.41	63	% burnt 200m	1.00	0.00
Fire severity									

Chapter 3 – Fire characteristics

Cat	26	-249.34	553.0	1.58	0.13	22	unburnt	1.00	0.43
							low-moderate	1.00	0.03
							high-extreme	1.00	0.78
Painted button-quail	24	-66.85	183.3	0.00	0.98	60	unburnt	1.00	0.86
							low-moderate	1.00	0.24
							high-extreme	3.51	0.03

Proportion of fire severity

Short-beaked echidna	44	-640.61	1374.1	0.03	0.36	32	% low-moderate		
							200m	3.81	0.00
Swamp wallaby	51	-2731.54	5571.5	0.00	0.31	25	% low-moderate		
							200m	8.99	0.00
Bare-nosed wombat	48	-846.95	1796.6	0.00	1.00	68	% low-moderate		
							200m	6.23	0.00
Cat	23	-251.57	551.8	0.38	0.23	21	% high-extreme		
							200m	1.00	0.25
Eastern grey kangaroo	47	-1126.76	2353.7	0.00	0.92	49	% high-extreme		
							200m	6.14	0.00

Vegetation type

Satin bowerbird	35	-325.40	724.2	0.00	0.74	48	wet unburnt	1.00	0.83
							wet burnt	1.00	0.02
							dry unburnt	1.00	0.17
							dry burnt	1.00	0.00
Small dasyurids	42	-294.14	677.9	0.00	0.93	76	wet unburnt	2.21	0.04
							wet burnt	1.00	0.00
							dry unburnt	5.22	0.01
							dry burnt	1.00	0.00
Superb lyrebird	47	-927.72	1954.9	0.00	1.00	62	wet unburnt	1.00	0.00

							wet burnt	4.64	0.00
							dry unburnt	1.00	0.00
							dry burnt	3.46	0.01
Wonga pigeon	36	-265.16	605.2	0.00	1.00	72	wet unburnt	3.02	0.00
							wet burnt	1.00	0.00
							dry unburnt	1.00	0.78
							dry burnt	1.00	0.00

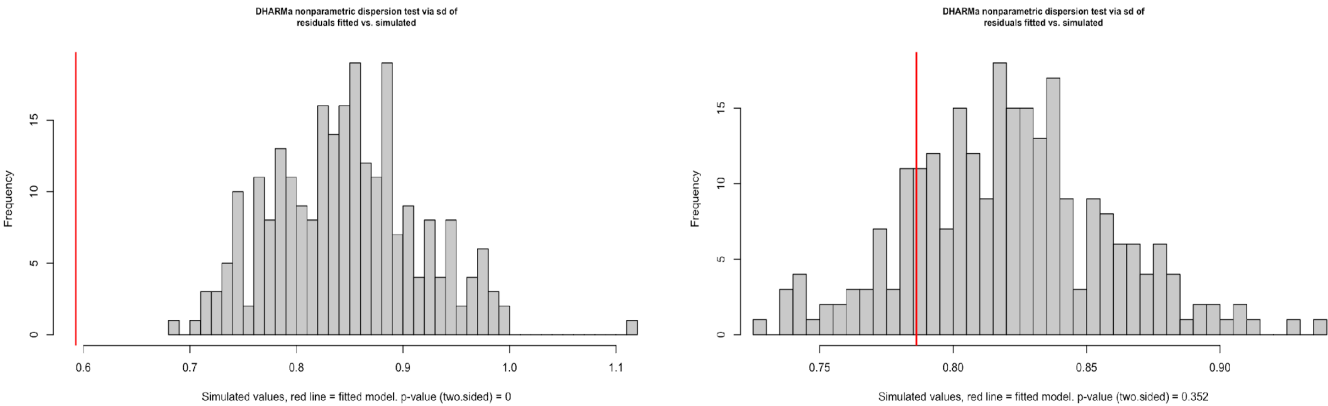


Fig. S1. Residual plots for the swamp wallaby (*W. bicolor*) data, comparing model fits using a negative binomial distribution (left) and a Gaussian distribution (right).

Chapter 4 – Adapting to novel fire regimes: Using movement to inform conservation of a threatened arboreal mammal

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Manuscript submitted and under review.

My contribution to this data chapter was substantial. I conceptualised ideas and led the fieldwork, collected and analysed the data, and wrote and edited all drafts, in consultation with my co-authors.



Southern greater glider (Petauroides volans) captured for collaring. Vivianna Miritis.

Abstract

Megafires are becoming increasingly common across the globe due to climate change and human activities. This rapid departure from historical fire regimes is creating novel challenges for animal populations, and their ability to persist may depend on fire-driven adaptations. Understanding how species respond and adapt to altered fire regimes is key to their conservation management, but for many species such mechanisms are poorly understood. Using GPS collars, we studied the effect of the 2019–20 Australian megafires on the space use and movement behaviour of southern greater gliders (*Petauroides volans*). We tracked eight animals in burnt forest and seven animals in unburnt forest to compare home range size and movement patterns. Our analysis revealed that despite severe habitat disturbance, greater gliders exhibited home range fidelity and their home range size, did not differ between unburnt and burnt sites. However, individuals in the burnt forest had higher movement rates and took more direct linear paths. Our study provides empirical evidence of how a fire-sensitive species is persisting in severely burnt habitat and may be able to do so by adjusting its movement patterns to meet its resource needs. We show that plasticity can provide some opportunity for adaptation to disturbance, but species that exhibit home range fidelity or otherwise fixed behavioural strategies, will continue to be challenged by severe and frequent environmental changes. We therefore recommend that conservation efforts for such species prioritise safeguarding unburnt habitat and, where necessary, consider provisioning critical supplementary resources to minimise wildfire impacts.

Introduction

Wildfires are a crucial ecological disturbance, shaping landscape structure, species distributions, and habitat availability in ecosystems across the globe (He et al. 2019). However, climate change and anthropogenic disturbance are driving changes in fire regimes (Bowman et al. 2020), with many regions experiencing a shift towards more frequent and severe wildfires (Stephens et al. 2013; Jones et al. 2022; Linley et al. 2022). Record-breaking megafires (>10,000 ha) are becoming more common in forest ecosystems worldwide (Attiwill & Binkley 2013; Duane et al. 2021). The Australian 2019–20 megafires are a prime example, which were unprecedented in their size and severity (Wintle et al. 2020; Nolan et al. 2021) and are regarded as Australia’s worst fire season on record (Khan 2021). These fires highlighted the need for better information on species’ responses to fire, in particular, megafires (Ward et al. 2020).

Megafires can significantly alter the availability and quality of wildlife habitat, affecting animal behaviours, particularly their movements and space use (Nimmo et al. 2019). Quantifying wildlife movement can provide critical insights into habitat quality (Fahrig 2007) and consequent energy costs to animals exploiting different habitats (Sparrow & Newell 1998). Slow and tortuous movements may indicate higher habitat quality, as individuals meet their needs without extensive exploration (Whittington et al. 2004; Cant et al. 2005; Haynes & Cronin 2006), while frequent and more linear movements may indicate lower habitat quality, as animals range further to locate and access resources (Cant et al. 2005). Furthermore, information on animal home ranges can be important for predicting population dynamics and behaviours (Maher & Lott 2000; Börger et al. 2008), and the adaptability of species to disturbances (Faille et al. 2010). This spatial information can greatly inform conservation strategies by providing insights on the potential of species to persist in post-fire landscapes.

Arboreal mammals are strongly influenced by the quality of habitat, especially the availability of food and shelter trees (Reckless et al. 2017) and are highly sensitive to forest disturbance (Whitworth et al. 2019; Cudney-Valenzuela et al. 2023), including fire (Mendonça et al. 2015). Australia’s southern greater glider (*Petauroides volans*; hereafter ‘greater glider’) is one such species. The greater glider is the largest gliding marsupial in the world and was once considered a common and widespread species (Lindenmayer et al. 2011). However, recent studies have documented local extinctions and range contractions (Smith & Smith 2018; McLean et al. 2018; Lindenmayer & Sato 2018) due to multiple threats including climate change, wildfires, land clearing, and logging (Lindenmayer et al. 2013; McLean et al. 2018; Wagner et al. 2020). As a

result, *P. volans* was listed as Vulnerable to extinction in 2016 and uplisted to Endangered in 2022, under Australian environmental legislation (Department of the Environment 2023). Furthermore, close to one-third of all greater glider habitat was burned in the 2019–20 megafires, with over half of the records of this species since 2000 occurring in areas that were impacted by the fires (Ashman et al. 2021).

Greater gliders have small home ranges, generally averaging <3 ha (Pope et al. 2004; McGregor et al. 2023), are poor at dispersing (Suckling 1982; Pope et al. 2004), and are considered to have strong home range fidelity (Tyndale-Biscoe & Smith 1969a). Being a strict folivore that feeds on eucalypt leaves (Fleay 1947; Menkhorst & Knight 2004), these small sedentary home ranges likely evolved in response to the year-round abundance of this resource (Mueller & Fagan 2008). However, as behaviours like range fidelity did not evolve in highly dynamic environments, species that forego the use of higher quality habitat in favour of their established ranges are likely to face challenges when the habitat they occupy is frequently disturbed (Faille et al. 2010; Abrahms et al. 2018; Merkle et al. 2022). One way that animals are adapting to rapid environmental change is through phenotypic plasticity (Wong & Candolin 2015; Jones et al. 2023; Merkle et al. 2022). Plasticity can aid survival following disturbance through behavioural responses like increases in daily movement and home range size to meet foraging needs (Kreling et al. 2021). The importance of plasticity in animal responses to altered fire regimes is increasingly recognised as a critical but poorly understood phenomenon (Jones et al. 2023). As such, research into these behavioural strategies can provide insights on the mechanisms that may facilitate or hinder adaptation to environmental change (Wong & Candolin, 2015), guiding the development and prioritisation of conservation actions (Jones et al. 2023).

To measure the response of greater gliders to megafire, we collected spatial data using GPS collars at sites heavily impacted by Australia's 2019–20 fires and sites that had remained unburned. According to Smith et al. (2007), greater gliders can have larger than average home ranges in disturbed forest. Therefore, we predicted that range fidelity would be negatively influenced by the fires and that greater gliders would have larger home ranges in burnt forest to maintain access to sufficient resources within their home ranges. We also assessed whether greater gliders altered their movement rates and turning angles in response to the fires. This is novel as GPS collars that enable collection of very fine-scale data were not previously accessible for this species. We predicted that greater gliders in burnt forest would display higher movement rates and adopt more direct linear paths through the more open landscape. These

predictions are based on the premise that post-fire landscapes often necessitate increased foraging effort due to reduced resource availability, potentially leading to larger home ranges and increased nightly movements (Nimmo et al. 2019).

Materials and methods

Study area

Our research was conducted in Tallaganda State Forest (35.52° S, 149.45° E) located in the Great Dividing Range in south-eastern Australia (Fig. 1). The State Forest covers approximately 5,700 ha and is surrounded by the adjoining Tallaganda National Park and Tallaganda State Conservation Area which collectively cover ~21,879 ha (herein referred to as ‘Tallaganda’), as well as private property. Tallaganda has a temperate climate with a mean annual minimum temperature of 6°C and maximum temperature of 19°C (Bureau of Meteorology 2023). The 2019–20 megafires, primarily the North Black Range fire which was ~38,000 ha in size, burnt over 6,000 ha in the northern-most area of the State Forest and National Park from November 2019 to January 2020 (Fig. 1).

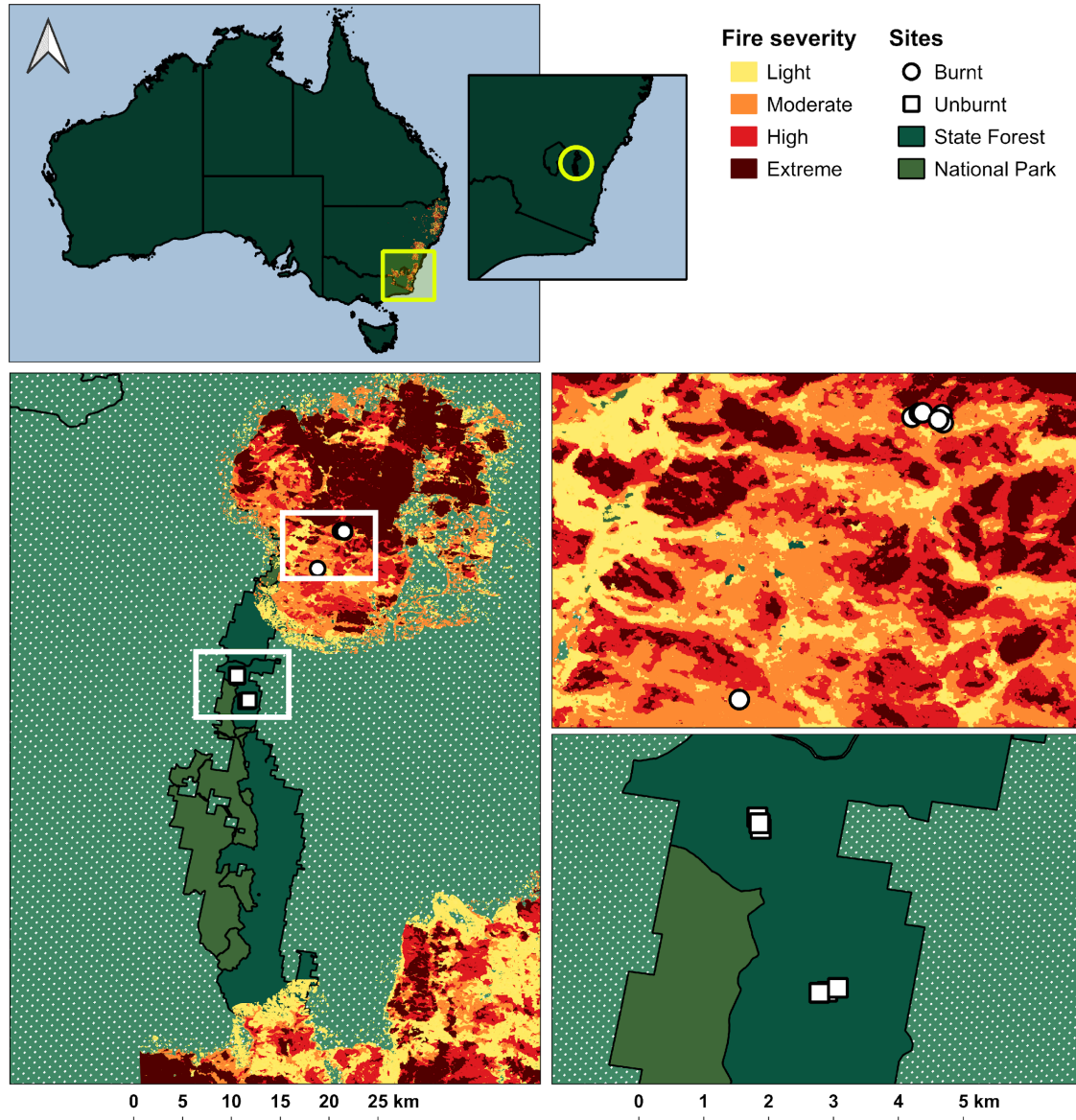


Fig. 1. Location of Tallaganda State Forest in south-eastern Australia (top-left), location of collared animals in burnt and unburnt forest (bottom-left; Department of Planning, Industry and Environment 2020), with detail of locations (bottom-right).

Study design and data collection

Spotlight surveys

In mid-July 2022, around 29 months post-fire, we conducted spotlight surveys across forested areas in Tallaganda to identify suitable sites for capturing greater gliders. We targeted areas based on existing records of greater gliders (Atlas of Living Australia 2022). We selected areas that had been burned at either

high severity (>90% canopy scorched with <50% canopy consumption) or extreme severity (>50% canopy consumption; Fig. 1), which we determined using the Fire Extent Severity Mapping layer (Department of Planning, Industry and Environment 2020; Gibson et al. 2020). We selected areas that were predominantly burned at high and extreme severity as these burns have the most impact on the canopy (Fig. 2), and greater gliders are particularly sensitive to this fire severity (Lindenmayer et al. 2013).



Fig. 2. Unburnt forest (left) and burnt forest (right) at sites selected for greater glider collaring.

Spotlight surveys were conducted from the road, whereby a minimum of two observers looked out opposite windows of a motor vehicle moving no more than 10 km/h using handheld spotlights. Once an animal was located, the GPS coordinates of its location were recorded. We used the records from the spotlight surveys to finalise our animal capture sites. We selected for burnt and unburnt sites that were similar in tree species composition and disturbance history. Unburnt sites had been selectively logged in 2010 and 2018, while burnt sites had been burned by prescribed fire in 2010 and selectively logged in 2014.

Collar deployment and retrieval

We returned to the selected sites in September and October 2022 to capture and collar greater gliders. The capture process was carefully designed to minimise stress and risk to the animals. About two hours before sunrise each day, we revisited the locations chosen based on the spotlight surveys and searched for animals using spotlights on foot. Once an animal was sighted, we observed it under a dim light until it retreated to its denning hollow (~1 hour later). When the den hollow was identified, we marked the tree with flagging tape, photographed the tree, and highlighted the specific den in the image to facilitate later referencing. We then returned in the afternoon with professional climbers, who ascended to the dens. If the animals were within reach, climbers carefully extracted them from the hollows. In cases where the animals were inaccessible, climbers waited until dusk and captured animals as they emerged.

During this period, we captured a total of 23 animals. Upon capture, we recorded animal sex, age, weight, coat colour, body condition, and presence of young. Body condition was assessed visually by examining the animal's coat, parasite load, weight, and muscle mass, and scored as 'poor' or 'good'. Of the 23 individuals captured, we deemed 15 individuals suitable for collaring based on their weight (>1000 g), ensuring that the 40 g GPS collars (Lotek Litetrack 40, New Zealand) did not exceed 4% of the animals' body weights. We collared one individual per tree even if more than one was found in a den. We collared eight animals in burnt sites and seven in unburnt sites. The collared gliders were then tracked for a period of 30 days. Greater gliders are exclusively nocturnal, so the GPS collars were set to record at 30-min intervals from sunset to sunrise each night. Eleven collars remained in operation for the entire survey period, while four collars detached from animals after 6–22 days of operation. We used the collars' built-in VHF transmitter to track the individuals 3–5 days after they were collared to check on their welfare and ensure the collars were working. When it was time to recapture the animals (30 days post-collar deployment) we used the VHF to track the animals to their dens and retrieved the collars using the climbing procedure described earlier. We reweighed each individual, reassessed their body condition, and re-checked the females for young.

Data preparation

Home range

Data preparation and analysis were completed in R v4.3.1 (R Core Team 2023). Home range size was estimated using the continuous time-movement modelling (ctmm) package (Fleming & Calabrese 2022).

Continuous time-movement models estimate animal space use while also accounting for spatial and temporal autocorrelation, a common feature in animal movement data whereby observations sampled more closely in space or time tend to be more similar (Silva et al. 2021). We estimated the initial movement model parameters with the `ctmm.guess` function and then fitted the data with two movement models: an Independent Identically Distributed (IID) model and an Ornstein-Uhlenbeck-Foraging (OUF) model. The best movement model was selected for each individual using the `ctmm.select` function, which ranks models using Akaike's information criterion corrected for a small sample size (AICc; Calabrese et al. 2016). The optimal model was then used to compute a Weighted Autocorrelated Kernel Density Estimator (wAKDE). We used wAKDE to adjust for uneven sampling rates (Fleming et al. 2018) where the GPS loggers failed to acquire fixes. Home range extent was defined based on a 95% confidence interval.

We chose the `ctmm` method because it offers superior home-range estimates to other methods (Fleming et al. 2015), and because our primary focus was to compare home-range sizes within the scope of this study, rather than to compare absolute values with other studies. However, as previous studies have used minimum convex polygons (MCP) and kernel density estimates (KDE) to estimate glider home range size, we have included a table in the supporting information for reference (see Table S1 in *Supplemental Information*).

Movement rate and tortuosity

We used the `adehabitatLT` package (Calenge 2023a) to obtain step lengths for each greater glider, which represent the distance moved between consecutive points. For the movement rate models, we calculated a standardised step length by dividing step length by the time elapsed between successive observations, and then multiplied it by 60 (distance moved per hour). For the nightly movement rate models, we computed the total distance moved each night by summing all step lengths within each night and standardising it to a 12-hour period. To exclude potentially erroneous data, we removed combinations of animal and night with fewer than seven points.

We used the `adehabitatLT` package to obtain absolute turning angles, which represent the sharpness of turns. We used absolute rather than relative angles because we were interested in the sharpness of turns (or the deviation from a straight path), rather than the actual direction of the turns (left or right). Turning angles calculated from consecutive points that were more than one hour apart were removed.

Data analysis

We used generalised linear mixed models (GLMMs) and generalised additive mixed models (GAMMs) fitted with the ‘mgcv’ package in R (Wood 2017) to assess how home range size and movements vary according to burn status and animal sex. For the home range analysis, we included burn status (burned or not burned during the 2019–20 fires) and sex (male or female; Table 1). For the movement analysis, we assessed movement rate and turning angles in relation to burn status and sex. Preliminary analysis showed that home range size influenced movement rate (Estimate = 0.13, $p < 0.01$) but not turning angles (Estimate = -0.03, $p = 0.17$), therefore we included home range as a variable in the movement rate models (Table 1). To account for variation between nights and individuals, we used spline basis functions (‘re’) as random effects in the movement rate and turning angle models (Table 1). For models that assessed hourly movements (time of night), we used additional cyclic cubic splines (‘cc’) to account for recurring patterns in animal behaviour throughout each night. The home range and movement rate models were fitted using the Gamma family with a log link function. Turning angle models were fitted using the Gaussian family.

Table 1. Explanatory variables in the GLMM and GAMM analyses for each model (+ denotes inclusion of the variable in the model).

Model	Burn status (unburnt, burnt)	Sex (male, female)	Individual s(ID)*	Night s(nightID) *	Time of night s(Hour)	Home range s(HR)
Home range	+	+				
Movement rate (nightly)	+	+	+	+		+
Movement rate (hourly)	+	+	+	+	+	+
Turning angles	+	+	+	+		
Turning angles (hourly)	+		+	+	+	

* represents random effects

Results

We captured a total of 23 greater gliders, 15 of which were fitted with GPS collars. During collar deployment and retrieval, we found six of the 15 greater gliders denning with other adult/sub-adult individuals (Table 2). Animal weights remained relatively consistent from collar deployment to collar retrieval (Table 2). All the females with young recorded during the collar deployment were recaptured with their young upon collar retrieval. All animals collared had good body condition at both capture and

recapture. None of the animals in our study dispersed, and all showed short-term site fidelity. Collared animals exhibited some degree of home range overlap with other collared individuals (Fig. 3), but this does not necessarily indicate temporal overlap. We did not find any of the collared animals denning together. We identified 1–3 den sites for each individual during the deployment and retrieval of the collars as well as during radio-tracking (Fig. 3). Some greater glider dens were identified during the spotlight surveys but as we did not capture individuals from those dens, we could not confirm which gliders used them. These dens, along with those used by known individuals, have been included in Figure 3.

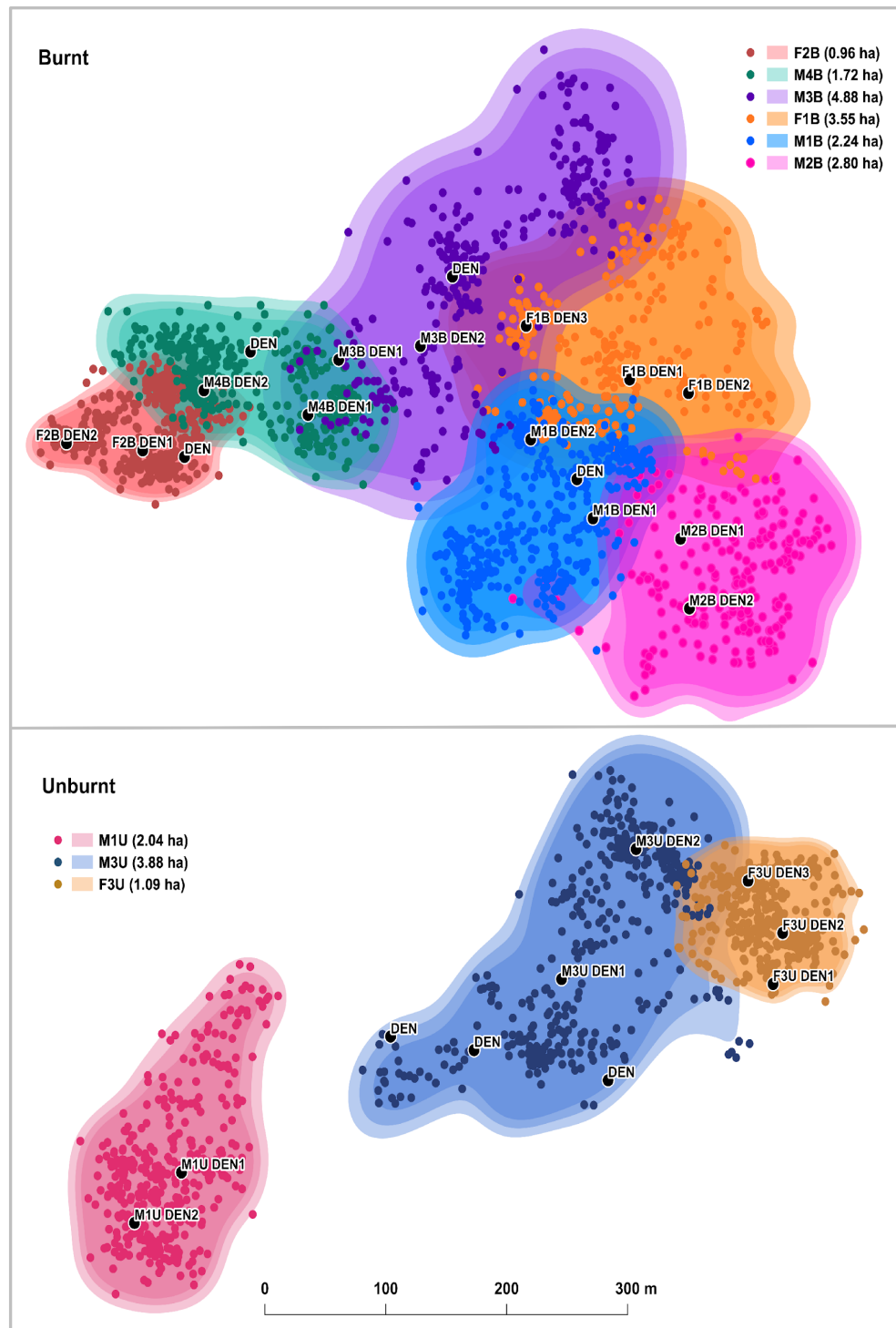


Fig. 3. Home-ranges (ha) for a subset of individuals in burnt and unburnt forest derived from continuous time-movement modelling (ctmm). Inner and outer shading of each polygon indicates 95% confidence intervals. Includes GPS points for each individual and den.

Table 2. Estimated home range (HR) size of greater gliders at Tallaganda State Forest from continuous time-movement models for each individual (ID) with 95% confidence intervals (CI). Table shows: n = number of GPS points, W1 = weight at deployment, W2 = weight at retrieval, Den = number of adult/sub-adult individuals in den, Y1 = young presence and age at deployment, Y2 = young presence and age at retrieval, PY = pouch young, FPY = furred pouch young, BY = back young, SA = sub-adult.

ID	n	Fire	Sex	Age	W1 (g)	W2 (g)	Den	Y1	Y2	HR (ha)	95% CI
F1B	317	Burnt	F	Adult	1400	1375	1	PY	FPY	3.55	2.91, 4.25
F2B	430	Burnt	F	Adult	1500	1330	1	FPY	BY	0.96	0.81, 1.11
F3B	357	Burnt	F	Adult	1295	1240	1	FPY	BY	1.17	1.02, 1.33
F4B*	105	Burnt	F	Adult	1540	-	2	PY	-	0.70	0.48, 0.96
M1B	395	Burnt	M	Adult	1140	1180	2	No	No	2.24	1.83, 2.69
M2B	240	Burnt	M	Adult	1155	1140	3	No	No	2.80	2.30, 3.34
M3B	337	Burnt	M	Adult	1340	1400	1	No	No	4.88	3.90, 6.02
M4B	376	Burnt	M	Adult	1310	1330	1	No	No	1.72	1.41, 2.06
F1U*	102	Unburnt	F	Adult	1460	-	1	FPY	-	1.39	0.92, 1.96
F2U*	151	Unburnt	F	Adult	1275	-	1	BY	-	1.13	0.88, 1.39
F3U	359	Unburnt	F	Adult	1520	1530	1	BY	BY	1.09	0.92, 1.26
F4U*	332	Unburnt	F	Adult	1150	-	1	No	-	0.99	0.77, 1.23
M1U	393	Unburnt	M	Adult	1220	1230	3	SA	SA	2.04	1.66, 2.46
M2U	457	Unburnt	M	Adult	1260	1545	2	No	No	2.38	1.94, 2.87
M3U	441	Unburnt	M	Adult	1265	1370	2	No	No	3.88	3.23, 4.58

*Collar was dropped.

We collected 4792 GPS points from the 15 animals tracked across burnt and unburnt sites. On average, each collar recorded 12 fixes per individual per night. Average home range size was 2.06 ha, but varied widely among the individual greater gliders, ranging from 0.70 to 4.88 hectares (Table 2). On average, individuals in burnt areas had larger home ranges (2.25 ha) than those in unburnt areas (1.84 ha), but this was not statistically significant (Table 3). Male greater gliders had larger home ranges on average (2.85 ha) than females (1.37 ha), irrespective of burn status, and this was statistically significant (Table 3).

Table 3. Relationships between fire variables and greater glider activity. Table shows intercept (β), statistical significance of the predictor variables (P) or smooth terms (P , F), estimated degrees of freedom (edf), and percentage deviance explained (D).

Response variable	Predictor variables	β	P	edf	F	D
Home range						44.3%
	Fire (Burnt)	0.20	0.48			
	Sex (Male)	0.73	0.02			
Movement rate (nightly)						27.8%
	Fire (Burnt)	0.11	0.03			
	Sex (Male)	0.00	0.98			
Movement rate (hourly) by time of night						8.9%
	Sex (Male)	-0.01	0.93			
	Fire (Burnt)	0.14	0.01			
	Time (Burnt)		<0.0	7.61	8.51	
			1			
	Time (Unburnt)		<0.0	4.91	8.95	
			1			
Turning angle						
	Sex (Male)	-0.05	0.27			3.1%
	Fire (Burnt)	0.10	0.03			
	Time (Burnt)		0.10	6.27	1.39	
	Time (Unburnt)		<0.0	6.76	3.15	
			1			

Reference levels: Unburnt and Female.

Mean nightly distance travelled by greater gliders in burnt forests was 513 m per night (95% CI: 445, 590) and 462 m in unburnt forest (95% CI: 402, 531; Fig. 4a). Additionally, greater gliders in the unburnt forest made sharper turns (mean = 100 degrees, 95% CI: 89, 111) than those in the burnt forests (mean = 106 degrees, 95% CI: 95, 116; Fig. 4c). When looking at these movements with time of night, we found that greater gliders had higher movement rates at the start and end of the night, at around 7:00 pm and 4:00 am AEST respectively, and this was more pronounced in burnt sites (Fig. 4b). We also found that turning angles increased and decreased in sharpness throughout the night, and this tended to coincide with movement rate, whereby at times of higher movement rate (around 6PM–8PM and 4AM–5AM) greater

gliders tended to take sharper turns (Fig. 4d). Sex did not significantly influence movement rate or turning angle (Table 3).

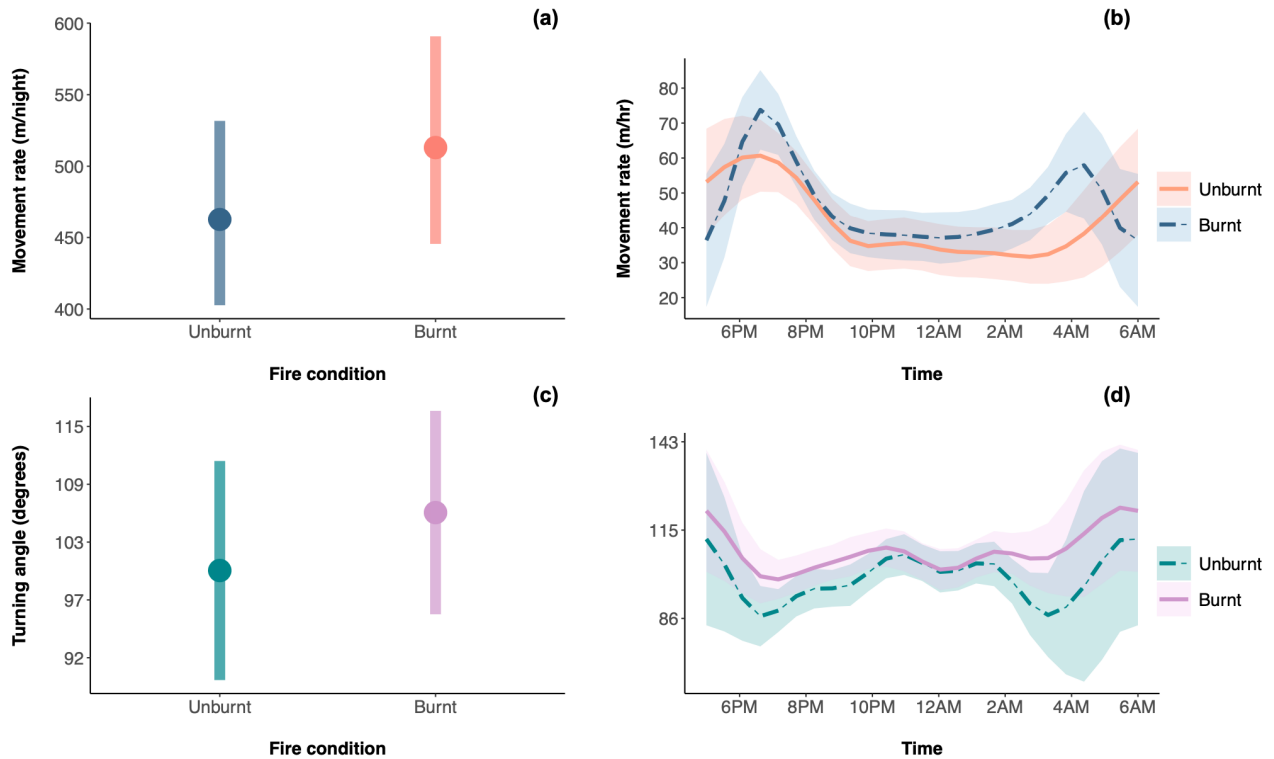


Fig. 4. Movement models predicted by generalised mixed models. In plots **a** and **c**, dots represent predicted values and whiskers denote standard errors. In plots **b** and **d** shading represents 95% confidence intervals.

Discussion

Understanding variation in animal movement patterns is important in applied and theoretical ecology, providing insights into species' responses to environmental disturbances such as megafires. The 2019–20 Australian megafires presented a unique opportunity to assess animal behaviour in response to novel fire regimes to better guide conservation management. Greater gliders exhibited strong home range fidelity; however, phenotypic plasticity with regard to their movement patterns may be facilitating their persistence within a landscape burned at high severity.

Despite the extent and severity of the fires, greater glider home range size was not significantly larger in burnt forest in comparison to unburnt forest. This finding provides no support for our prediction that

home range fidelity would be affected by the fires, resulting in expanded home ranges in burnt forest. While greater gliders have been reported to have larger than average home range sizes in logged forest with low resource availability (Smith et al. 2007), such a pattern was not supported for the burnt forest in our study. Given this species is not typically associated with recently burnt forest, especially following high-severity burns (Lindenmayer et al. 2013; Chia et al. 2016; Campbell-Jones et al. 2022), it is highly unlikely that these animals migrated to the burnt sites post-fire but rather survived the fires and are continuing to persist within their established pre-fire home ranges. Supporting this, Tyndale-Biscoe & Smith (1969a) found that greater gliders did not relocate to undisturbed forest following logging, which ultimately led to their death. That study also concluded that greater gliders were limited in their ability to disperse, and post-disturbance survival was often dependent on the persistence of individuals remaining within portions of their original home range (Tyndale-Biscoe & Smith 1969a). This type of home range fidelity has also been observed in other species; for example, experimental manipulation of great tit (*Parus major*) habitat revealed that established pairs did not relocate from poor quality habitat even when high quality alternative habitats were available (Krebs 1971). This persistence can not only stop animals from relocating but can also confine them to smaller home ranges as they avoid degraded habitat (Faille et al. 2010).

Further, we found that home range size was strongly influenced by sex; male greater gliders had significantly larger home ranges (2.85 ha) than females (1.37 ha). These sex differences in home range size align with some previous studies on greater gliders (Pope et al. 2004; Smith et al. 2007), as well as other arboreal mammals around the world (e.g., Fridell & Litvaitis 1991; Hanski et al. 2000; Kuo & Lee 2012). In relation to megafires this is notable as sex can influence home range fidelity (Faille et al. 2010). A key resource for greater gliders, especially female greater gliders, is den hollows (Gibbons & Lindenmayer 2002; Smith et al. 2007; Lindenmayer et al. 2013). While fires can accelerate the formation of tree hollows (Adkins 2006), severe wildfires often result in mass tree mortality and collapse, with consequent net loss of large hollow-bearing trees (Lindenmayer et al. 2012). Female greater gliders prioritise dens more so than males and restrict their home ranges to retain a higher number of dens around them (Smith et al. 2007). This behaviour is likely associated with the rearing of their offspring which stay dependent on their mothers after leaving the pouch (Tyndale-Biscoe & Smith 1969b). In particular in our study, we observed joeys sheltering in their dens while their mothers foraged, and this has been documented previously (Fleay 1947). Similar home range fidelity associated with young-rearing can be found in other species; for

example, Faillie et al. (2010) showed that despite habitat disturbance, female caribou (*Rangifer tarandus caribou*) displayed strong home range fidelity, and this was particularly evident during calf-rearing. In the context of our study, the availability of surviving den trees may be generally confining greater gliders within their pre-fire range, and this may be more pronounced for females.

Greater gliders in burnt forest had higher nightly and hourly movement rates than gliders in unburnt forest, but they also exhibited more direct movements throughout the night. This supported our prediction that greater gliders would have higher movement rates and more direct linear paths in burnt sites. While home range fidelity may constrain the ability of animals to relocate following disturbance events like fires, our results suggest that greater gliders adjusted their behaviour in an effort to meet resource requirements. More specifically, individuals in burnt forest may be travelling more frequently and further within their home ranges to meet foraging needs. Similarly, Kreling et al. (2021) found that black-tailed deer (*Odocoileus hemionus columbianus*), which had strong site fidelity, increased their nightly movement rates in response to resource scarcity following a megafire that burnt through their home ranges. The authors also reported weak evidence of straighter and more directed movements after the fire, likely reflecting the direct movements between remaining vegetation patches (Kreling et al. 2021). In our study, the straighter movement paths of gliders in burnt forest, may similarly be indicating that individuals are minimising time spent in riskier or resource-poor habitat (Nimmo et al. 2019) within their home ranges.

Furthermore, greater glider activity was higher at the start and end of the night, with reduced movement through the middle of the night. Due to their folivorous diet, greater gliders often need to remain stationary for extended durations to aid digestion and conserve energy (Hume 1999). This behaviour indicates a limited foraging window, which may be particularly challenging in fire-affected forest if individuals spend foraging time navigating suboptimal habitat in search of food. While we did not find a clear difference in body condition between animals in burnt and unburnt forest, increased energetic costs in limited high-quality habitat can lead to longer-term impacts on individual health, reproductive success, and consequent population viability (Widyastuti et al. 2022). Greater gliders are considered to be near the minimum size able to sustain a strictly folivorous diet (Hume 1999). The low fermentation rates of eucalypt leaves, coupled with the small stomach size of greater gliders, restrict glider food consumption and the energy they can derive from food (Hume, 1999). Given these dietary limitations, drastic landscape changes such as

those resulting from megafires that influence forage availability and increase movement rates could be detrimental for greater glider populations (see Lindenmayer et al. 2011).

Conservation implications

Our study is an important first step in understanding how megafire affects the movements and behaviour of an endangered arboreal mammal. We show that greater gliders display altered movement patterns in burnt forests persisting beyond two years post-fire, suggesting ongoing impacts on this species well after the fire event. We also show that greater gliders exhibit some behavioural adaptation to extensive wildfires. Future studies would benefit from a larger sample size, tracking animals immediately post-fire, and tracking over different seasons, each of which should provide additional insights into the movements and space use of this species.

We show that plasticity can provide some opportunity for adaptation to disturbance; however, with greater gliders being at the physiological limit of their strictly folivorous diet, increased movement rates in response to environmental change may present new challenges. This is likely to be further compounded by a climate-induced reduction in leaf nutrition, which is already pushing folivorous species like greater gliders to forage more to meet nutritional demands (Youngentob et al. 2011; Wagner et al. 2021). We therefore recommend that the most effective immediate management action for such species is to protect remaining habitat from habitat destruction such as logging. This is particularly so because logging can increase the risk of further high-severity fires in native Australian forests (Lindenmayer et al. 2021). Furthermore, in the wake of future fire events, greater gliders may benefit from active restoration and targeted interventions in degraded habitats including the provision of nest boxes to supplement loss of hollow bearing trees.

Our study also contributes new data on greater glider home range size and shows that home ranges were small and did not significantly differ between burnt and unburnt forest. Our findings emphasise that although greater gliders have shown an ability to persist by adapting their movements, they and similar species exhibiting fixed behavioural strategies like home range fidelity, will likely be challenged by severe and frequent habitat disturbance. Additionally, we found that home range sizes estimated using the weighted Autocorrelated Kernel Density Estimator were almost always smaller than those estimated using

MCP and KDE techniques (Table S1). This suggests that previous research may have overestimated space use by this species.

Arboreal mammals, including greater gliders, are important components of healthy ecosystems. Protection of viable habitat will be crucial for the long-term sustainability of greater glider populations and, by extension, the overall health of eastern Australian forest ecosystems. Greater glider conservation needs, such as mature hollow bearing trees, encompass the requirements of many other species within the forest ecosystem. Thereby, protecting and managing forests to support healthy greater glider populations will indirectly benefit numerous other flora and fauna.

Author contributions

The study's conception and design were a collaborative effort of all authors. Vivianna Miritis and Kita Ashman collected the data. Vivianna Miritis conducted the GIS work, and analysis. Tim Doherty contributed to the data analysis, and Dale Nimmo provided constructive feedback. Vivianna Miritis interpreted the results in consultation with all authors. Vivianna Miritis led the writing of the manuscript. All authors critically contributed to the final draft and gave approval for publication.

Acknowledgements

We acknowledge the Ngarigo and Walbunja Aboriginal peoples, the Traditional Owners of the lands and waters on which this work was conducted, and extend that respect to their Elders past and present. We thank Dr Karen Marsh, Dr Kara Youngentob and Dr Denise McGregor for providing local knowledge and assistance during the planning of this project. We also thank the numerous volunteers that assisted with fieldwork. Field methods were approved by The University of Sydney's Animal Ethics Committee (2020/1821) and the Forestry Corporation of NSW (RES100157). Funding for equipment and fieldwork for this research was provided by the World Wide Fund for Nature Australia and the NSW Environmental Trust. TSD was supported by the Australian Research Council (DE200100157).

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Supporting information

Table S1. Home range estimates derived from minimum convex polygons (MCP100%), kernel density estimates (KDE95%), and continuous time-movement modelling (ctmm95%). MCP and KDE estimates were calculated using the adehabitatHDR package (Calenge 2023b).

Individual	Sex	Fire	n	MCP(100%)	KDE (95%)	Ctmm (95%)
F1B	F	Burnt	317	3.00	3.92	3.55
F2B	F	Burnt	430	1.03	1.07	0.96
F3B	F	Burnt	357	2.43	1.39	1.17
F4B	F	Burnt	105	0.64	0.71	0.70
M1B	M	Burnt	395	2.41	2.52	2.24
M2B	M	Burnt	240	3.98	2.99	2.80
M3B	M	Burnt	337	6.43	5.47	4.88
M4B	M	Burnt	376	1.89	2.01	1.72
F1U	F	Unburnt	102	1.32	1.40	1.39
F2U	F	Unburnt	151	1.10	1.78	1.13
F3U	F	Unburnt	359	1.67	1.24	1.09
F4U	F	Unburnt	332	1.68	1.11	0.99
M1U	M	Unburnt	393	2.60	2.37	2.04
M2U	M	Unburnt	457	2.85	2.87	2.38
M3U	M	Unburnt	441	5.28	4.81	3.88

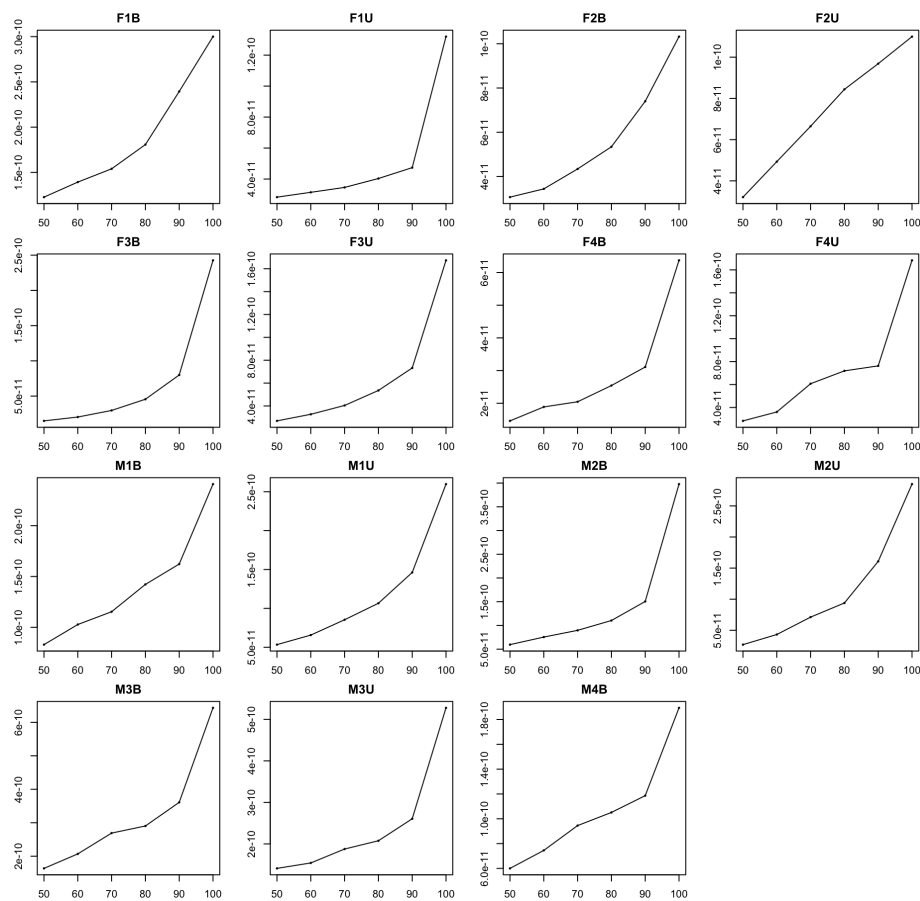


Fig. S1. Asymptote plots for 100% minimum convex polygons (MCP100%) for each individual.

Chapter 5 – Nest boxes as a recovery tool for hollow-using mammals following extensive wildfires

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Manuscript in preparation for submission.

My contribution to this data chapter was substantial. I conceptualised ideas and led the fieldwork, collected and analysed the data, and wrote and edited all drafts, in consultation with my co-authors.



Feathertail gliders (Acrobatus pygmaeus) in nest box. Vivianna Miritis.

Abstract

Tree hollows provide crucial habitat for vertebrate species globally, and support over 300 bird, mammal and reptile species in Australia. However, hollow-bearing trees are declining due to threats such as increasing fire frequency and severity. Nest boxes are increasingly being used in conservation efforts to assist fauna, yet their effectiveness for arboreal mammals remains poorly understood, particularly in burnt landscapes. Following the record breaking 2019–20 megafires in Australia, our field experiment evaluated the effectiveness of nest boxes in supporting wildlife. We deployed 54 nest boxes across nine sites, comprising six burnt and three unburnt sites, and compared these to equivalent control sites without nest boxes. We used baited camera traps to survey arboreal mammals 2 months prior to nest box deployment and 24 months post-deployment. We also assessed nest box occupancy by physically checking boxes and with motion sensing cameras over two years. Nest box cameras showed that boxes were being visited as early as 1 month post-deployment, but occupancy did not occur for more than 9 months post-deployment based on the physical checks. At 24 months post-deployment, nest box mean occupancy was 61% in burnt sites and 50% in unburnt sites. The camera trap surveys revealed an increase in arboreal mammal activity over time in burnt sites irrespective of nest box presence. Conversely, in unburnt sites, activity was steady over time but higher in sites with nest boxes. Our findings suggest that nest boxes may provide a modest benefit for fire-impacted arboreal mammals, but also emphasise that conservation strategies should prioritise the protection and preservation of mature trees with natural cavities.

Introduction

Tree hollows are critical to vertebrate species in forest and woodland habitats around the world (Carvalho et al., 2014; Evelyn and Stiles, 2003; Marsden and Pilgrim, 2003; van der Hoek et al., 2017). However, hollow-bearing trees are declining worldwide due to multiple threats (e.g., Carnicer et al., 2011; Cockle et al., 2010; Laurance et al., 2000; Politi et al., 2010), including altered fire regimes (Banks et al., 2011; Radford et al., 2021). While fire can play a role in accelerating the formation of tree hollows (Adkins, 2006), frequent and severe wildfires often cause tree death and collapse, with consequent loss of large hollow-bearing trees (Banks et al., 2011; Lindenmayer et al., 2012; Salmons et al., 2018).

In Australia, hollows are used by more than 300 vertebrate species, of which 83 are mammals and 40 of which are considered arboreal or scansorial (Gibbons and Lindenmayer, 2002). Once hollows are lost, recruitment of suitable hollows for vertebrate fauna is slow, generally taking over 100 years to form in eucalypts (Gibbons and Lindenmayer, 2002). Australian arboreal mammals are highly sensitive to the loss of hollows, and species occurrence and richness is dependent on forests that support numerous hollow-bearing trees (Lindenmayer et al., 2013). Arboreal mammals are critical to functioning ecosystems, providing ecosystem services such as the transport of seeds, pollination of plants, and redistribution of nutrients (Brockelman et al., 2022; Goldingay et al., 1991). Therefore, extensive and severe wildfires that remove hollows imperil arboreal mammals and consequently the ecosystem functions they provide. As such, management interventions following extensive wildfires are crucial for the conservation of such species, and by extension, the overall health of forest ecosystems.

In 2019–20, Australia experienced its worst fire season on record with fires unparalleled in their extent and severity (Bowman et al., 2020). Record-breaking wildfires are becoming more common around the world (White and Seginak, 2000) and are expected to increase in occurrence under climate change (Jones et al., 2022). While the protection and retention of hollow-bearing trees is the best option for hollow-using fauna, many species readily use artificial hollows, such as nest boxes (Harley, 2006; Smith and Agnew, 2002; Ward, 2000). As such, nest boxes could be valuable in the management of fire-impacted hollow-dependent mammals and were recommended as priority response to the Australian megafires (see Dickman et al., 2020).

Nest boxes bypass the time needed for hollows to develop naturally, and may provide immediate benefits (Lindenmayer et al., 2009). Research indicates that nest boxes serve as effective tools for detecting various species and investigating the ecological behaviours of animals dependent on tree hollows (Bladon et al., 2002; Ward, 2000). Additionally, they have been shown to act as functional replacements for natural hollows in habitats where such hollows are limited (Arlettaz et al., 2010; Smith and Agnew, 2002). However, their success has also been variable, and this has made them a topic of contention (Harley and Spring, 2003; Le Roux et al., 2016; Lindenmayer et al., 2003). Furthermore, while numerous international studies have shown the value of nest boxes following fire for avian species (Smith et al., 2007; White and Seginak, 2000), far less is known about the effectiveness of nest boxes for the recovery of arboreal and scansorial mammals (hereafter ‘arboreal mammals’).

The objective of this study was to assess the efficacy of nest boxes as a recovery tool for small arboreal mammals (<400 g) following the catastrophic 2019–20 megafires. Our specific aims were to 1) assess which species of arboreal mammals would visit and use the nest boxes, 2) assess the rate of occupancy following nest box deployment, 3) investigate if occupancy is influenced by whether a site has been impacted by the fires or not, and 4) assess arboreal mammal recovery in burnt sites with and without nest boxes. We achieved these aims over a two-year period through a combination of physical nest box checks and comparative camera surveys conducted before and after the nest boxes were deployed.

Materials and methods

Study area

We conducted this study in Murrumbidgee National Park (35.61° S, 150.30° E) in the state of New South Wales on the south-eastern coast of Australia. The park is approximately 1,970 ha and has a temperate climate with mean maximum temperatures around 17°C in winter and 26°C in summer (Bureau of Meteorology, 2023). The 2019–20 Australian wildfires, primarily the Currowan fire which burnt over 300,000 ha, burnt more than 80% of the park in December 2020.

Nest box design

Nest boxes were a standard rectangular shape and made from Cyplas recycled plastic (Hollow Log Homes, Noosaville, QLD, Australia; Fig. 1). ‘Large’ nest boxes were 265 mm H x 170 mm W x 165 mm D with a 51 mm diameter entry hole, and ‘small’ nest boxes were 215 mm H x 125 mm W x 130 mm D with a 25 x 45

mm diameter entry hole. We chose two nest box sizes to accommodate a broad range of species—the small boxes generally suit species <50 g and the large boxes suit species 50–400 g. Using two nest box sizes with different entry diameters also minimised the likelihood of smaller species being excluded by larger ones, which can occur when a single nest box design is used (Goldingay et al., 2007). Small boxes had a side entry and large boxes had a rear entry with flanges on each side to create a gap between the box and tree.



Fig. 1. Nest boxes used in this study. Left photo shows large nest box and right photo shows small nest box.

Study design

We used a crossed experimental design with both burnt ($n = 12$) and unburnt ($n = 6$) sites, and sites with and without nest boxes (half of the sites in each fire treatment). Burnt sites were in forest that experienced either low (<10% burnt understorey with >90% green canopy) or moderate severity fire (20–90% canopy scorch) based on the Fire Extent and Severity Mapping (FESM) layer (Department of Planning, Industry and Environment [DPIE], 2020). Sites were separated by a minimum of 1000 m (Fig. 2). In February 2021 (~14 months post-fire), we installed four large and two small nest boxes at each of six burnt sites and three unburnt sites, arranged in a 2 x 3 grid at 50 m spacing (54 nest boxes in total; Fig. 2). Nest boxes were installed 3–4 m from the ground and secured to each tree using a plastic-coated wire wrapped around the trunk (Fig. 1). To minimise exposure to direct sunlight, nest boxes were generally positioned facing south.

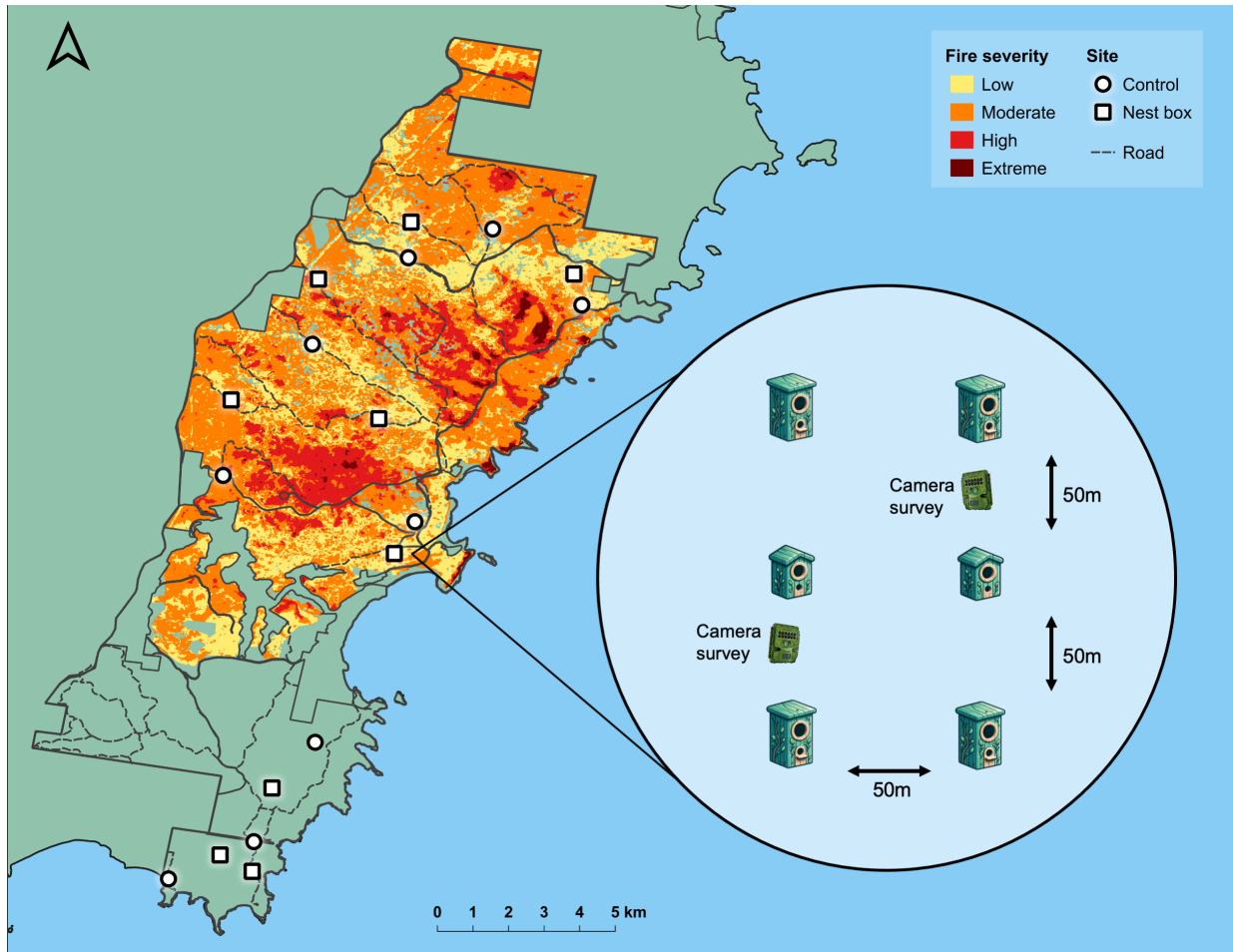


Fig. 2. Murrumbidgee National Park showing control and nest box sites in burnt and unburnt forest. All sites included a grid of six nest box points and two camera survey points. Map includes burn severity (FESM; DPIE, 2020).

Camera surveys

In December 2020, prior to nest box installation, and in February 2023, post-nest box installation, we deployed 36 motion-sensing cameras (HF2X, Reconyx, Holmen, WI, USA) across all 18 sites. We used the mapped grid of nest box locations to deploy the cameras so that their positions were consistent across all sites (Fig. 2). At sites with nest boxes, cameras were ~25 m away from the nearest box to minimise disturbance. Each camera was strapped to a tree, 3–4 m above the ground, and faced a bait canister secured to a tree 2–3 m away at the same height. Baits were made by soaking a rag in barley malt extract syrup and placing it inside a PVC pipe bait canister that was screwed into position using a saddle bracket. We chose malt extract as an alternative to commonly used honey baits, as it has the same high energy content, and

eliminates the possible spread of pathogens associated with honey, to bees in the area (Shimanuki, 1983). Cameras were set to motion trigger on a continuous schedule, on 'high' sensitivity, and 'fast shutter' night mode, and took five consecutive photos per trigger with no delay between triggers. Cameras remained in operation for 1–2 months for both surveys.

Nest box checks and nest box cameras

We inspected nest boxes to confirm animal occupancy in November 2021 (9 months post-installation) and February 2023 (24 months). Occupancy was defined as an animal being inside the nest box at the time of inspection or evidence of current occupancy such as nesting material or scats. Nest boxes were physically inspected using a ladder.

In addition to nest box inspections, we deployed 30 motion-sensing cameras (HF2X, Reconyx, Holmen, WI, USA) to monitor a subset of the 54 nest boxes. We used the cameras to monitor activity around the nest boxes and to help with species identifications that may have been difficult through physical inspections alone. The cameras were deployed for a subset of nest boxes because not all nest boxes had nearby trees suitable for camera placement. Each site had 2–3 cameras monitoring nest boxes, and these stayed in operation from February 2021 until February 2023. The cameras used the same settings as the survey cameras which included a continuous schedule, high sensitivity, fast shutter night mode, and five consecutive photos per trigger.

Camera image tagging and data preparation

All animals were identified to species level where possible; however, for the *Antechinus* species (*Antechinus agilis* and *A. stuartii*) and *Acrobatus* species (*Acrobates frontalis* and *A. pygmaeus*) identification was only possible to genus level. For the nest box cameras, we noted whether an animal was observed visiting, or using, the nest box. We extracted the image metadata, site name, species name, and image date and time, using the package 'camtrapR' (Niedballa et al., 2016) in R (v. 4.3.1; R Core Team, 2023). We classified 'independent images' as images taken more than 5 min after any image of the same species. This interval was based on visual inspection of site-specific plots which showed the break points between consecutive animal images (see Figure S1 in Supporting Information).

Camera survey data analysis

We fitted generalised linear mixed models (GLMMs) using the glmmTMB package in R (Brooks et al., 2017) to assess the activity of the targeted arboreal mammals before and after the deployment of nest boxes in burnt and unburnt sites. We assessed the impact of ‘survey’ (pre-nest box deployment and 24-months post-deployment), ‘burn status’ (burnt or not during the 2019–20 fires), and ‘site’ (control vs nest box) on the response variable ‘activity’ of arboreal mammals. Activity referred to the number of independent observations per species per site divided by camera trap effort (days operating) for that survey period. We included ‘camera’ as a random effect to control for repeated measures. Activity was modelled using a zero-inflated gamma distribution, with a log(link) function.

Results

Nest box occupancy

Out of the 54 nest boxes deployed, the mean occupancy rate was 10% in November 2021 (9 months post-deployment), increasing to 57% by February 2023 (24 months post-deployment). Considering burn status, the mean occupancy rate in unburnt sites was 17% with no occupancy in burnt sites in November 2021; by February 2023, the mean occupancy rates had risen to 50% in unburnt sites and 61% in burnt sites. By the end of the study, the mean occupancy rate for small boxes was higher than that for large boxes, at 78% and 47%, respectively.

The most common nest box occupant across all nest boxes over the period of deployment was the antechinus (*Antechinus agilis* and *A. stuartii*; 26% mean occupancy), followed by the feathertail glider (*A. frontalis* and *A. pygmaeus*; 22% mean occupancy). Sugar gliders (*Petaurus breviceps*) and bush rats (*Rattus fuscipes*), which could only use large boxes, each had a mean occupancy of 11% of these boxes. Small boxes across all sites were preferred by antechinus (50% mean occupancy) and feathertail gliders (39% mean occupancy), but large nest boxes were also used by both (14% mean occupancy). During the physical checks, two nest boxes had antechinus present without nests.

When accounting for burn status and the box size accessible by each species, we found that antechinus and sugar glider occupancy tended to be slightly higher in burnt sites in comparison to unburnt (Fig. 3). In contrast, mean bush rat occupancy was five times higher in unburnt sites, while feathertail glider occupancy was equal between burnt and unburnt (Fig. 3).

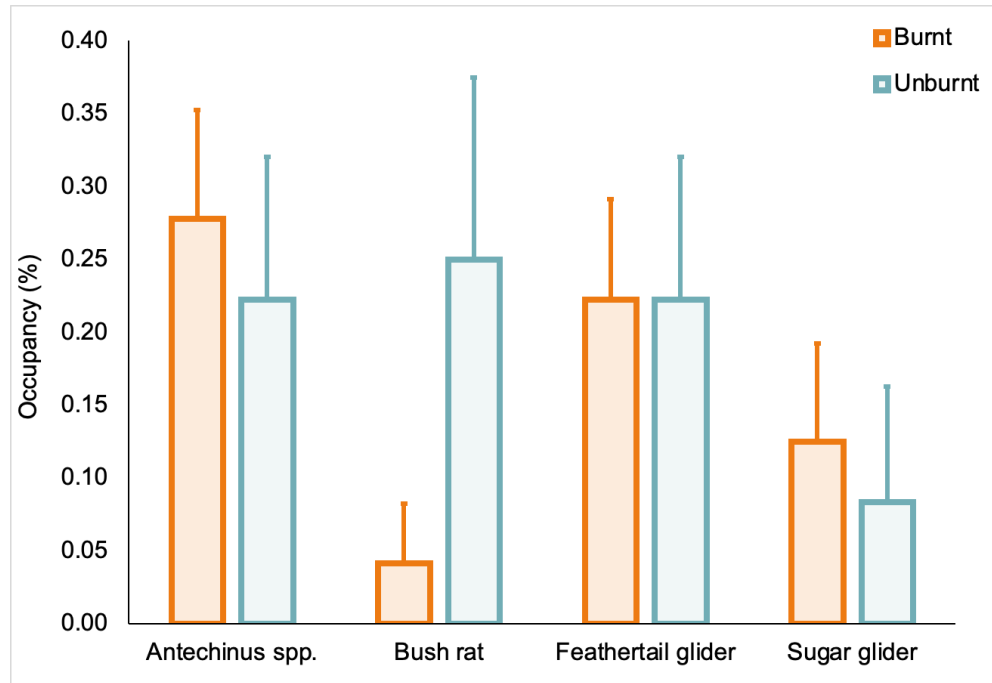


Fig. 3. Mean nest box occupancy rates by species, shown with standard error bars, in burnt and unburnt sites 24 months following nest box installation.

Nest box cameras

Of the 30 cameras, 21 detected animals, yielding 273 independent animal observations. These comprised 25 different species, including eight mammals and 17 birds. Birds visited the nest boxes but did not use them. Despite the nest boxes being intended for smaller arboreal mammals (<400 g), they were regularly visited by larger arboreal mammals, including common and mountain brushtail possums (*Trichosurus vulpecula* and *T. cunninghami*), and on two occasions by yellow-bellied gliders (*Petaurus australis*).

The most frequently detected species was the feathertail glider ($n = 83$ independent observations), followed by the sugar glider ($n = 37$), antechinus ($n = 32$) and bush rat ($n = 3$). Eastern pygmy possums were not observed during physical checks but were recorded on camera visiting nest boxes ($n = 2$). Sugar gliders, despite being too large to enter them, were observed visiting two of the small nest boxes on multiple occasions ($n = 16$).

Fifteen cameras operated for 24-months, which we used for comparison with the physical nest box checks (Table 1). At these sites, eleven cameras detected target species (arboreal mammals <400 g) compared to five nest boxes (Table 1). The cameras generally detected more species visiting or using the nest boxes

compared to the physical checks (Table 1). Cameras also detected species at the nest boxes earlier, with 10 cameras in comparison to one nest box detecting species by the first round of checks (<290 days post-nest box deployment; Table 1).

Table 1. Arboreal mammal detections by nest boxes and their corresponding camera. ‘Species’ columns show numbers of species detected by cameras and nest boxes. ‘Day’ columns show days post-nest box deployment to first mammal detection at nest box.

Nest box/ Camera ID	Species (camera)	Day (camera)	Species (nest box)	Day (nest box)	Nest box size	Burn status
NB1	2	25	0	-	Large	Burnt
NB2	0	-	0	-	Large	Burnt
NB3	1	59	1	734	Small	Burnt
NB4	1	107	0	-	Large	Burnt
NB5	3	91	1	734	Small	Burnt
NB6	1	177	0	-	Large	Burnt
NB7	0	-	0	-	Large	Burnt
NB8	0	-	0	-	Large	Burnt
NB9	4	274	2	276	Large	Burnt
NB10	3	276	1	734	Small	Unburnt
NB11	2	128	1	734	Large	Unburnt
NB12	1	454	0	-	Large	Unburnt
NB13	1	286	0	-	Large	Burnt
NB14	3	25	0	-	Large	Burnt
NB15	0	-	0	-	Large	Burnt

Camera surveys

Our models showed that, in unburnt forest, arboreal mammal activity was relatively stable at control sites (Fig. 4), with no significant change between the pre-nest box survey (‘survey 1’) and post-nest box survey (‘survey 2’; Table 2). However, in survey 2, activity was significantly higher at nest box sites compared to control sites (Fig. 4). By contrast, burnt sites had a significant increase in activity from survey 1 to survey 2 across both treatment and control sites, but the presence of nest boxes did not appear to affect the response (Fig. 4; Table 2).

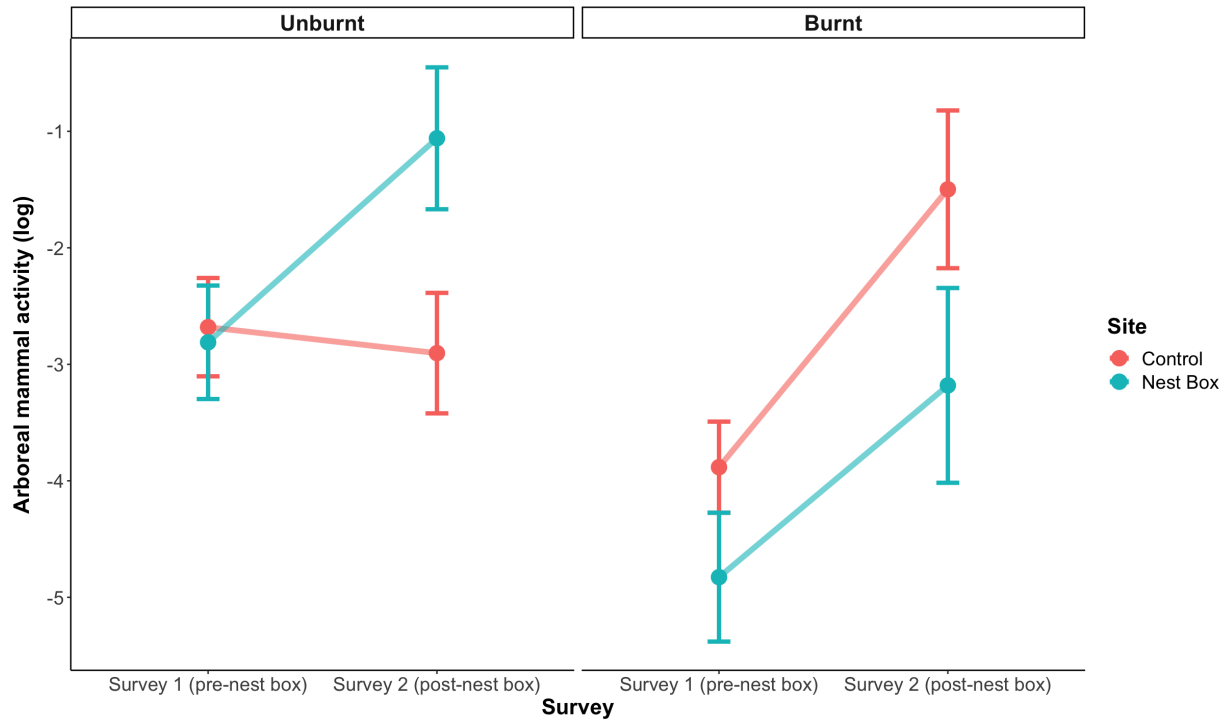


Fig. 4. Arboreal mammal activity before nest box deployment (survey 1) and 24 months after nest box deployment (survey 2) in unburnt and burnt forest.

Table 2. Effect of nest box presence on arboreal mammal activity in burnt and unburnt forest derived from generalised linear mixed models.

Model factors	Estimate	SE	<i>z</i>	<i>P</i>
Unburnt sites				
(Intercept)	-2.681	0.422	-6.352	<0.001
Survey 2 (post-nest box)	-0.223	0.517	-0.431	0.666
Nest box site	-0.130	0.487	-0.267	0.780
Survey 2:Nest box site	1.751	0.609	2.874	<0.001
Burnt sites				
(Intercept)	-3.883	0.391	-9.934	<0.001
Survey 2 (post-nest box)	2.385	0.677	3.523	<0.001
Nest box site	-0.944	0.553	1.708	0.088
Survey 2:Nest box site	-1.646	0.836	-1.969	0.049

Reference levels: Survey 1 (pre-nest box surveys), and control sites.

Discussion

Nest boxes, as artificial habitats, have been used increasingly in conservation efforts to assist fauna in landscapes that have been altered due to anthropogenic or natural disturbances such as fires (Lindenmayer et al., 2009). However, the success of these interventions for arboreal mammals has been variable. The 2019–20 Australian fires presented an opportunity to test the effectiveness of nest boxes as a recovery tool for arboreal mammals (<400 g) following extensive wildfires. We found that nest box occupancy was 11% higher in burnt sites in comparison to unburnt sites two years following the fires. However, nest boxes did not appear to hasten recovery compared to control sites in burnt areas.

In our study, nest box occupancy was low (10%) 9-months post-nest box deployment but increased more than five-fold (57%) by 24-months. Delayed occupancy of nest boxes is consistent with other studies (Lindenmayer et al., 2016). Notably, we found that nest boxes in burnt sites were not occupied 9 months post-deployment in comparison to unburnt sites which had some (17%) initial occupancy. However, 24 months post-deployment, this had shifted to nest box occupancy in burnt sites being higher (61%) in comparison to unburnt sites (50%). The nest box cameras detected a greater number of species compared to physical checks, which was expected given the continuous monitoring capabilities of cameras, and these results were similar to those in previous research (Honey et al., 2021). Cameras showed that animals were visiting nest boxes well before occupying them. This finding contrasts the conclusions of other studies suggesting that delayed occupancy of nest boxes may be the result of animals having not discovered them (Lindenmayer et al., 2016). Our data imply that discovery does not account for occupancy delays in this instance, and instead it is likely that behavioural or ecological factors are influencing the timing of nest box use.

The results from the camera surveys showed that arboreal mammal activity increased rapidly over time in burnt sites while in unburnt sites it remained relatively stable throughout the study. However, the presence of nest boxes in unburnt sites was associated with increased arboreal mammal activity by the second survey (24 months post-nest box installation). By contrast, in burnt sites, the increase in arboreal mammal activity was not associated with nest box presence. These findings suggest that nest boxes may be beneficial in stable habitats where key resources have not been extensively impacted, while in highly disturbed burnt forest, other factors may influence arboreal mammal recovery more than hollow availability. Supporting this interpretation, some studies have shown that species like sugar gliders are

more likely to occupy nest boxes in areas with a high availability of natural hollows (Le Roux et al., 2016; Lindenmayer et al., 2016). Further, species responses to fires are variable and can differ considerably. While the presence of certain species is closely associated with the availability of hollows (Lindenmayer et al., 2013), others are also strongly influenced by factors such as vegetation cover (Fordyce et al., 2016) or availability of specific food resources (Bladon et al., 2002). Therefore, the effectiveness of nest box programs in environments affected by fire will likely vary depending on species-specific ecological characteristics and needs.

Despite nest box design not being a key focus of our research, we did find that small nest boxes were favoured at our sites (78% occupancy) compared to large boxes (47% occupancy). These findings are in contrast to research in human-modified landscapes in south-eastern Australia (Le Roux et al., 2016). In our study, this is likely because feathertail gliders and antechinus were the most frequently detected species and the small nest box design is better suited to such species. Specifically, small nest boxes had a smaller entrance size, which can strongly influence nest box occupancy (Beyer and Goldingay, 2006; Le Roux et al., 2016). Entrance size physically dictates which species can fit through but can also serve an ecological role by limiting interspecific competition. Specifically, smaller apertures deter larger species, thereby mitigating competitive exclusion and facilitating occupancy by smaller, often less dominant, species (Gibbons and Lindenmayer, 2002). As such, our study reaffirms the importance of nest box design and that design features such as entry diameter should not be overlooked when nest boxes are being considered as conservation tools.

Conservation implications

Our research suggests that nest boxes provide a modest benefit to hollow-using arboreal mammals in burnt forest. However, our findings showed that nest boxes increase activity in adjacent unburnt areas, which could serve as source populations for faunal recovery in burnt forest once environmental conditions are suitable. Therefore, increasing the carrying capacity of unburnt areas with strategic nest box placement may be an effective conservation tool.

Our findings suggest that in burnt forest the effectiveness of nest boxes likely varies due to the different fire susceptibilities and specific ecological requirements of individual species. For species that depend on multiple hollows and show reduced presence in environments with fewer hollow-bearing trees, nest boxes

could facilitate population persistence or recovery. Conversely, species with specific needs such as specialised diets, may not benefit from nest boxes if their food sources remain scarce post-fire. Therefore, we advise against implementation of nest box programs without taking into consideration the specific ecological needs of the species they are intended for. Further to this, we reiterate that nest boxes cannot replace mature hollow-bearing trees, which provide additional resources for wildlife (Lindenmayer et al., 2014). Therefore, retention of natural hollows and protection of remaining unburnt native forest against further degradation, such as logging, should be prioritised.

Our study also reaffirms the importance of nest box design to best benefit arboreal mammals. The data suggest that nest boxes are not a 'one-size-fits-all' solution; their design and deployment should be species and context-specific. Further to this, a key issue with the provision of nest boxes is the risk of creating additional nesting or sheltering habitat for pest species (Gibbons and Lindenmayer, 2002; Lindenmayer et al., 2009). However, all the species observed in our study were native and this may be because the nest boxes used had characteristics that make them unsuitable for pest species (Goldingay et al., 2015).

Finally, our research indicates that continuous monitoring with cameras, coupled with periodic physical checks, can provide a better understanding of nest box visits and use. Moreover, camera surveys were particularly useful in assessing species activity before and after nest box deployment. Therefore, cameras can serve as an important tool for nest box programs that aim to track population recovery.

Author contributions

Vivianna led the study's conception and design, collected and analysed the data, and drafted the manuscript. TD made important contributions to the data analysis. All authors made important contributions to the final draft.

Acknowledgements

We acknowledge the Murramarang peoples, the Traditional Owners of the lands and waters on which this work was conducted, and extend that respect to their Elders past and present. We thank the NSW National Parks and Wildlife Service staff, Michael Phelan and David Cunningham, for providing local knowledge, assistance, and equipment during the course of this project. Field methods were approved by the University of Sydney Animal Ethics Committee (2020/1821) and the Department of Planning, Water and

Industry (SL102361). Funding for this research was provided by the NSW Environmental Trust and the Holsworth Wildlife Research Endowment. TSD was supported by the Australian Research Council (DE200100157).

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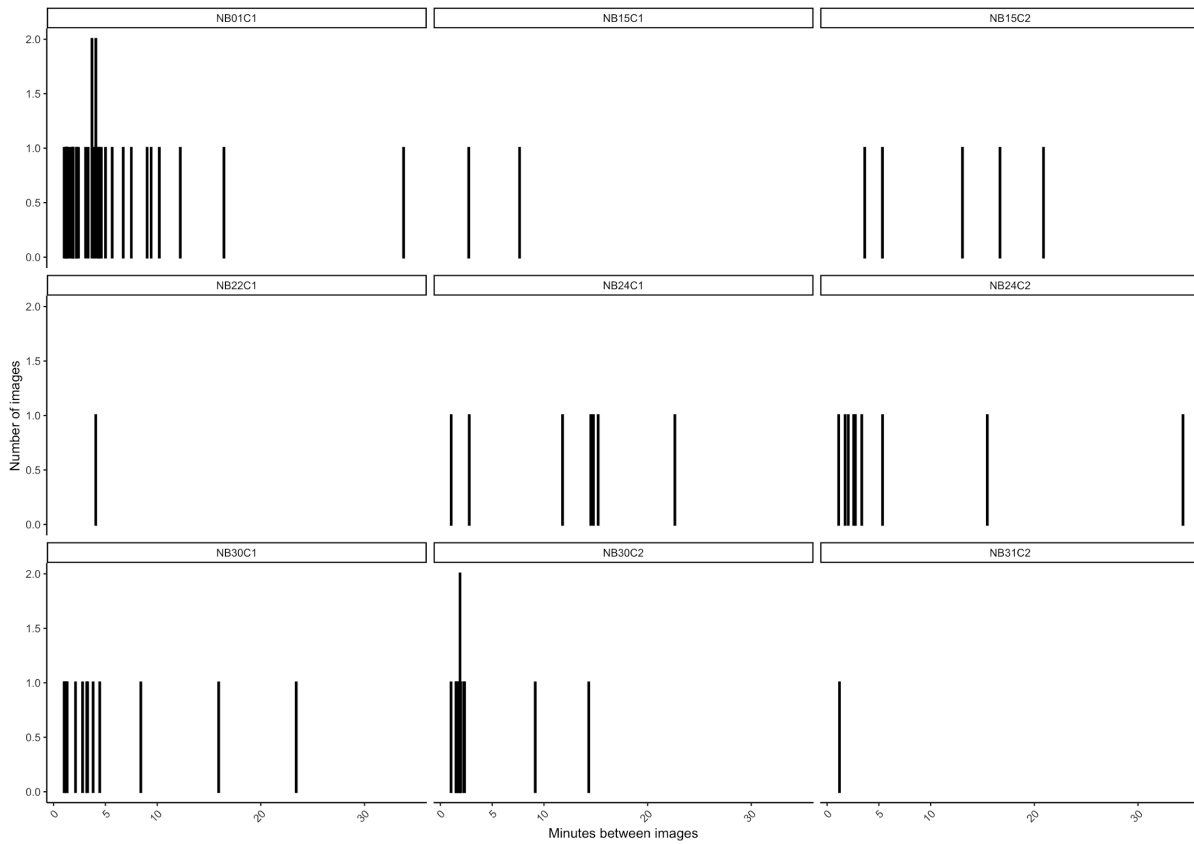
Supporting information

Fig. S1. Plots showing the time gaps between consecutive images at camera sites. Cameras with image gaps >30 min have been excluded. Plot shows high frequency of images with a gap of <5 min, as such we classed image gaps >5 min apart as ‘independent’.

Chapter 6 – Summary

Nowhere is the challenge of adaptation greater for animals than in the case of modern wildfires (Kreling et al., 2021). The Australian 2019–20 megafires were unprecedented in scale, severity, and duration, and highlighted the paucity of key information that could allow practitioners to assess the impacts of such fires on animal species. As such, key management recommendations were proposed by several authors that would guide a better understanding of the impacts of these megafires and future fires to come (see Dickman, 2021; Dickman et al., 2020; van Eeden et al., 2020; Ward et al., 2020; Wintle et al., 2020). These recommendations included initiating rapid fauna assessments, long-term monitoring, analysis of fire impacts on different species' persistence, and evaluating the effectiveness of post-fire management strategies. More broadly, rapidly quantifying the potential impacts of megafires and implementing immediate conservation responses have been increasingly recognised as critical strategies for protecting biodiversity and facilitating recovery in fire-prone ecosystems globally (Kelly et al., 2020).

Using these recommendations, I developed four aims that I have addressed in the previous data chapters of this thesis. As outlined in Chapter 1, these aims were to:

1. Assess the recovery of vertebrate species, primarily mammals, over time (Chapters 2 and 3),
2. Investigate if recovery is influenced by specific fire variables, such as fire severity and extent (Chapter 3),
3. Assess how some species are adapting to novel fire regimes and whether these adaptations are sufficient in aiding population persistence (Chapter 4),
4. Investigate the efficacy of nest boxes as a management tool for facilitating mammal recovery following fire events (Chapter 5).

In the previous chapters I have provided an overview of the ecological impacts of the Australian 2019–20 megafires on terrestrial and arboreal vertebrates. I have examined the emergent challenges in biodiversity conservation and management strategies in the face of increasingly frequent and intense fire events. This included providing a detailed assessment of the post-fire responses and adaptations of fauna, the efficacy of a commonly used management tool, and discussions on the broader implications of these fires for Australian fauna as well as fauna species worldwide. In this concluding chapter, I contextualise the results of each data chapter, and provide key management implications and suggestions for future research.

In Chapters 2 and 3, I assessed the post-fire recovery of vertebrate species following the 2019–20 Australian fires over two years. Chapter 2 focused on small mammals and their abundance, diversity, and species-specific responses to the fires using live-trapping surveys. In this chapter I found that species diversity increased with time since the fires and was higher in burnt sites by the end of the study. However, this increase in diversity occurred because of the occurrence of an invasive species, the house mouse (*Mus musculus*), which had a strong preference for burned forest, especially where severe burns had occurred. By the end of the study the most commonly captured species in burnt forest were generalist species, the bush rat (*Rattus fuscipes*) and house mouse, while species that were more specialised in their diet and habitat needs, like the antechinuses (*Antechinus agilis*, *A. stuartii* and *A. mimetes*) were less abundant in forest impacted by the fires. These results provide important data on post-fire succession of small mammals, especially in response to megafire, and highlight the need for sustained management for the recovery of species with habitat and dietary specialisations.

In Chapter 3, I expanded my analysis to explore how more-nuanced fire variables and vegetation type influence vertebrate species recovery over time. This included interrogation of an extensive dataset from remote camera traps which operated continuously for 3 to 27 months following the fires. I analysed the responses of 14 animal species/groups which encompassed mammalian predators, small and medium-sized mammals, large herbivores, and birds. My analysis showed that the responses of co-occurring vertebrate species to fire are variable, and time since the fires with nuanced fire metrics including fire severity, proportional area of habitat burnt, and vegetation type by burn status, capture more of the complexity of post-fire successional changes than do simple contrasts between burnt and unburnt habitat. The results suggested that some species will benefit while others will be disadvantaged by novel fire regimes, and also highlighted the importance of using multi-faceted approaches to account for the complex responses of animal species to fires.

In Chapter 4, I explored the idea of fire-driven animal adaptation; this is a mechanism that is increasingly recognised for its importance in mediating the impacts of novel fire regimes, but is poorly understood (Jones et al., 2023). Using fine-scale data collected from GPS collars, I assessed the effect of the fires on the space use and movement behaviour of the southern greater glider (*Petauroides volans*). I selected this species because of its sensitivity to fires, its rapid and ongoing population declines, and because close to one-third of its habitat was burned by the megafires (Ashman et al., 2021). Notably, during my study, in

October 2022, *P. volans* was declared as Endangered under the Environment Protection and Biodiversity Conservation Act 1999. The data I collected provided empirical evidence to indicate how a fire-sensitive species is persisting in severely burnt habitat and may be able to do so by adjusting its movement patterns to meet its resource needs. However, the results also showed that greater gliders exhibited home range fidelity, a behavioural strategy that has evolved under the selection pressures exerted by historical fire regimes. The results emphasised that greater gliders are exhibiting some ability to adapt and persist after a fire, but suggest further that species that continue to exhibit fixed behavioural strategies such as home range fidelity, and forego higher quality habitat in favour of their established ranges, will be challenged by ongoing, and increasingly severe and frequent habitat disturbances.

In Chapter 5, I investigated the efficacy of nest boxes in facilitating mammal recovery post-fire. I selected nest boxes because they are a commonly recommended and used management tool, and were recommended as priority response to the megafires (see Dickman et al., 2020). I deployed 54 nest boxes across burnt and unburnt sites and monitored them over two years through physical checks and camera monitoring. I also implemented remote camera surveys monitoring arboreal mammal activity at sites with and without nest boxes. Two years after deployment, more than half the nest boxes were occupied in burnt forest. However, the camera surveys also revealed that arboreal mammal activity increased over time in burnt forest irrespective of nest box presence. This result was in contrast to results from sites not impacted by the fires, which had steady activity over time but higher activity in sites with nest boxes. These results presented some interesting findings in that nest boxes provide a modest benefit for fire-impacted arboreal mammals but may serve as an effective tool for increasing the carrying capacity of unburnt areas, which could facilitate recolonisation when burned habitat becomes suitable. Our study also highlighted the benefits of using multiple monitoring approaches (physical nest box checks and camera surveys) to better understand the effectiveness of this management tool.

Broader implications

This thesis enhances our understanding of the responses of vertebrate species to megafires and adds to the growing literature on the ecological effects of contemporary fire regimes. The dataset collected throughout is unique in that it documented the continuous short- to medium-term post-fire succession of a variety of species, and this is particularly valuable given this was Australia's most catastrophic wildfire season on record. It was also one of the few studies that collected data so soon after the fires (<3 months post-fire).

The importance of timely monitoring is increasingly being recognised as a key factor for capturing species' responses to fires. For example, a quantitative review of fox and cat activity post-fire found that the probability of a positive response to fire decreased with time since fire for both cats and foxes (Doherty et al., 2023). Similarly, in the results of this thesis, peak fox activity occurred just three months post-fire (Chapter 3). While there may be logistical constraints with surveying recently burnt areas, these findings suggest that there is a critical time period in accurately capturing the responses of certain species. Further, these findings emphasise that predator impacts on vulnerable prey species are likely to be most elevated in the initial months post-fire, and feral predator control, a priority action in response to the fires (Dickman et al., 2020), is likely to be most effective during this period.

A subtle theme throughout this research was the influence of generalist and specialist traits on the response of various species to burnt forest. The impact of environmental change being mediated by species' capacity to exploit a range of environmental conditions is not a new concept (see Clavel et al., 2011; Devictor et al., 2008). However, species specialisations are an important and often undervalued mechanism impacting persistence in post-fire environments (Dickman and Happold, 2022). In my research, numerous species displayed fire-sensitive responses, including the antechinuses (*Antechinus agilis*, *A. stuartii*, *A. mimetes*) and the wet-forest birds (*Menura novaehollandiae*, *Leucosarcia melanoleuca*, *Ptilonorhynchus violaceus*) which all had lower abundance or activity in burned forest throughout the study (3–27 months post-fire; Chapters 2 and 3). These species all share common traits in that they are quite specific in their resource requirements (i.e., hollow-bearing trees, invertebrates, fruits), all of which are impacted by fires. As discussed in Chapter 5, specialised requirements also likely influenced the effectiveness of nest boxes in burnt forest as nest boxes can only fulfil one ecological need which may be more important to some species than others. Indeed, recent literature has highlighted the necessity for population monitoring across a wide range of species, to enhance understanding of how traits will interact with changing environmental conditions and influence animal survival and population responses to future disturbance (Ensley et al., 2023). A strong focus on conservation has been placed around protecting threatened species; however, there is compelling evidence that proactive management and early recognition of the threats to common species should be equally prioritised and managed. Greater gliders are a key example; Lindenmayer et al. (2011) warned against conservation complacency for this at-the-time common but specialised species, and now just over a decade later it is federally listed as Endangered.

Limitations and future research

In this thesis I have reported the variable short- to medium-term responses of a range of animal species and provided future research recommendations throughout. More broadly, this research sets the foundation for longer-term studies which will be required to continue understanding the long-term succession of species, as the impacts of these megafires will extend for decades.

Fire ecology

This thesis has covered a broad scope of aims relevant to contemporary fire regimes. However, there are many aspects of the fire regime, including fire return intervals, season, rainfall, and Indigenous burning practices which are highly relevant to fire ecology and would be informative for future research to include when assessing species responses. In particular, Australia's fire-prone landscapes and the biodiversity within them have evolved hand-in-hand with Indigenous cultural burning. The transformation of these landscapes since European occupation reinforces the need for reintroducing Indigenous fire management, which will also play an important role in managing fuel loads and biodiversity across southeast Australian forests (Steffensen, 2020). Moreover, reintegrating these practices could provide a means to start healing the deep-rooted ecological and cultural disruptions experienced by Indigenous peoples (Fletcher et al., 2021). Such research will be important for developing effective and ecologically sensitive fire management strategies and for continuing to acknowledge the historical stewardship of Indigenous communities over these landscapes.

Geographic and topographic features

Including environmental variables such as geographic and topographic features could provide a better understanding of animal species' responses to fire, and may be particularly useful in wildfire studies where pre-fire data is not available. This would involve considering factors like elevation, slope, aspect, soil type, and proximity to water bodies, all of which can influence the local climate, vegetation structure, and, consequently, the composition of the animal community and their reactions to fire.

Wildfire versus megafire

Future research could compare faunal responses to megafires and other types of fires, including smaller wildfires and prescribed burns. This is a difficult proposition given the unpredictable nature of wildfires but may best be achieved through approaches such as longitudinal surveys and meta-analysis of existing

data. Such research would help clarify whether unprecedented megafires result in correspondingly unprecedented effects on wildlife.

Post-fire wildlife management

Extending the understanding of remedial management strategies would also be highly beneficial. In this thesis I have investigated the efficacy of nest boxes as a management tool; however, other strategies including provision of food resources would benefit from further research. To date, there hasn't been much research on the effectiveness of providing food and water in situ for affected wildlife (wildlife provisioning; Jones et al., 2023). However, following the 2019–20 megafires fires volunteers, members of the community, wildlife organisations, and state government, felt compelled to help by supplementing food and water. This included state-funded aerial food drops and the development of brief guidelines for supplementing food and water after fires (NSW Department of Planning and Environment, 2020). A substantial amount of research is required to determine the beneficial or negative outcomes of wildlife provisioning as a response to habitat disturbances (Jones et al., 2023). Some research even suggests that wildlife provisioning can trigger population increases of opportunistic generalist species and reduce community diversity (Oro et al., 2013). As such, further research will be important to better understand the impacts of wildlife provisioning and to inform effective post-fire management strategies.

Predicting declines and extinction risks

Predicting species decline and assessing extinction risks in response to altered fire regimes are becoming increasingly important areas of study, particularly in light of the rapid population declines of species that were previously considered common and widespread (Lindenmayer et al., 2011). The work of Ensbey et al. (2023), which involved using animal traits and expert estimates of population loss following the 2019–20 megafires, provides an important foundation for predicting species responses and potential extinction risks due to altered fire regimes. However, further research is needed to understand how species traits are interacting with changing environmental conditions. Moreover, other important research areas to consider, which could complement remedial management strategies like wildlife provisioning, include the assessment of critical resources for species, and evaluations of how these resources were impacted by the fires, and how they may be impacted by future frequent and severe fires.

Conclusion

For millions of years fires have brought life and death, in a cycle that has shaped the evolution and ecology of countless species and landscapes. It is a complex and intricately balanced environmental force, but the balance has shifted. Through this thesis I have explored and answered numerous research questions on contemporary fire regimes. However, further research will continue to develop our understanding of this dynamic and complex ecological process.

Witnessing the immediate aftermath of the Australian megafires was sombre. There is something very stark about standing in a forest that is completely silent. Leafless scorched trees extending for kilometres. The ground, covered in only in black ash. I hope this is not the future of the world's forests. This is a critical reflection on the consequences of environmental complacency and highlights the need for unified efforts in conservation and management to provide a better future for these rich ecosystems.

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Inspecting a hollow. Kai Wild

