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RESEARCH ARTICLE

Animal mortality during fire

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Abstract

Earth's rapidly warming climate is propelling us towards an increasingly fire-prone future. Currently, knowledge of the extent and characteristics of animal mortality rates during fire remains rudimentary, hindering our ability to predict how animal populations may be impacted in the future. To address this knowledge gap, we conducted a global systematic review of the direct effects of fire on animal mortality rates, based on studies that unequivocally determined the fate of animals during fire. From 31 studies spanning 1984–2020, we extracted data on the direct impacts of fire on the mortality of 31 species from 23 families. From these studies, there were 43 instances where direct effects were measured by reporting animal survival from pre- to post-fire. Most studies were conducted in North America (52%) and Oceania (42%), focused largely on mammals (53%) and reptiles (30%), and reported mostly on animal survival in planned (82%) and/or low severity (70%) fires. We found no studies from Asia, Europe or South America. Although there were insufficient data to conduct a formal meta-analysis, we tested the effect of fire type, fire severity, fire regime, animal body mass, ecological attributes and class on survival. Only fire severity affected animal mortality, with a higher proportion of animals being killed by high than low severity fires. Recent catastrophic fires across the globe have drawn attention to the plight of animals exposed to wildfire. Yet, our systematic review suggests that a relatively low proportion of animals (mean predicted mortality [95% CI] = 3% [1%–9%]) are killed during fire. However, our review also underscores how little we currently know about the direct effects of fire on animal mortality, and highlights the critical need to understand the effects of high severity fire on animal populations.

KEYWORDS
death, disturbance, megafire, Pyrocene, survival, systematic review, tracking, wildfire

1 | INTRODUCTION

Fire has shaped the diversity of life on Earth for hundreds of millions of years (Bowman et al., 2009; He et al., 2019). Many terrestrial ecosystems are fire prone, and fire shapes the structure, function and composition of these systems (Bond & Keeley, 2005; Bowman et al., 2009; He et al., 2019; Pausas & Keeley, 2009). Some plants and animals benefit from fire (He et al., 2019) and the environmental heterogeneity it creates (Parr & Andersen, 2006). However, global fire regimes are changing (Bowman et al., 2020). Climate change is rapidly heating and drying the planet (Karl & Trenberth, 2003), and ignition patterns and fuel structures are changing (Pausas & Keeley, 2021), resulting in increased wildfire frequency and intensity (Di Virgilio et al., 2019; Jolly et al., 2015; Wu et al., 2021). Consequently, changing fire regimes threaten >1000 animal species with extinction worldwide (Kelly et al., 2020).

Fire influences animal populations via direct and indirect effects (otherwise termed first- and second-order effects respectively; Engstrom, 2010). The direct effects of fire involve mortality during the fire event (Whelan et al., 2002). As fire passes through a landscape, animals within the perimeter of the fire die if they are unable to flee or seek adequate shelter (i.e. via smoke inhalation, radiant heat or being directly consumed by flames) (Nimmo et al., 2019, 2021). The capacity to survive fire likely depends on animal traits (e.g. evolutionary exposure to fire [Nimmo et al., 2021; Pausas & Parr, 2018]; ability to flee [Nimmo et al., 2019]; ecological attributes, i.e. use of and access to non-flammable refugia), aspects of the environment (e.g. refuge availability [Banks et al., 2017], fuel loads and moisture) and fire behaviour (e.g. fires of higher severity [Whelan et al., 2002]) (Figure 1: conceptual framework). The indirect effects of fire are those related to the changes that fire brings about through the combustion of habitat, the resulting loss of food and shelter, and the successional dynamics that fire initiates (Engstrom, 2010). Population declines immediately following fire are presumed to involve a combination of direct mortality and emigration, or reduced survival due to increased rates of predation and resource limitations in the post-fire landscape (Engstrom, 2010; Whelan et al., 2002).

Although fire affects 300–500 million ha of land globally each year (Forkel et al., 2019), there is surprisingly little knowledge of fire as an agent of direct animal mortality (Nimmo et al., 2021). Yet, interest in the topic has increased in recent years following megafires—fires that are extreme in size (e.g. >10,000 ha) and severity (Stephens et al., 2014)—in Australia, California, Siberia and the Amazon (Barlow et al., 2020; Escobar, 2019; Nolan et al., 2020; van Eeden et al., 2020). The unprecedented scale of these recent fires (Boer et al., 2020; Duane et al., 2021) resulted in substantial proportions of many species' ranges—and in some instances entire geographic ranges—lying within the perimeter of a single fire (Ward et al., 2020). Understanding the likely proportional population toll of such fires is important in order to reassess the conservation status of species (Legge et al., 2020; Wintle et al., 2020), to help prioritize conservation management actions in the aftermath (Geary et al., 2021; Wintle et al., 2020), and to begin to grapple with the likely timescales of recovery. It is, therefore, timely to appraise what we know about the direct effects of fire on animal populations.

To address this knowledge gap, we systematically reviewed empirical studies that examined the impact of fire on the mortality rates of animals globally. Only individual animals that were able to be tracked continuously through the passage of fire—typically via radio-tracking—qualified for inclusion in our systematic review. These studies can detect fire-induced mortality with high certainty, whereas studies of changes in animal population size before/after fire typically do not differentiate between survival/mortality and immigration/emigration, creating uncertainty regarding the proportion of animals that survived the passage of fire (i.e. vs. animals that emigrated outward from the firegrounds immediately prior to or following the fire's passage). Likewise, some recent studies have documented the—sometimes very high—numbers of animals killed in fires (Tomas et al., 2021), but we do not directly consider such studies because they lack a before–after component, so cannot provide evidence of proportional population losses, or survival rates of individual animals, in fire.

Our principal objectives were to:

1. Characterize and summarize the direct effects of fire on animal mortality rates and analyse the extracted data to clarify which traits of the animals and fires are important in explaining variation in the direct impacts of fire; and
2. Identify the major knowledge gaps regarding how fires directly cause animal mortality and suggest how these may be addressed by future research.

2 | MATERIALS AND METHODS

2.1 | Systematic review

Our study involved a systematic review of the literature investigating the direct effects of fire on the mortality of animals to identify broad publication trends and, for a subset of these studies, analyse whether traits of the animals and/or fire mediate the immediate outcomes for animals impacted by fire.

2.1.1 | Search criteria

For the purposes of this study, animals were defined as non-human organisms in the kingdom Animalia. We only considered studies that measured the effect of a fire on the mortality of a known number of animals, such that their fate before and after the passage of fire was explicit and quantifiable. Because we were interested only in the direct effects of fire on animal mortality, we did not include studies that only estimated abundance or survival before and after a fire, or at burnt and unburnt sites based on trapping or observational data (see Whelan et al., 2002). We chose to exclude these studies because fleeing and/or emigration is a common response to fire (Nimmo et al.,

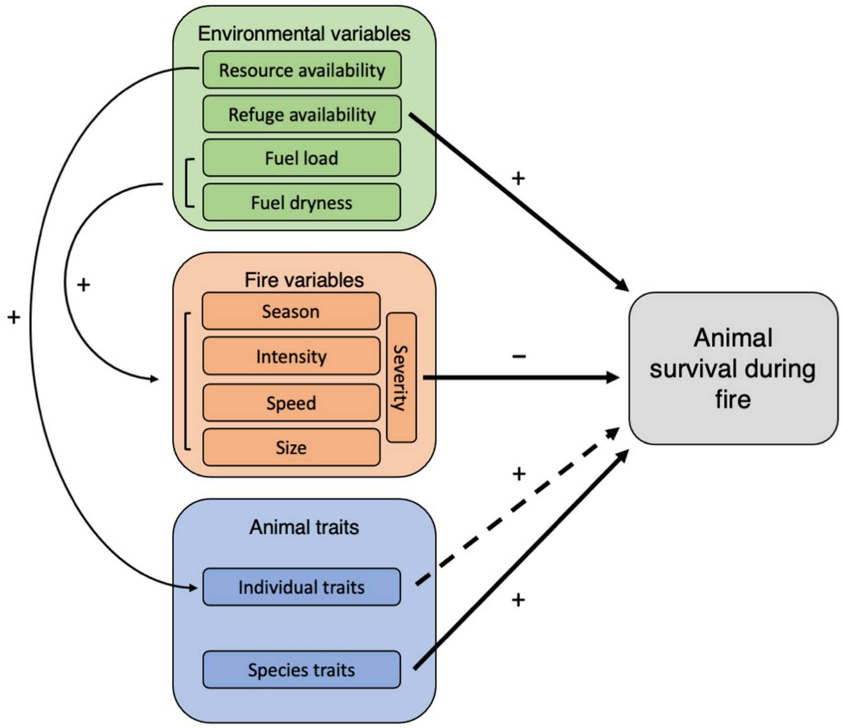

FIGURE 1 Conceptual framework of factors affecting animal survival during fire. Direction of effects is driven by assuming each variable is maximized. *Environmental variables* can affect survival both directly (proximate driver; thick arrows) and indirectly (distal driver; thin arrows) by influencing *fire variables* and *animal traits*. *Resource availability* directly improves the condition of individuals, which may improve individual survival. *Refuge availability* may directly improve animal survival by providing unburnt refugia at various spatial scales that allows animals to avoid fire (Robinson et al., 2013). *Fuel load* and *fuel dryness* provide combustible material for fire in the landscape and directly increase the chances of fires being of high severity. *Fire variables* likely strongly affect the survival of animals during fire with more severe fires reducing the extent or incidence of unburnt refuges and consuming more flammable shelter sites. *Fire severity* is driven by *fire season* (prevailing weather conditions), *intensity* (burn temperature), *speed* (driven by wind) and *size* (driven by distribution of fuel), and likely has a strong influence on animal survival during fire, with fires of high severity significantly reducing animal survival during fire. *Animal traits* likely influence animal survival via several pathways. *Individual traits*, such as age, satiation, reproductive status, physiological condition, prior experience and individual differences in innate fire avoidance behaviours, may affect the chances that an individual survives during fire (Nimmo et al., 2021). The dotted line denotes uncertainty. *Species traits*, such as mobility, size, ecological attributes and evolutionary exposure to fire, likely have a strong influence on whether individuals survive fire events (Nimmo et al., 2021; Pausas & Parr, 2018). Animals that are more able to avoid the lethal effects of fire, due to their innate ability to detect and appropriately respond, shelter in fire-safe refugia because of their size or ecology, or simply their ability to rapidly flee to a safe distance, are likely to increase their likelihood of surviving during fire [Colour figure can be viewed at wileyonlinelibrary.com]

2019), and these studies are typically unable to disassociate mortality from emigration (see Sergio et al., 2019). Although both vertebrates and invertebrates could have been captured by our search criteria, only individual animals that were able to be tracked through the passage of fire—typically via radio-tracking—qualified for inclusion in our systematic review. Because of this criterion, no invertebrate studies were captured here. Fire refers to both wildfire and planned (i.e. prescribed and experimental) burns. Publication date was unbounded.

2.1.2 | Literature search

We systematically searched Web of Science and Scopus databases in November and December 2020, using combinations of search terms relating to animals, fire and survival/mortality (Supporting Information 1). To increase the specificity of results, we also refined these searches by including/excluding unrelated search categories (Supporting Information 1). We supplemented our literature search with further unstructured searches of published and grey literature (e.g. via Google Scholar and reference lists of returned studies). All searches were conducted in English. Our structured search returned 3548 studies, and seven extra studies were found using less structured methods. After duplicate records were removed, we retained 2919 studies for review. We used the R package METAGEAR (Lajeunesse, 2016) to screen studies by title and abstract only and assess them against our inclusion criteria. This package was used to assess study titles and abstracts independently of all other information to reduce potential sources of bias. Following this screening, 62 studies were deemed appropriate for full text review, however, after examining the full texts, only 31 of these studies met our search criteria (see Figure S1.1 for the PRISMA diagram). All studies used in the systematic review are provided in Data Sources.

2.1.3 | Data extraction

For each study, we recorded the number of animals monitored through the passage of fire and the number killed directly by fire. We categorized each study based on the type of fire studied (e.g. planned fire or wildfire) and the severity of the fire event (e.g. low and high severity fire; Table S1.1). Fire severity is context specific (Keeley, 2009), and was applied as closely to how it was defined in the source publications. In a few cases, we contacted source study authors to confirm whether we applied the appropriate fire category to their study. Generally, low severity fires burnt in cooler conditions and left some unburnt groundcover, and unburnt canopy (in vegetation types that include a tree layer), whereas high severity fires burnt in warmer, more dangerous fire conditions and consumed most or all groundcover, and most or all canopy (in vegetation types that include a tree layer). Within each study, we categorized each study taxon based on its taxonomic class (e.g. bird, reptile, mammal or amphibian), family and species. We recorded ecological attributes (e.g. terrestrial, arboreal and volant) of all study taxa (Table S1.1). For all species, we recorded body masses using taxonomically appropriate databases (see Table S1.1). Some studies investigated multiple fires and/or their effects on multiple species. For this reason, we extracted 'instances' of the direct effects of fire on the mortality of a single species during a fire event from each study. For animals to qualify as monitored through the passage of fire, each individual must have been present in the area immediately prior to the area burning (see Table S1.1). We recorded geographical attributes of all instances (e.g. study continent, country, specific study location; Table S1.1). Based on study location, we then assigned all studies to a broad terrestrial biome following Olson et al. (2001).

2.2 | Data analysis

We used the extracted data to visualize the spread of studies through time and space, and assessed them for temporal and/or geographical bias. We assessed whether traits of the study species, fire or fire regime affected the proportion of a population that died during fire. We removed instances with very small samples sizes ($n < 5$ individuals monitored through the passage of fire), after which we retained 29 of 43 instances of the direct effects of fire on mortality. We used generalized linear mixed models to test the effect of predictor variables on the proportion of animals that died during the passage of each fire, which we modelled as the number of animals that died during the fire (1s) and animals that survived the fire (0s) during a fixed number of Bernoulli trials (total number of animals monitored). Due to the small sample size (i.e. 29 instances), we fitted a series of univariate models relating the proportion of animals that died in relation to: fire type (levels: planned vs. wildfire), fire severity (levels: low vs. high severity), log-transformed body mass (continuous), ecological attributes (levels: terrestrial, arboreal vs. volant) and animal class (levels: amphibian, bird, mammal vs. reptile). To test whether the fire regime of a study region affected animal survival, we assigned each study a fire activity index (see Pausas & Ribeiro, 2017). Fire activity indices (from 0 to 1) were assigned to each ecoregion (Olson et al., 2001) using MODIS hotspot data (Collection 5 Active Fire Products; Giglio, 2013) collected between 2000 and 2015 by scaling averaged fire activity and radiative power data by the area of each ecoregion (see Pausas & Ribeiro, 2017 for full methods). We then fitted a model testing whether the proportion of animals that died was affected by fire activity. Additionally, to test whether fire activity affected the vulnerability of animals to fire severity (i.e. are animals from fire-prone regions better able to survive high severity fires?) we fitted this model with and without an interaction with fire severity. As some individual species featured in multiple instances, we included species as a random effect. All analyses were performed using R version 4.0.3 (R Core Team, 2021) with the *lme4* package (Bates et al., 2007). We then used the *ggeffects* package to predict the outcome of variables that had a significant effect on mortality (Lüdecke, 2018).

3 | RESULTS

3.1 | Systematic review

Our systematic review returned 31 studies spanning 1984–2020 investigating the direct impacts of fire on the mortality rates of 31 species from 23 families (Figure 2). We found that studies tracking animals through the passage of fire have increased through time (Figure 2a). We observed a substantial geographical bias in the literature (Figures 2a and 3), with most studies coming from the United States (North America) and Australia (Oceania) (52% and 42% respectively). There was only a single study from each of Senegal and South Africa (each 3% of studies; Africa), and we detected no studies of fire-induced mortality on animals from Asia, Europe or South America (Figures 2a and 3), despite there being vast fire-prone regions across these continents (Kelly et al., 2020).

Most studies focussed on the direct effects of fire on the mortality rates of mammals and reptiles (53% and 30% of instances respectively), rather than birds and amphibians (12% and 5% respectively; Figures 2b and 4). For all animal classes, most studies investigated the direct effects of planned and low severity fires (82% and 70% of instances respectively), with relatively few investigating wildfire and high severity fire (19% and 30% respectively; Figure 4). The majority of studies focused on the direct effects of planned and low severity fire on mammals (42% respectively; Figure 4). We found no studies on direct impacts of wildfire or high severity fire on the mortality of amphibians (Figure 4).

The families most frequently studied were Muridae (rodents; five instances) and Viperidae (vipers; five instances; Figure 2b). In only five species (16%) were the direct impacts of fire on mortality assessed in multiple studies (Figure 5). Across all studies, there was an enormous range in the body sizes of the animal species studied, from 7.9 g red-backed fairy-wrens (*Malurus melanocephalus*) (Murphy et al., 2010; Sommer et al., 2018) to the world's largest terrestrial animal—the 4400 kg African bush elephant (*Loxodonta africana*) (Woolley et al., 2008). Most studies investigated the direct

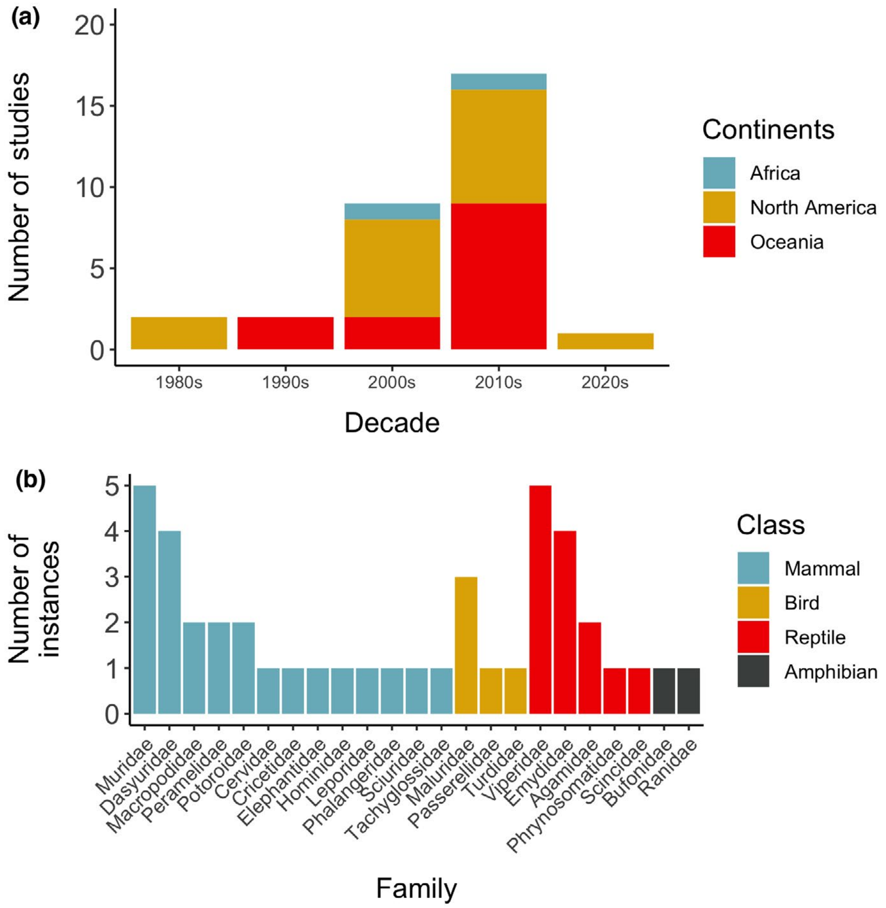

FIGURE 2 (a) Number of published studies in the systematic review dataset (total 31) per continent, per decade; and (b) number of instances that a species from each family grouped by animal class appeared in a study in the systematic review dataset [Colour figure can be viewed at wileyonlinelibrary.com]

effects of fire on the mortality of animals that are currently listed as *Least Concern* according to the *IUCN Red List of Threatened Species* (74% of species; see Supporting Information). Two *Near Threatened* (Bachman's sparrow *Aimophila aestivalis* and gopher frog *Lithobates capito*), one *Vulnerable* (eastern box turtle *Terrapene carolina carolina*) and four *Endangered* species (African bush elephant *Loxodonta africana*, northern bettong *Bettongia tropica*, pygmy bluetongue lizard *Tiliqua adelaidensis* and savanna chimpanzee *Pan troglodytes verus*) were studied (6%, 3% and 13% of species respectively).

The direct impacts of fire on animal mortality have been investigated in seven of the 14 global terrestrial biomes. We found examples of the direct effects of fire on wildlife mortality in planned fire and wildfire, and low and high severity fire, for most of these seven biomes (Figure 6). Despite half of all terrestrial biomes having been studied, most studies reported instances of planned and low severity fire in temperate broadleaf and mixed forests (42% of instances respectively; Figure 6). Currently, there has been no study of the impacts of fire on animal mortality in 50% of terrestrial biomes and, of those that have been studied, there is no information on the impacts of high severity fire or wildfire in 43% (Figure 6).

3.2 | Factors affecting mortality during fire

Overall, within-study sample sizes of species monitored through the passage of fire tended to be relatively small (53% of instances monitored fewer than 10 individuals). Most studies (65% of instances) recorded no direct mortality caused by fire (Figure 5). Across all fires, the mean (95% CI) predicted direct effect of fire on animal mortality was 3% (1%–9%), and observed mortality ranged from 0 to 40% for studies tracking five or more individuals (Figure 7). Generalized linear mixed models revealed no apparent effects of fire type ($F_{1,28} = 1.13$, $p = .293$), body mass ($F_{1,28} = 1.55$, $p = .217$), ecological attributes ($F_{1,28} = 0.42$, $p = .362$) or animal class ($F_{1,28} = 0.26$, $p = .702$) on the direct effects of fire on animal mortality. Additionally, there was no apparent interactive effect of regional fire activity and fire severity on animal mortality ($F_{2,16} = 0.88$, $p = .336$), nor a main effect of regional fire activity after the interaction was removed ($F_{1,16} = 0.61$, $p = .438$). There was, however, a significant effect of fire severity on animal mortality ($F_{1,28} = 5.77$, $p = .016$; Figure 7), with a greater predicted proportion of animals dying in high severity fires (mean mortality [95% CI] = 7% [2%–21%]) than low severity fires (2% [1%–7%]).

4 | DISCUSSION

4.1 | Direct effects of fire on animal mortality

Our characterization and summary of the literature has revealed how little we know about the direct effects of fire on animal populations. Our systematic review identified only 43 instances in 31 studies that quantified fire-induced animal mortality through the passage of a fire.

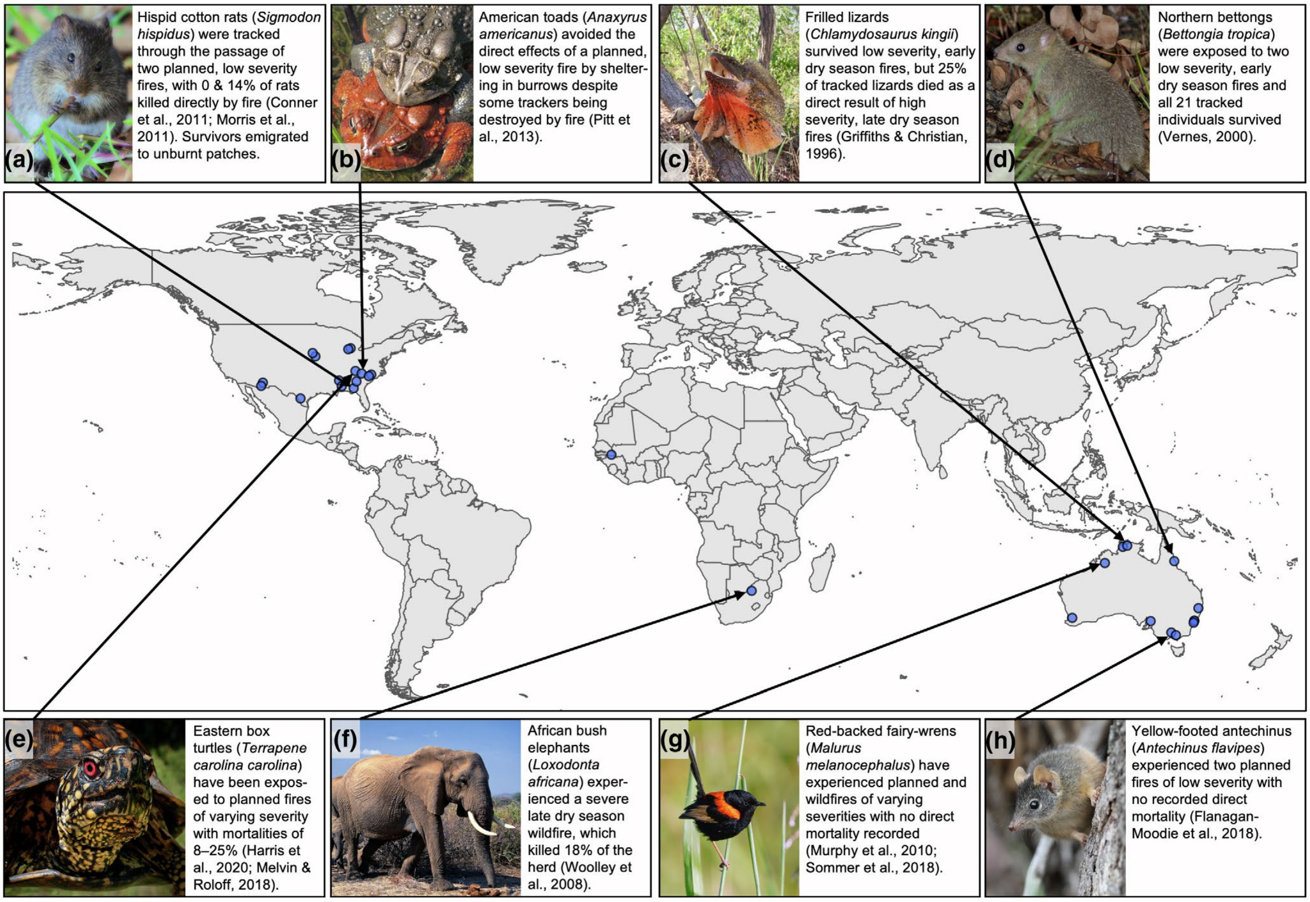

FIGURE 3 Global map of study locations. Species-specific examples of the direct effect of fire on animal mortality appear in boxes. Photograph credits: (a) James Leon Young CC BY-SA 2.0; (b) Vicki's Nature CC BY-NC-ND 2.0; (c) Alana de Laive; (d) Stewart Macdonald; (e) Brookhaven National Laboratory CC BY-NC-ND 2.0; (f) flickrfavorites CC BY 2.0; (g) David Cook Wildlife Photography CC BY-NC 2.0; (h) patrickkavanagh CC BY 2.0 [Colour figure can be viewed at wileyonlinelibrary.com]

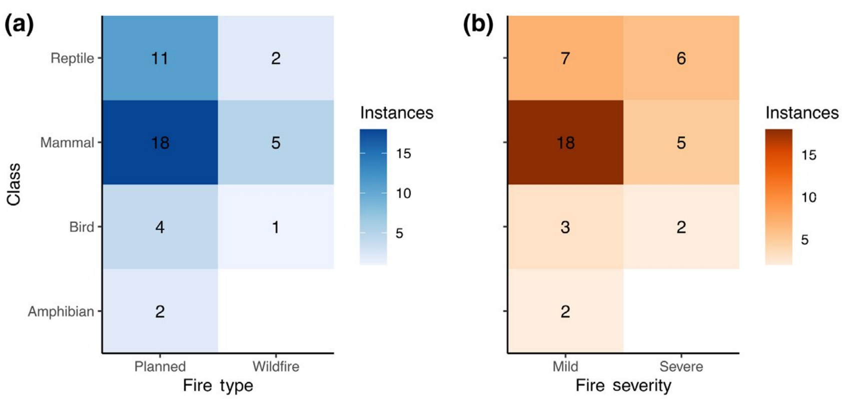

FIGURE 4 Counts of the number of instances (a) a fire type (planned or wildfire) and (b) a fire severity (low or high) was studied for each animal class [Colour figure can be viewed at wileyonlinelibrary.com]

We found that the vast majority of studies assessed the effects of planned fire—which tended to be of low severity—on the mortality of animals. Hence, our understanding of how high severity fire affects animal mortality is particularly limited. Despite megafires being of growing conservation concern globally (Wintle et al., 2020), we found only one study documenting the impacts of megafire on animal mortality rates (i.e. Banks et al., 2012). Our overall finding was that a surprisingly low proportion of animals were killed directly by fire (3% on average)—although a higher proportion of animals died during studies of high severity fires (7% on average). That such low proportions of animals were killed in the fires considered in the studies we compiled does not necessarily mean that some fires, especially fires of high severity and large extent, do not kill many animals. Indeed, a recent study based on systematic counts of burnt corpses indicates that millions of vertebrate animals were killed in a ~40,000 km^2 area exposed to fires in the Pantanal, South America (Tomas et al., 2021).

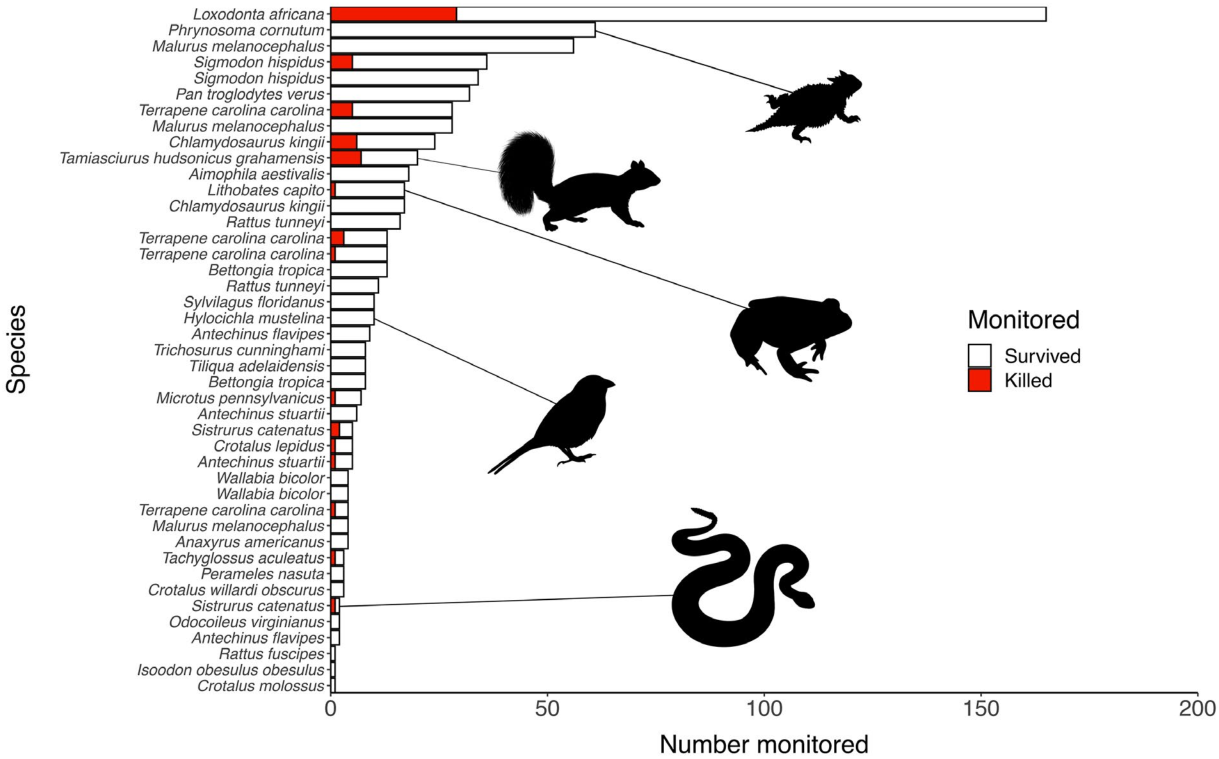

FIGURE 5 Direct effects of fire on the mortality of wildlife showing proportion killed by fire in each instance. Species that appear multiple times reflect multiple studies, or multiple instances, where the direct impact of fire was observed [Colour figure can be viewed at wileyonlinelibrary.com]

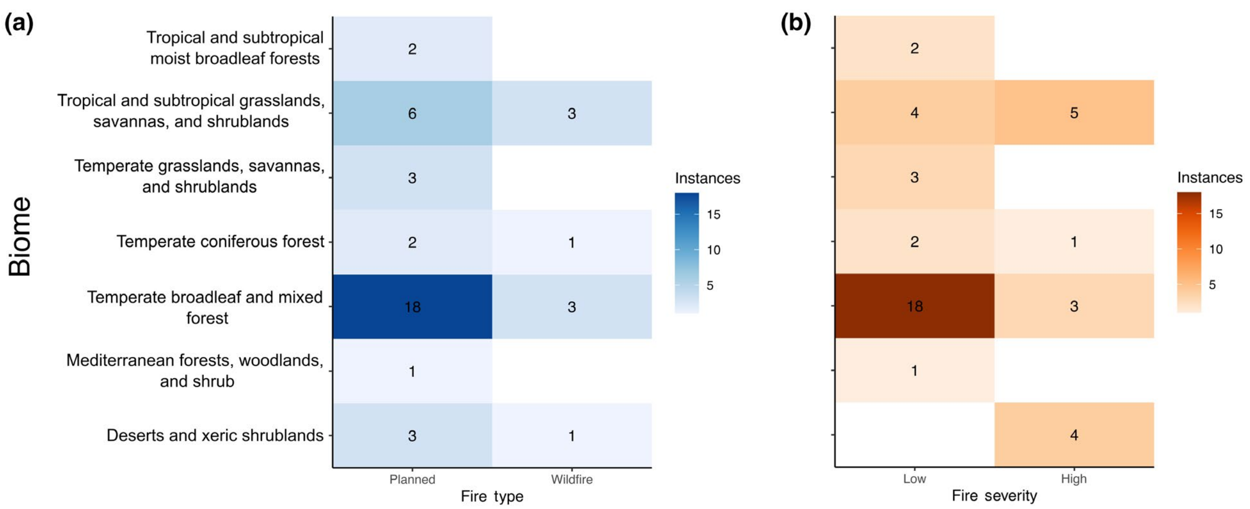

FIGURE 6 Counts of the number of instances (a) a fire type (planned or wildfires) and (b) a fire severity (low or high) was studied in each biome. Biomes are taken from Olson et al. (2001) [Colour figure can be viewed at wileyonlinelibrary.com]

Studies of the direct impacts of fire on animal mortality tended to be characterized by small sample sizes (i.e. across all studies, 53% of instances tracked fewer than 10 animals), a geographic bias towards North America and Australia, and a taxonomic bias towards mammals and reptiles. While, to some extent, the geographic and taxonomic biases reflect biases throughout the ecological literature (Di Marco et al., 2017; Troudet et al., 2017) and the geographic bias may be due, in part, to our filtering of studies published in English, it may also be a result of the financial cost, labour-intensiveness and logistical difficulties inherent in tracking the movements and survival of individual animals in the wild using very high frequency (VHF) and Global Positioning System (GPS) technology. The taxonomic bias away from birds, amphibians and invertebrates may be explained by their generally small body size requiring often impractically small

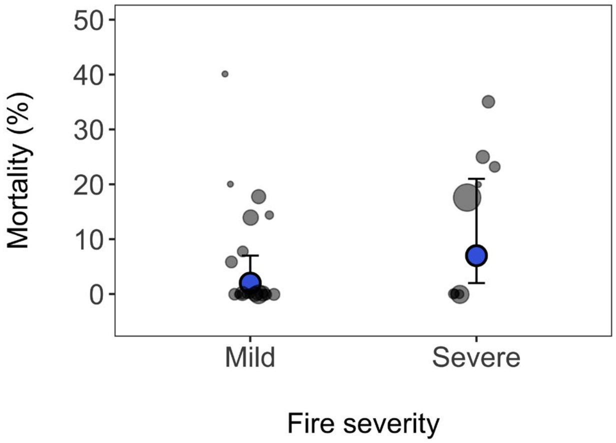

FIGURE 7 Mean predicted mortality (95% CI) of wildlife exposed to low and high severity fires (blue). Only studies that monitored five or more individuals through the passage of fire were included. Black dots represent observed direct effects of fire on animal mortality, with size of circle representing the number of animals monitored [Colour figure can be viewed at wileyonlinelibrary.com]

and prohibitively expensive transmitters. Encouragingly, this field of animal monitoring is rapidly growing and technological innovation is expected to progressively reduces tag weights and costs (Nimmo et al., 2019; Sergio et al., 2019). This could allow a rapid increase in our understanding of animal movement and survival through the passage of fire (Nimmo et al., 2019).

Many animal species that inhabit fire-prone ecosystems have evolved a range of adaptations for detecting and responding to fire, and such adaptations can reduce mortality (Nimmo et al., 2021; Pausas & Parr, 2018). Our study suggests that these adaptations are deployed highly effectively, at least in response to low severity fires. Some animals can detect the cues of incipient fire (e.g. Álvarez-Ruiz et al., 2021; Doty et al., 2018; Grafe et al., 2002; Nowack et al., 2018) and enact responses to reduce the risk of being consumed by the flames (Nimmo et al., 2021). Pausas and Parr (2018) identified a range of "fire response strategies" that enhance survival during fire, including rapid refuge seeking. Some of these behaviours are evident in the papers reviewed. For example, swamp wallabies (*Wallabia bicolor*) and savanna chimpanzees (*Pan troglodytes verus*) 'double back' through the fire front to shelter in areas that have already burned (Garvey et al., 2010; Pruetz & Herzog, 2017), while brown antechinus (*Antechinus stuartii*) 'shelter in place' in non-flammable refuges and enter torpor to reduce their need for limited resources in the depauperate and dangerous post-fire landscape (Stawski et al., 2015).

Although we found substantially higher mortality rates in relation to high severity fire, even here <10% of monitored animals died during fire, suggesting fire-avoidance behaviours can confer survival even during high severity events. However, we caution that 'high severity' fire was classified by the authors of the reviewed studies and may encompass the outcomes of a broad range of fire behaviours, from late dry season grassfires, relatively slow-moving crown fires to pyro-cumulonimbus storms that spread rapidly for tens of kilometres (Dowdy et al., 2017). The variability in mortality within our high severity class is likely to be significant, and we are almost entirely without quantification of the mortality toll of extreme severity fires, such as megafires. Yet, the single example that we do have, again reinforces the capacity of animals to survive even extreme fire behaviour. In 2009, Banks et al. (2012) attached transmitters to eight mountain brushtail possums (*Trichosurus cunninghami*) prior to the unanticipated 'Black Saturday' megafires in Victoria, Australia (Cruz et al., 2012). Despite the extreme severity of this uncontrolled wildfire, no direct mortality of possums was recorded in this study. Presumably, possums avoided fire-driven mortality by sheltering in deep tree hollows that reduced their exposure to extreme heat.

Our findings come with some important caveats. First, we have not attempted to quantify the full mortality toll of fire on animal populations, which requires consideration of both the direct and indirect effects of fire. While many animals may survive the passage of fire, some may sustain severe burns that reduce their subsequent fitness. Furthermore, the post-fire environment presents novel challenges that may have significant effects on the persistence of local populations (e.g. Leahy et al., 2015; Shaw et al., 2021). For example, although most American hispid cotton rats (*Sigmodon hispidus*) survived the passage of fire, most of the monitored populations fled to nearby unburnt plots, and those that did not flee suffered increased predation pressure in the burnt plots (Conner et al., 2011; Morris et al., 2011). Similarly, although all monitored pale field-rats (*Rattus tunneyi*) survived the passage of both low and high severity experimental burns in northern Australia, mortality due to predation increased after fire, probably due to loss of groundcover (Leahy et al., 2015). Furthermore, reduced resource and shelter availability post-fire can reduce animal body condition (Fenner & Bull, 2007), potentially increasing their vulnerability to predation. While this review documented immediate direct mortality effects of fire on wildlife, there is a need for quantification and exploration of subsequent and indirect effects of fire on animal survival, both positive and negative.

Second, small sample size is a limitation of our data—both the number of studies and the sample sizes within these studies. The current lack of available data on direct mortality from fire means that we found very few studies where large numbers of animals were impacted, but such events do occur (e.g. in a herd of 165 endangered African bush elephants, 29 (18%) died as a direct result of an uncontrolled wildfire in South Africa [Woolley et al., 2008]). A greater emphasis on collecting such data in future will allow scientists to better understand the factors that shape both large mortality events and the contexts and mechanisms that allow wildlife to survive fire.

Finally, both the direct and indirect impacts of fire on animal populations need to be considered within the broader context in which the event occurs. Climate change is rapidly altering global fire regimes (Bowman et al., 2020), resulting in increased wildfire frequency and intensity (Di Virgilio et al., 2019; Duane et al., 2021; Jolly et al., 2015; Wu et al., 2021). While individual fires may not cause significant mortality in fire-adapted species, changes in the fire regime, combined with other threats, may well add to the tapestry of threats that species face (Banks et al., 2011; Geary et al., 2019; Moir, 2021).

4.2 | Knowledge gaps and future research

There is an urgent need to understand the effects of high severity fire on animal populations. Our study underscores how little we know about the direct effects of fire on animal mortality rates. This knowledge gap limits our ability to understand fire as an evolutionary force and to assess the conservation consequences of population-level impacts of increasingly large and severe fires on vulnerable species. While it would be relatively straightforward to increase our understanding of the impacts of planned fire on wildlife, it is far more difficult to monitor the effects of large, unpredictable and uncontrolled wildfires on animals. The most obvious way to approach filling this knowledge gap would be to drastically increase the tracking of native wildlife, particularly in areas and times of severe wildfire danger. Addressing this gap will require ecologists working closely with fire managers to track the fate of animals from a broader array of taxonomic groups and geographic areas through the passage of fire, and months following fire. This is likely to be aided by advances in the technology for tracking animals, making the task cheaper and less logistically challenging (Cooke et al., 2004; Kays et al., 2015).

Future research hoping to advance our understanding of the direct effects of fire on animal survival would benefit from following a consistent and repeatable approach to monitoring animal survival during fire (e.g. see Geary et al., 2020). We found that fire severity affected animal survival during fire, but we predict that, with a greater number of studies encompassing a broader array of taxonomic groups, life histories and regions, more variables will be found to influence animal survival (see Figure 1). Animal survival during fire is likely exceptionally complex and context dependent, however, there are likely broad proximate and distal drivers that affect outcomes for individuals during fire (Figure 1). Environmental variables, such as resource and refuge availability and fuel conditions are likely to be strong proximate and distal drivers of animal survival during fire. For example, refuge availability may directly improve animal survival by providing unburnt refugia at various spatial scales that simply allows animals to avoid fire (Robinson et al., 2013), while large, continuous loads of dry fuel may indirectly reduce animal survival by stoking higher severity fires (Pausas & Keeley, 2021).

We found that fire severity had a strong influence on animal survival during fire, however, it is possible that the effects of fire behaviour on animal survival are more nuanced than what we detected. Factors, such as fire season (prevailing weather conditions), intensity (burn temperature), speed (driven by wind) and size (driven by distribution of fuel) likely affect the survival of animals during fire, and could easily be incorporated into future models to test their effects (Figure 1).

The relationship between animal traits and survival during fire can be divided into individual and species traits (Figure 1). Although there is very little empirical research demonstrating that survival during fire is influenced by individual traits, such as age, satiation, reproductive status, physiological condition, prior experience, and individual differences in innate fire avoidance behaviours (e.g. Álvarez-Ruiz et al., 2021), we predict that these factors could strongly modulate the outcomes for individuals (see Nimmo et al., 2021). Measuring how these differences affect survival in the field will be difficult and would require sampling large numbers of individuals, and may be most meaningfully measured in tightly controlled manipulative experiments. Species traits, however, such as mobility, size, ecological attributes, evolutionary exposure to fire, and adaptation to local fire regimes, likely have a strong influence on whether individuals survive during (Nimmo et al., 2021; Pausas & Parr, 2018). When sufficient data become available, these traits could quite easily be included as variables in future analyses to assess their effect on survival. Although we assessed the effects of some of these species traits and found they had no effect on mortality, we anticipate that they may become important with a larger dataset.

We hope our conceptual framework outlining the variables that likely influence the outcomes for individuals during fire may be leveraged to improve the design of observational and experimental studies aimed at filling these gaps in our understanding of the direct effects of fire on animal survival.

5 | CONCLUSIONS

Although we have much to learn about animal mortality rates during fire, the evidence suggests that most animals survive their direct effects, particularly during low severity fires. As such, management actions that address the challenges faced by animals in the post-fire landscape could be extremely valuable in reducing the longer term, indirect impacts felt by animal populations in the weeks, months and years following a fire event. Put simply, all is not lost after a fire—many animals survive, providing opportunity for conservation intervention aimed at reducing post-fire mortality. Efforts that reduce post-fire predation pressure, such as the addition of artificial refuges to the landscape (e.g. Bleicher & Dickman, 2020) and targeted invasive predator control (Geary et al., 2021), and those that replace resources consumed by fire, such as supplemental food and water stations and nest boxes, could be leveraged to reduce the vulnerability of populations of threatened species following high severity wildfires.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and methodology for the paper. C.J.J. reviewed the literature, collected data and performed the data analysis. C.J.J. and D.G.N. led the writing of the manuscript with contributions from all authors. All authors gave final approval for publication and agree to be accountable for the content.

DATA AVAILABILITY STATEMENT

Data are available through Zenodo (https://doi.org/10.5281/zenodo.5030560).

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REFERENCES

Álvarez-Ruiz, L., Belliure, J., & Pausas, J. G. (2021). Fire-driven behavioral response to smoke in a Mediterranean lizard. *Behavioral Ecology*, *32*(4), 662–667. https://doi.org/10.1093/beheco/arab010

Banks, S. C., Blyton, M. D. J., Blair, D., McBurney, L., & Lindenmayer, D. B. (2012). Adaptive responses and disruptive effects: How major wildfire influences kinship-based social interactions in a forest marsupial. *Molecular Ecology*, *21*(3), 673–684. https://doi.org/10.1111/j.1365-294X.2011.05282.x

Banks, S. C., Knight, E. J., McBurney, L., Blair, D., & Lindenmayer, D. B. (2011). The effects of wildfire on mortality and resources for an arboreal marsupial: Resilience to fire events but susceptibility to fire regime change. *PLoS ONE*, *6*(8), e22952. https://doi.org/10.1371/journal.pone.0022952

Banks, S. C., McBurney, L., Blair, D., Davies, I. D., & Lindenmayer, D. B. (2017). Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. *Ecography*, *40*(11), 1325–1338. https://doi.org/10.1111/ecog.02251

Barlow, J., Berenguer, E., Carmenta, R., & França, F. (2020). Clarifying Amazonia's burning crisis. *Global Change Biology*, *26*(2), 319–321. https://doi.org/10.1111/gcb.14872

Bates, D., Sarkar, D., Bates, M. D., & Matrix, L. (2007). The lme4 package. *R Package Version*, *2*(1), 1–29.

Bleicher, S. S., & Dickman, C. R. (2020). On the landscape of fear: Shelters affect foraging by dunnarts (Marsupialia, *Sminthopsis* spp.) in a sandridge desert environment. *Journal of Mammalogy*, *101*(1), 281–290. https://doi.org/10.1093/jmammal/gyz195

Boer, M. M., de Dios, V. R., & Bradstock, R. A. (2020). Unprecedented burn area of Australian mega forest fires. *Nature Climate Change*, *10*(3), 170–172. https://doi.org/10.1038/s41558-020-0710-7

Bond, W., & Keeley, J. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*(7), 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the earth system. *Science*, *324*(5926), 481–484. https://doi.org/10.1126/science.1163886

Bowman, D. M. J. S., Kolden, C. A., Abatzoglou, J. T., Johnston, F. H., van der Werf, G. R., & Flannigan, M. (2020). Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*, *1*(10), 500–515. https://doi.org/10.1038/s43017-020-0085-3

Conner, L. M., Castleberry, S. B., & Derrick, A. M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *Journal of Wildlife Management*, *75*(4), 938–944. https://doi.org/10.1002/jwmg.110

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., & Butler, P. J. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology & Evolution*, *19*(6), 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Cruz, M. G., Sullivan, A. L., Gould, J. S., Sims, N. C., Bannister, A. J., Hollis, J. J., & Hurley, R. J. (2012). Anatomy of a catastrophic wildfire: The Black Saturday Kilmore East fire in Victoria, Australia. *Forest Ecology and Management*, *284*, 269–285. https://doi.org/10.1016/j.foreco.2012.02.035

Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., Maina, J. M., Possingham, H. P., Rogalla von Bieberstein, K., Venter, O., & Watson, J. E. M. (2017). Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation*, *10*, 32–42. https://doi.org/10.1016/j.gecco.2017.01.008

Di Virgilio, G., Evans, J. P., Blake, S. A. P., Armstrong, M., Dowdy, A. J., Sharples, J., & McRae, R. (2019). Climate change increases the potential for extreme wildfires. *Geophysical Research Letters*, *46*(14), 8517–8526. https://doi.org/10.1029/2019GL083699

Doty, A. C., Currie, S. E., Stawski, C., & Geiser, F. (2018). Can bats sense smoke during deep torpor? *Physiology & Behavior*, *185*, 31–38. https://doi.org/10.1016/j.physbeh.2017.12.019

Dowdy, A. J., Fromm, M. D., & McCarthy, N. (2017). Pyrocumulonimbus lightning and fire ignition on Black Saturday in southeast Australia. *Journal of Geophysical Research: Atmospheres*, *122*(14), 7342–7354. https://doi.org/10.1002/2017JD026577

Duane, A., Castellnou, M., & Brotons, L. (2021). Towards a comprehensive look at global drivers of novel extreme wildfire events. *Climatic Change*, *165*. 43. https://doi.org/10.1007/s10584-021-03066-4

Engstrom, R. T. (2010). First-order fire effects on animals: Review and recommendations. *Fire Ecology*, *6*(1), 115–130. https://doi.org/10.4996/fireecology.0601115

Escobar, H. (2019). Amazon fires clearly linked to deforestation, scientists say. *Science*, *365*(6456), 853. https://doi.org/10.1126/science.365.6456.853

Fenner, A. L., & Bull, C. M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology*, *272*(4), 444–450. https://doi.org/10.1111/j.1469-7998.2007.00287.x

Forkel, M., Andela, N., Harrison, S. P., Lasslop, G., van Marle, M., Chuvieco, E., Dorigo, W., Forrest, M., Hantson, S., Heil, A., Li, F., Melton, J., Sitch, S., Yue, C., & Arneth, A. (2019). Emergent relationships with respect to burned area in global satellite observations and fire-enabled vegetation models. *Biogeosciences*, *16*(1), 57–76. https://doi.org/10.5194/bg-16-57-2019

Garvey, N., Ben-Ami, D., Ramp, D., & Croft, D. B. (2010). Survival behaviour of swamp wallabies during prescribed burning and wildfire. *Wildlife Research*, *37*(1), 1–12. https://doi.org/10.1071/WR08029

Geary, W. L., Buchan, A., Allen, T., Attard, D., Bruce, M. J., Collins, L., Ecker, T. E., Fairman, T. A., Hollings, T., Loeffler, E., Muscatello, A., Parkes, D., Thomson, J., White, M., & Kelly, E. (2021). Responding to the biodiversity impacts of a megafire: A case study from south-eastern Australia's Black Summer. *Diversity and Distributions*, ddi.13292. https://doi.org/10.1111/ddi.13292

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T., & Ritchie, E. G. (2020). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology*, *89*(4), 955–971. https://doi.org/10.1111/1365-2656.13153

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., & Tulloch, A. I. T. (2019). Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *Journal of Applied Ecology*, *56*(8), 1992–1997. https://doi.org/10.1111/1365-2664.13427

Giglio, L. (2013). *MODIS collection 5 active fire product user's guide. Version 2.5*. Department of Geographical Sciences, University of Maryland.

Grafe, T. U., Döbler, S., & Linsenmair, K. E. (2002). Frogs flee from the sound of fire. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1495), 999–1003. https://doi.org/10.1098/rspb.2002.1974

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*(6), 1983–2010. https://doi.org/10.1111/brv.12544

Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., & Bowman, D. M. J. S. (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, *6*(1), 7537. https://doi.org/10.1038/ncomms8537

Karl, T. R., & Trenberth, K. E. (2003). Modern global climate change. *Science*, *302*(5651), 1719–1723. https://doi.org/10.1126/science.1090228

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, *18*(1), 116–126. https://doi.org/10.1071/WF07049

Kelly, L. T., Giljohann, K. M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A. F., Buckland, S. T., Canelles, Q., Clarke, M. F., Fortin, M.-J., Hermoso, V., Herrando, S., Keane, R. E., Lake, F. K., McCarthy, M. A., Morán-Ordóñez, A., Parr, C. L., Pausas, J. G., … Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science*, *370*(6519), eabb0355. https://doi.org/10.1126/science.abb0355

Lajeunesse, M. J. (2016). Facilitating systematic reviews, data extraction and meta-analysis with the METAGEAR package for R. *Methods in Ecology and Evolution*, *7*(3), 323–330. https://doi.org/10.1111/2041-210X.12472

Leahy, L., Legge, S. M., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., & Johnson, C. N. (2015). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research*, *42*(8), 705. https://doi.org/10.1071/WR15011

Legge, S., Woinarski, J., Garnett, S., Nimmo, D., Scheele, B., Lintermans, M., Mitchell, N., Whiterod, N., & Ferris, J. (2020). Rapid analysis of impacts of the 2019–20 fires on animal species, and prioritisation of species for management response. (Report Prepared for the Wildlife and Threatened Species Bushfire Recovery Expert Panel 14 March 2020, p. 30).

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

Moir, M. L. (2021). Coextinction of *Pseudococcus markharveyi* (Hemiptera: Pseudococcidae): A case study in the modern insect extinction crisis. *Austral Entomology*, *60*(1), 89–97. https://doi.org/10.1111/aen.12506

Morris, G., Hostetler, J. A., Mike Conner, L., & Oli, M. K. (2011). Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations. *Oecologia*, *167*(4), 1005–1016. https://doi.org/10.1007/s00442-011-2053-6

Murphy, S. A., Legge, S. M., Heathcote, J., & Mulder, E. (2010). The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research*, *37*(2), 145–155. https://doi.org/10.1071/WR09007

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., … Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, *94*(3), 981–998. https://doi.org/10.1111/brv.12486

Nimmo, D. G., Carthey, A. J. R., Jolly, C. J., & Blumstein, D. T. (2021). Welcome to the Pyrocene: Animal survival in the age of megafire. *Global Change Biology*, *27*(22), 5684–5693. https://doi.org/10.1111/gcb.15834

Nolan, R. H., Boer, M. M., Collins, L., Resco de Dios, V., Clarke, H., Jenkins, M., Kenny, B., & Bradstock, R. A. (2020). Causes and consequences of eastern Australia's 2019–20 season of mega-fires. *Global Change Biology*, *26*(3), 1039–1041. https://doi.org/10.1111/gcb.14987

Nowack, J., Stawski, C., Körtner, G., & Geiser, F. (2018). Physiological and behavioral responses of an arboreal mammal to smoke and charcoal-ash substrate. *Physiology & Behavior*, *184*, 116–121. https://doi.org/10.1016/j.physbeh.2017.11.020

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the World: A new map of Life on Earth. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Parr, C. L., & Andersen, A. N. (2006). Patch mosaic burning for biodiversity conservation: A critique of the pyrodiversity paradigm. *Conservation Biology*, *20*(6), 1610–1619. https://doi.org/10.1111/j.1523-1739.2006.00492.x

Pausas, J. G., & Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience*, *59*(7), 593–601. https://doi.org/10.1525/bio.2009.59.7.10

Pausas, J. G., & Keeley, J. E. (2021). Wildfires and global change. *Frontiers in Ecology and the Environment*, *19*(7), 387–395. https://doi.org/10.1002/fee.2359

Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, *32*(2–3), 113–125. https://doi.org/10.1007/s10682-018-9927-6

Pausas, J. G., & Ribeiro, E. (2017). Fire and plant diversity at the global scale. *Global Ecology and Biogeography*, *26*(8), 889–897. https://doi.org/10.1111/geb.12596

Pruetz, J. D., & Herzog, N. M. (2017). Savanna chimpanzees at Fongoli, Senegal, navigate a fire landscape. *Current Anthropology*, *58*(S16), S337–S350. https://doi.org/10.1086/692112

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Robinson, N. M., Leonard, S. W. J., Ritchie, E. G., Bassett, M., Chia, E. K., Buckingham, S., Gibb, H., Bennett, A. F., & Clarke, M. F. (2013). REVIEW: Refuges for fauna in fire-prone landscapes: Their ecological function and importance. *Journal of Applied Ecology*, *50*(6), 1321–1329. https://doi.org/10.1111/1365-2664.12153

Sergio, F., Tanferna, A., Blas, J., Blanco, G., & Hiraldo, F. (2019). Reliable methods for identifying animal deaths in GPS - and satellite-tracking data: Review, testing, and calibration. *Journal of Applied Ecology*, *56*(3), 562–572. https://doi.org/10.1111/1365-2664.13294

Shaw, R. E., James, A. I., Tuft, K., Legge, S., Cary, G. J., Peakall, R., & Banks, S. C. (2021). Unburnt habitat patches are critical for survival and in situ population recovery in a small mammal after fire. *Journal of Applied Ecology*, *58*(6), 1325–1335. https://doi.org/10.1111/1365-2664.13846

Sommer, N. R., Moody, N. M., Lantz, S. M., Leu, M., Karubian, J., & Swaddle, J. P. (2018). Red-backed fairywrens adjust habitat use in response to dry season fires. *Austral Ecology*, *43*(8), 876–889. https://doi.org/10.1111/aec.12629

Stawski, C., Matthews, J. K., Körtner, G., & Geiser, F. (2015). Physiological and behavioural responses of a small heterothermic mammal to fire stimuli. *Physiology & Behavior*, *151*, 617–622. https://doi.org/10.1016/j.physbeh.2015.09.002

Stephens, S. L., Burrows, N., Buyantuyev, A., Gray, R. W., Keane, R. E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K. G., & van Wagtendonk, J. W. (2014). Temperate and boreal forest mega-fires: Characteristics and challenges. *Frontiers in Ecology and the Environment*, *12*(2), 115–122. https://doi.org/10.1890/120332

Tomas, W. M., Berlinck, C. N., Chiaravalloti, R. M., Faggioni, G. P., Strussmann, C., Libonati, R., Abrahão, C. R., Alvarenga, G. D. V., Bacellar, A. E. D. F., Batista, F. R. D. Q., Bornato, T. S., Camilo, A. R., Castedo, J., Fernando, A. M. E., de Freitas, G. O., Garcia, C. M., Gonçalves, H. S., Guilherme, M. B. D. F., Layme, V. M. G. & Morato, R. (2021). Counting the dead: 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal Wetland, Brazil [Preprint]. In Review. https://doi.org/10.21203/rs.3.rs-859794/v1

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, *7*(1), 9132. https://doi.org/10.1038/s41598-017-09084-6

van Eeden, L. M., Nimmo, D. G., Herman, K., Ehmke, G., Driessen, J., O'Connor, J., Bino, G., Taylor, M., & Dickman, C. R. (2020). *Impacts of the unprecedented 2019–2020 bushfires on Australian animals*. Report prepared for WWF-Australia, Ultimo NSW. https://www.wwf.org.au/ArticleDocuments/353/WWF_Impacts-of-the-unprecedented-2019-2020-bushfires-on-Australian-animals.pdf.aspx

Ward, M., Tulloch, A. I. T., Radford, J. Q., Williams, B. A., Reside, A. E., Macdonald, S. L., Mayfield, H. J., Maron, M., Possingham, H. P., Vine, S. J., O'Connor, J. L., Massingham, E. J., Greenville, A. C., Woinarski, J. C. Z., Garnett, S. T., Lintermans, M., Scheele, B. C., Carwardine, J., Nimmo, D. G., … Watson, J. E. M. (2020). Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nature Ecology & Evolution*, *4*(10), 1321–1326. https://doi.org/10.1038/s41559-020-1251-1

Whelan, R. J., Rodgerson, L., Dickman, C. R., & Sutherland, E. F. (2002). Critical life cycles of plants and animals: Developing a process-based understanding of population changes in fire-prone landscapes. In R. A. Bradstock, J. E. Williams, & A. M. Gill (Eds.), *Flammable Australia: The fire regimes and biodiversity of a continent* (pp. 94–124). Cambridge University Press.

Wintle, B. A., Legge, S., & Woinarski, J. C. Z. (2020). After the megafires: What next for Australian wildlife? *Trends in Ecology & Evolution*, *35*(9), 753–757. https://doi.org/10.1016/j.tree.2020.06.009

Woolley, L.-A., Millspaugh, J. J., Woods, R. J., Janse van Rensburg, S., Mackey, R. L., Page, B., & Slotow, R. (2008). Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE*, *3*(9), e3233. https://doi.org/10.1371/journal.pone.0003233

Wu, C., Venevsky, S., Sitch, S., Mercado, L. M., Huntingford, C., & Staver, A. C. (2021). Historical and future global burned area with changing climate and human demography. *One Earth*, *4*(4), 517–530. https://doi.org/10.1016/j.oneear.2021.03.002

DATA SOURCES

Banks, S. C., Blyton, M. D. J., Blair, D., McBurney, L., & Lindenmayer, D. B. (2012). Adaptive responses and disruptive effects: How major wildfire influences kinship-based social interactions in a forest marsupial. *Molecular Ecology*, *21*(3), 673–684. https://doi.org/10.1111/j.1365-294X.2011.05282.x

Bond, B. T., Burger, L. W., Leopold, B. D., Godwin, K. D., & Jones, J. C. (2002). Short-term response of eastern cottontails to prescribed fire in east-central Mississippi. *Proceedings of the Fifty-Sixth Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *56*, 187–197.

Conner, L. M., Castleberry, S. B., & Derrick, A. M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *Journal of Wildlife Management*, *75*(4), 938–944. https://doi.org/10.1002/jwmg.110

Cross, M. D., Root, K. V., Mehne, C. J., McGowan-Stinski, J., Pearsall, D., & Gillingham, J. C. (2015). Multi-scale responses of eastern massasauga rattlesnakes (*Sistrurus catenatus*) to prescribed fire. *The American Midland Naturalist*, *173*(2), 346–362. https://doi.org/10.1674/amid-173-02-346-362.1

Durbian, F. E. (2006). Effects of mowing and summer burning on the massasauga (*Sistrurus catenatus*). *The American Midland Naturalist*, *155*(2), 329–334. https://doi.org/10.1674/0003-0031(2006)155[329:EOMASB]2.0.CO;2

Fenner, A. L., & Bull, C. M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology*, *272*(4), 444–450. https://doi.org/10.1111/j.1469-7998.2007.00287.x

Flanagan-Moodie, A. K., Holland, G. J., Clarke, M. F., & Bennett, A. F. (2018). Prescribed burning reduces the abundance of den sites for a hollow-using mammal in a dry forest ecosystem. *Forest Ecology and Management*, *429*, 233–243. https://doi.org/10.1016/j.foreco.2018.07.023

Garvey, N., Ben-Ami, D., Ramp, D., & Croft, D. B. (2010). Survival behaviour of swamp wallabies during prescribed burning and wildfire. *Wildlife Research*, *37*(1), 1–12. https://doi.org/10.1071/WR08029

Geluso, K. N., & Bragg, T. B. (1986). Fire-Avoidance Behavior of Meadow Voles (*Microtus pennsylvanicus*). *American Midland Naturalist*, *116*(1), 202–205. https://doi.org/10.2307/2425953

Griffiths, A. D., & Christian, K. A. (1996). The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology*, *21*(4), 386–398. https://doi.org/10.1111/j.1442-9993.1996.tb00625.x

Harris, K. A., Clark, J. D., Elmore, R. D., & Harper, C. A. (2020). Direct and indirect effects of fire on eastern box turtles. *The Journal of Wildlife Management*, *84*(7), 1384–1395. https://doi.org/10.1002/jwmg.21920

Hellgren, E. C., Burrow, A. L., Kazmaier, R. T., & Ruthven, D. C. (2010). The effects of winter burning and grazing on resources and survival of Texas horned lizards in a thornscrub ecosystem. *Journal of Wildlife Management*, *74*(2), 300–309. https://doi.org/10.2193/2009-090

Hope, B. (2012). Short-term response of the long-nosed bandicoot, *Perameles nasuta*, and the southern brown bandicoot, *Isoodon obesulus obesulus*, to low-intensity prescribed fire in heathland vegetation. *Wildlife Research*, *39*(8), 731–744. https://doi.org/10.1071/WR12110

Humphries, W. J., & Sisson, M. A. (2012). Long distance migrations, landscape use, and vulnerability to prescribed fire of the gopher frog (*Lithobates capito*). *Journal of Herpetology*, *46*(4), 665–670. https://doi.org/10.1670/11-124

Ivey, T. L., & Causey, M. K. (1984). Response of white-tailed deer to prescribed fire. *Wildlife Society Bulletin*, *12*(2), 138–141. https://www.jstor.org/stable/3781603

Koprowski, J. L., Leonard, K. M., Zugmeyer, C. A., & Jolley, J. L. (2006). Direct effects of fire on endangered Mount Graham red squirrels. *The Southwestern Naturalist*, *51*(1), 59–63. https://doi.org/10.1894/0038-4909(2006)51[59:DEOFOE]2.0.CO;2

Leahy, L., Legge, S. M., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., & Johnson, C. N. (2015). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research*, *42*(8), 705–716. https://doi.org/10.1071/WR15011

Melvin, T. A., & Roloff, G. J. (2018). Reliability of postfire surveys for eastern box turtles. *Wildlife Society Bulletin*, *42*(3), 498–503. https://doi.org/10.1002/wsb.911

Morris, G., Hostetler, J. A., Mike Conner, L., & Oli, M. K. (2011). Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations. *Oecologia*, *167*(4), 1005–1016. https://doi.org/10.1007/s00442-011-2053-6

Murphy, S. A., Legge, S. M., Heathcote, J., & Mulder, E. (2010). The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research*, *37*(2), 145–155. https://doi.org/10.1071/WR09007

Nowack, J., Cooper, C. E., & Geiser, F. (2016). Cool echidnas survive the fire. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828), 20160382. https://doi.org/10.1098/rspb.2016.0382

Pitt, A. L., Tavano, J. J., Baldwin, R. F., & Waldrop, T. A. (2013). Effects of fuel reduction treatments on movement and habitat use of American toads in a southern Appalachian hardwood forest. *Forest Ecology and Management*, *310*, 289–299. https://doi.org/10.1016/j.foreco.2013.08.032

Powell, L. A., Lang, J. D., Conroy, M. J., & Krementz, D. G. (2000). Effects of forest management on density, survival, and population growth of wood thrushes. *The Journal of Wildlife Management*, *64*(1), 11. https://doi.org/10.2307/3802970

Pruetz, J. D., & Herzog, N. M. (2017). Savanna chimpanzees at Fongoli, Senegal, navigate a fire landscape. *Current Anthropology*, *58*(S16), S337–S350. https://doi.org/10.1086/692112

Seaman, B. D., & Krementz, D. G. (2000). Movements and survival of Bachman's sparrows in response to prescribed summer burns in South Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *54*, 227–240.

Smith, L. J., Holycross, A. T., Painter, C. W., & Douglas, M. E. (2001). Montane rattlesnakes and prescribed fire. *The Southwestern Naturalist*, *46*(1), 54–61. https://doi.org/10.2307/3672373
Sommer, N. R., Moody, N. M., Lantz, S. M., Leu, M., Karubian, J., & Swaddle, J. P. (2018). Red-backed fairywrens adjust habitat use in response to dry season fires. *Austral Ecology*, *43*(8), 876–889. https://doi.org/10.1111/aec.12629
Stawski, C., Körtner, G., Nowack, J., & Geiser, F. (2015). The importance of mammalian torpor for survival in a post-fire landscape. *Biology Letters*, *11*(6), 20150134. https://doi.org/10.1098/rsbl.2015.0134
Sutherland, E. F. (1998). *Fire, resource limitation and small mammal populations in coastal eucalypt forest* (PhD thesis). University of Sydney.
Vernes, K. (2000). Immediate effects of fire on survivorship of the northern bettong (*Bettongia tropica*): An endangered Australian marsupial. *Biological Conservation*, *96*, 305–309. https://doi.org/10.1016/S0006-3207(00)00086-0
Woolley, L.-A., Millspaugh, J. J., Woods, R. J., Janse van Rensburg, S., Mackey, R. L., Page, B., & Slotow, R. (2008). Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE*, *3*(9), e3233. https://doi.org/10.1371/journal.pone.0003233

SUPPORTING INFORMATION

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