Megafire: the Darwinian guillotine?

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ABSTRACT

Southern Australia's 2019–20 wildfire season was unprecedented, but the ecological toll remains poorly understood. Estimates of three billion animals being affected by the fires attracted global attention, but how many of those animals succumbed to the flames? A recent systematic review of fire-induced mortality showed that a surprisingly high proportion of vertebrates typically survive fire (>90%), and a growing body of research is demonstrating behavioural adaptations that might facilitate survival during fire. Behaviours that favour survival are likely to be selected for in fire-prone landscapes and could be fine-tuned over time in relation to fire behaviour and specific fire regimes. Megafires that burn vast areas could act as mass selection events, rapidly filtering 'fire-naive' individuals from populations. Applying an evolutionary and behavioural lens to fire ecology will provide novel insights that help predict the ramifications of changing fire regimes on animal species.

Key words: Australia, behavioural ecology, mortality, movement ecology, wildfire, wildlife

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Introduction

"Unprecedented". Not just unusual. More than extreme. Never recorded in history. During southern Australia's 2019–20 fire "season from hell" (Wintle *et al.* 2020), "unprecedented" was the word of the day. Yet any notion that the term's use was hyperbolic was promptly razed. The megafires were fanned by unprecedented climatic conditions–Australia's hottest and driest years on record (Abram *et al.* 2021). The fires burned an unprecedented area of a continental forest biome (~12 M ha; Boer *et al.* 2020; Wintle *et al.* 2020), and broke records for their radiative power (Abram *et al.* 2021), a measure of fire intensity (Keeley 2009), and included an unprecedented number of pyroconvective storms (Kablick III *et al.* 2020). These intense fires left an unprecedented area burnt at high severity (1.8 M ha; Collins *et al.* 2021), and the smoke from the fires blanketed cities for weeks and months, bringing about an unprecedented public health burden (Borchers Arriagada *et al.* 2020).

As the magnitude of the fires became evident, attention quickly turned to the potential ecological toll. In terms of wildlife, the first assessments revealed that > 800 vertebrate species potentially lay in the path of the fires (Ward *et al.* 2020), including 21 threatened species, and some species, such as Kate's leaf-tailed gecko (*Saltuarius kateae*), that had their entire geographic range burnt (Legge *et al.* 2021).

But it was not estimates of the number of species affected by the wildfires that seemed to attract the most attention, but rather, the number of individual animals. In January 2020, Professor Chris Dickman's estimate that half a billion animals (specifically, birds, mammals, and reptiles) had been affected by the fires drew global attention. But the fires were still spreading, and so the number grew, reaching 1 billion by the fire season's end. The estimates were admittedly back-of-the-envelope. Some ecologists wondered: why such interest in estimating the number of animals in the fire's path? Many of the individuals would be of common species of no conservation concern, and hence the number had little relevance to conservation. But the number serves more as a communication tool than a direct input to conservation. The extent of fires can be measured and communicated in km^2, acres, and hectares, but putting such figures in perspective often requires a benchmark. For instance, x number of football fields. Even then, it is difficult to imagine what 12 million football fields of burned forest looks like, or what it means for the forest's biota. Moving from area to the number of individuals is simple because estimates of animal density are defined by area, but it turns a unit of measurement into a living entity: an individual animal. It is possible to imagine an individual animal dying in the flames or toiling within the fire scar, and then multiply that death and suffering by–as the final, revised estimate suggested– three billion animals affected (van Eeden *et al.* 2020).

Animal mortality during fire

What do you mean by "affected"? Do you not mean "killed", as was widely reported? Professor Dickman's estimates, and the follow-up estimates of van Eeden *et al.* (2020), were of the number of individual animals within the fire-grounds. The language in describing the estimate was careful: it stipulated the number of animals affected, not killed, by the fires. It is a reasonable assumption that animals within the fire-grounds would be affected by the fires in some way, hence the careful choice of words. But how many of those individuals were actually killed?

That number is far more difficult to estimate. Many studies have estimated changes in abundance of species before and after fire: could they be used to predict fire-induced mortality? Not reliably. Such studies typically cannot differentiate between animals that die in the fire, those that change their behaviour (and hence become more/less detectable after fire), and those that flee an area after the fire. That is, they tend to measure apparent survival rather than actual survival (Lebreton *et al.* 1992). Given the increasing evidence of behavioural changes following fire (Geiser *et al.* 2018; Stawski *et al.* 2015a) and evidence of mass emigration from burned areas (Swan and Wilson 2015), changes in local abundance before and after fire are likely not fit for purpose when estimating survival. Instead, a smaller subset of studies on animals and fire is more useful—those that track the fate of individual animals through the course of a fire event. These studies use animal tracking technologies, such as radio or GPS collars, to identify animals that were in the path of a fire as it approached. By following the fate of the tracked animals after the fire's passage, researchers can identify which animals were able to out-manoeuvre the fire and live to see another day, and which were not so fortunate. This allows researchers to estimate the mortality rate during fire: the proportion of sampled animals that died in the path of the fire.

Studies that track animals through fire have been both deliberate, planned projects, as well as opportunistic studies in which an unexpected fire passed through an existing animal tracking programme (Garvey *et al.* 2010). Yet, these studies are scattered throughout an increasingly voluminous literature. In a systematic review of studies that tracked the fate of individual animals through fire, Jolly *et al.* (2022) located 31 peer-reviewed research papers comprising 43 cases, mostly from North America and Australia. While studies often tracked relatively low numbers of individuals (i.e., 53% tracked < 10), they showed substantial variability in mortality rates. The majority of studies (65%) recorded no fire-induced mortality. Yet other studies recorded 40% mortality. On average (95% CI), fires killed 3% (1–9%) of tracked individuals, but this proportion rose to 7% (2–21%) when considering the studies that tracked the fate of individuals through intense (cf. mild) fires.

The importance of fire intensity in mediating animal mortality is highlighted by a study of frill-necked lizards (*Chlamydosaurus kingii*) in fire-prone savanna woodlands of northern Australia (Griffiths and Christian 1996). During a low-intensity fire, 17 lizards were radio-tracked, all of which survived by climbing to the relative safety of the tree canopy, away from the flames of the low-intensity surface fire. During an intense fire in the same region, 24 lizards were tracked, a quarter of which died employing the same tactic, as the flames reached higher. Animals that used a different tactic—taking up refuge in non-flammable termite mounds—survived.

Although Jolly *et al.* (2022) improved our understanding of animal mortality during fire, they did not get us much closer to estimating the number of animals that died in the 2019–20 Australian wildfires. The data are too limited to make that leap. Of particular concern is the lack of studies of animal survival through "megafires". The definition of megafire varies (Tedim *et al.* 2018), but a common definition is fires that burn > 10,000 ha. We found only one such study (Banks *et al.* 2011). Thus, we have almost no understanding of mortality rates during large, intense fires, let alone the unprecedented 2019–20 wildfires. Before attempting to estimate a body count for unprecedented fires, we need an empirical understanding of animal mortality across a far greater range of fire types, including megafires.

With that said, what can we make of Jolly *et al.*'s (2022) key finding that, on average, just ~3% of animals die during fire? How does such a large proportion of individuals survive the passage of such a lethal threat? There are many adaptations and exaptations that help: for instance, a burrowing habit is common in fire-prone landscapes (Pausas and Parr 2018), buffering animals from the immediate threat of fire. An analogous approach to fire survival is seen in many plants (Pausas 2019). But unlike plants, animals can move rapidly in response to stimuli, including fire (Nimmo *et al.* 2019). As illustrated by the frill-necked lizard case study, the decisions, and movements, that animals make as fire approaches can be the difference between life and death.

Animal movement and behaviour in response to fire have not been major foci of fire ecologists to date (Keith 2022; Nimmo *et al.* 2019), but that is beginning to change. Recent studies have highlighted that a suite of animals from fire-prone landscapes can detect and recognise the cues of fire: the acrid smell of smoke (Álvarez-Ruiz *et al.* 2021), the crackling sounds (Grafe *et al.* 2002), and stark visuals. Detecting and recognising fire cues gives animals an early warning of, and head-start on, approaching fire. Upon smelling smoke, captive Australian sleepy lizards (*Tiliqua rugosa*) become uneasy, flicking their tongues and pacing their tanks (Mendyk *et al.* 2020). Smoke also rouses Gould's long-eared bats (*Nyctophilus gouldi*) and fat-tailed dunnarts (*Sminthopsis crassicaudata*) from torpor (Doty *et al.* 2018; Stawski *et al.* 2015b). A recent study showed that Mediterranean skinks (*Psammodromus algirus*) from fire-prone shrublands respond far more acutely to smoke than individuals of the same species from dune ecosystems that rarely burn (Álvarez-Ruiz *et al.* 2021).

These studies collectively suggest that animals in fire-prone landscapes may be under selection for "fire-savvy" individuals: those that can detect and recognise the threat implied by fire's proximity, and then respond in a way that maximises their chance of survival if the fire arrives (Nimmo *et al.* 2021; Pausas and Parr 2018). The frill-necked lizards that fled to termite mounds during the intense fire had the opportunity to pass on their genes, whereas the ill-fated lizards that took to the canopy did not. As this process is repeated across landscapes and populations, throughout the 300–500 million hectares of land that burns annually (Forkel *et al.* 2019), it is reasonable to hypothesise that natural selection is carving out a fire-savvy phenotype.

The extent to which this occurs probably relates to a region's fire history (Nimmo *et al.* 2021). Where intense fires are frequent, the selection is likely to be most intense. Where fire is low intensity and infrequent, or entirely absent, selection is likely to be limited or non-existent. Hence, fire regimes should predict responsiveness to fire cues, and be tailored to particular fire types and behaviour (Nimmo *et al.* 2021). A lack of selection for fire-savvy individuals could result in "fire-naivety", akin to predator-naivety (Sih *et al.* 2010), in which animals fail to detect, recognise, or appropriately respond to the cues of incipient fire, much as a native mammal can overlook the telltale signs of a nearby stalking invasive predator (Carthey and Banks 2014). This is a concern given that a defining feature of the 2019–20 wildfires was the occurrence of fire—including high intensity fire—in vegetation types where it is rare and typically low intensity (Collins *et al.* 2021). For instance, rainforests are often thought of as fire-resistant, with average intervals of > 100 years between (typically low-intensity, understorey) fires (Murphy *et al.* 2013). This fire regime probably equates to limited selection for fire-savvy phenotypes. The 2019–20 wildfires burned an unprecedented area of rainforest vegetation at high severity, consuming rainforest canopies (Collins *et al.* 2021). The intensity of these canopy fires was undoubtedly far greater than what these ecosystems usually experience. Fire-naive populations exposed to such uncharacteristic fire behaviour are highly unlikely to enjoy the high survival rates reported by Jolly *et al.* (2022), but that remains to be tested.

The post-fire gauntlet

Of course, fire can also lead to animal mortality indirectly, by affecting resources (food, water, shelter sites) and by resetting the stage for species interactions (Geary *et al.* 2018). Indeed, it is possible that most of the mortality related to fire occurs soon after it has passed. Predators quickly arrive, hunting exposed prey across landscapes devoid of vegetation (Hovick *et al.* 2017; McGregor *et al.* 2016). These predation events can cause significant mortality (Leahy *et al.* 2016). Some species abruptly change their movement patterns upon recognising the cues of recent fire, such as ash beds and charcoal, perhaps to avoid predation (Stawski *et al.* 2015a,b, 2017). Is this the result of selection arising from these regular pulses of predation risk (Nimmo *et al.* 2021)? The post-fire landscape may act as an additional filter to the fire event, further winnowing the pre-fire population towards a fire-savvy phenotype (Figure 1).

If fire drives the evolution of behavioural responses, then megafires burning millions of hectares have the

Figure 1. Surviving fire may rely on an animal's ability to read multiple cues before and immediately after fire. In this example, lizards that can recognise and respond appropriately to fire cues and post-fire risks are white, "fire naïve" animals are light grey, and those that respond only to fire cues (and not post-fire risks) are dark grey. Fire acts a selection force, favouring fire savvy individuals. Figure by Alana de Laive.

potential to act as a "Darwinian guillotine": a stark and "mercifully brief" evolutionary apparatus that sorts fire-savvy and fire-naive animals through life and death across vast areas (sensu Lunney *et al.* 2008). While megafires might comprise a small fraction of fires, they often account for the vast majority of burned area (Attiwill and Binkley 2013). Megafire could act as a 'mass selection event', rapidly filtering out fire-naive animals from populations (Nimmo *et al.* 2022).

Megafires may represent a significant extinction risk for fire-naive species, particularly when the majority of their distribution lies within the fire scar. For other species, megafires could hasten the dominance of fire-savvy phenotypes, allowing populations to rapidly adapt to changing fire regimes. If this is true, and survival during and after megafire is a non-random process that favours animals that are fire-savvy, then the signature of that selection should be evident in the behaviours of the remaining population: they should be more responsive to fire cues and post-fire cues than those in areas that escaped the fire. Furthermore, if animal survival during megafires is driven by heritable variation in fire cue detection and related anti-fire behavioural responses, then the offspring from animals within megafires will retain this elevated level of responsiveness, relative to subsequent generations from unburned areas.

Conclusions

Applying a behavioural and evolutionary lens to animal–fire interactions is long overdue (Pausas and Parr 2018), and will help scientists understand and predict the impacts of changing fire regimes on animal species. Importantly, recognising the roles of evolution in animal responses to fire will allow us to understand how animal populations might adapt as fire regimes shift. But Keith (2022) highlights another advantage—recognising fire as an ecological process with evolutionary consequences that shape behavioural phenotypes—rather than a catastrophe by definition—could help move beyond the "disaster paradigm" that has characterised so much commentary on fires in Australia and globally (also see Bradstock 2008). Transcending the disaster paradigm might lead us to ask different questions, and hence arrive at different answers, that could be more productive in terms of identifying priorities and conservation solutions. We will certainly need all the tools at our disposal to ensure that biodiversity in fire-prone landscapes persists through the age of megafire.

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