Welcome to the Pyrocene: animal survival in the age of megafire

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Abstract

Planet Earth is entering the age of megafire, pushing ecosystems to their limits and beyond. While fire causes mortality of animals across vast portions of the globe, scientists are only beginning to consider fire as an evolutionary force in animal ecology. Here, we generate a series of hypotheses regarding animal responses to fire by adopting insights from the predator-prey literature. Fire is a lethal threat, thus there is likely strong selection for animals to recognise the olfactory, auditory, and visual cues of fire, and deploy anti-fire responses that maximise survival probability. If fire defences are costly, it follows that intraspecific variation in anti-fire traits should correspond with variation in fire behaviour and regimes. Species and populations inhabiting ecosystems that rarely experience fire may lack these traits, placing 'fire naïve' populations and species at enhanced extinction risk as the distribution of fire extends into new ecosystem types. We outline a research agenda to understand behavioural responses to fire and to identify conservation interventions that could be used to overcome fire naivety.

1. INTRODUCTION

Fire has shaped Earth's ecosystems for >400 million years (D. M. J. S. Bowman et al., 2009) and burns 300–500 million hectares of land annually (Forkel et al., 2019). Earth's warming and drying climate, combined with changes in land use and biota, is propelling the planet towards a more flammable future (Pyne, 2020). Fire is expanding its distribution, creeping—sometimes tearing—into landscapes long considered fire-free (Bowman et al., 2020). Recent megafires in Australia, California, Siberia, and the Amazon herald the potential emergence of a new epoch, the 'Pyrocene' (Pyne, 2020).

Remarkably, given its distribution and frequency, we understand very little of how fire acts as an evolutionary force on animals (Pausas & Parr, 2018). Fire can drive mortality of animals across vast areas, and in doing so undoubtedly exerts strong selective pressure on animal populations (Nimmo et al., 2019; Pausas & Parr, 2018). Fires produce cues: odours, sights, and sounds that signal its presence in the landscape. The ability of animals to recognise and respond to these cues is a matter of life and death. Species that lack an eco-evolutionary history with fire may be naive to its lethality, unable to recognise fire cues as a sign of impending danger until it's too late.

2. WHERE THERE'S SMOKE…

When staff at the Aubudon Zoo in the United States burned their lunch, they quickly noticed that they weren't alone in smelling the smoke. In nearby tanks, Australian sleepy lizards *Tiliqua rugosa* began frantically pacing their enclosures, rapidly flicking their tongues, and trying to escape (Mendyk et al., 2020). This uncharacteristic behaviour motivated staff to check sleepy lizards in tanks outside the affected room. Those lizards remained sleepy. Another 13 reptile species were housed in the smoke-affected room, mostly from regions where fire is rare or absent; none changed their behaviour (Mendyk et al., 2020).

The unusual behaviour of the lunchroom sleepy lizards appeared to be triggered by the smoke, and the rapid tongue flicking suggested the lizards sensed chemical cues emitted by burned pastry. The vast majority of these lizards were captive-born, suggesting an innate olfactory response (Mendyk et al., 2020). The sleepy lizards' Australian home is a fire-prone continent, where the selective pressure to avoid mortality by fire is strong. Fire regularly kills sleepy lizards, and many other animals(Friend, 1993).

Sleepy lizards aren't alone—a growing diversity of animal species from fire-prone landscapes have been found to sense incipient fire (Geiser et al., 2018; Stawski, Körtner, et al., 2015). This capacity to detect, recognise, and respond to olfactory cues raises obvious parallels with another widespread and lethal selective force—predation.

3. FIRE ECOLOGY MEETS PREDATOR ECOLOGY

Prey animals are able to detect the cues of predators with which they share a sufficiently long evolutionary history (Carthey & Blumstein, 2018). Such cues may be olfactory, such as predator scent marks, scats, or urine (Wisenden, 2000), visual, such as sighting the predator itself (Arteaga-Torres et al., 2020), or acoustic, such as hearing the predator's mating or territorial calls(Hettena *et al.* 2014). The cues of fire include acrid odours (olfactory), smoke plumes and flames (visual), and crackling sounds (auditory).

Evidence is accumulating that—as they respond to predatory cues—animals can recognise these fire cues as a sign of impending threat**.** Eastern pygmy possums (*Cercartetus nanus*) and Gould's long-eared bats (*Nyctophilus gouldi*), from Australia's fire-prone forests and woodlands, arouse from torpor when exposed to smoke (Doty et al., 2018; Nowack et al., 2016; Stawski, Körtner, et al., 2015). Eastern red bats (*Lasiurus borealis*) arouse in response to the sounds of fire (Scesny, 2006), which also motivates reed frogs (*Hyperolius nitidulus*), from fire-prone African savanna, to flee to nearby fire-resistant cover (Grafe et al., 2002). While not yet studied, it is likely that multi-modal risk assessment, where cues from different modalities are integrated to form a unified percept is likely used to integrate fire cues to reduce uncertainty (Munoz & Blumstein, 2012).

As with animal predator cues, recognition of fire cues may be innate, driven by natural selection (Atherton & McCormick, 2020), or acquired through learning (Griffin, 2004). The responses of the Audubon Zoo sleepy lizards suggest an innate recognition of compounds in smoke, as many of the individuals lacked ontogenetic experience with fire (Mendyk et al., 2020). That 13 other species in the same room did not react suggests that the sleepy lizard's response is probably not merely a generic response to novel stimuli but a fine-tuned response to a cue with a specific interpretation. While most other examples of animals responding to fire cues come from wild-caught animals (Geiser et al., 2018)—and therefore cannot distinguish between learned and innate responses—captive bred fat-tailed dunnarts (*Sminthopsis crassicaudata*) arouse from torpor when exposed to smoke, also suggesting an innate response (Stawski, Matthews, et al., 2015).

The capacity to detect a cue also depends on the cue's strength and environmental factors which affect a cues' spatial range (Garvey et al., 2016). As with animal predators, fire cue modalities differ in the amount of early warning they provide of an approaching fire. In general, olfactory cues travel furthest, followed by auditory and visual cues, which in some instances will signal immediate danger (Figure 1). However, the spatial range of cues, and hence their value as an early warning signal, likely depends on fire behaviour, environmental context, and its interaction with an individual's perceptual range. For example, in dense forest, the visual cues of fire might not enter an animal's perceptual range until it is very nearby, whereas in open, topographically simple landscapes, rising smoke plumes could enter an animal's perceptual range from a considerable distance (tens of kilometres), providing ample warning of enhanced fire risk.

Having detected and recognised a cue, prey must decide whether to respond, based on a risk-benefit analysis that weighs the potential costs of responding against the likely benefits (Lima, 1998). Typical anti-predator responses include vigilance (Ito & Mori, 2010), avoiding high-risk areas (Carrascal & Alonso, 2006), hiding (Blumstein & Pelletier, 2005), and reducing movement or freezing (Caro, 2005). A number of anti-fire behaviours are evident in the literature, each aimed at avoiding fire-induced mortality. These broadly range from seeking refuge in non-flammable shelter sites (e.g. deep crevices, burrows, water bodies, and adjacent vegetation) to fleeing the fire front as it approaches (Figure 2). Anti-fire behaviours also include complex social behaviours, such as cotton rats (*Sigmodon* sp.) uncharacteristically squeaking to young and even carrying juveniles away from approaching fire (Komarek, 1969).

Using a framework of behavioural decision-making under predation risk, we can hypothesise how animals might trade off safety against perceived risk from a fire, as well as against energetic and missed opportunity costs of responding to fire-related cues. The decision to deploy an anti-fire behaviour, or the type of behaviour deployed, can differ depending on phases of the predation sequence (Endler, 1991). Acting earlier (e.g. entering a burrow upon detecting a distant fire cue) results in higher missed opportunity costs, but improves survival probability. Reacting to distant fire cues could result in considerable opportunity costs, particularly in landscapes in which fire is a frequent occurrence (e.g. spinifex sandplains or tropical savannas). An imperfect ability to predict fire behaviour means that anti-fire behaviours could be deployed when there is little chance of the fire reaching an individual's location. Choosing to act late (i.e. when fire is in the immediate vicinity of an animal) results in fewer opportunity costs, but can require higher energetic costs (e.g. fleeing a fire front), and likely comes with a lower survival probability (Figure 1). The deployment of anti-fire responses might depend on fire behaviour (is it approaching rapidly?), the environmental context (are there non-flammable refuges nearby?), and the traits of the individual (e.g. mobility, body size), which dictate escape options.

An individual's physical state could also dictate decision-making in the face of incipient fire. Hungry, diseased, pregnant, or lactating animals may delay responding to a fire for longer than fit and healthy, satiated individuals (Trimmer et al., 2017). This is significant given that megafires have often followed periods of prolonged ecological stress (i.e. droughts and heat waves (Abram et al., 2021)) that would also impact on animal physical fitness. The strength and shape of the relationship between cue modality, intensity (strength, volume, apparency), and the increasing immediacy of the threat (Figure 1), will likely depend on the strength of the relationship between fire and mortality risk, dictated by species’ traits and ecosystem characteristics. For example, from the perspective of burrowing animals in landscapes characterised by small, low intensity fires (e.g. fuel limited ecosystems), the threat implied by a certain cue modality or intensity would be lower, and might elicit a lower response, than for an animal within flammable vegetation in an environment where fires are typically large and intense (e.g. tall temperate forests), where any hint of a fire cue might be cause for immediate and high-level action. Animals might combine information on fire cues with other environmental information that could help measure fire risk—such as wind speed, air temperature, even fuel moisture—to help balance the costs and benefits of responding to fire cues.

4. FIRE NAIVETY

Because not all populations live in areas that burn, there may have been no historic selection driving anti-fire responses. In the same way that animals are considered predator naive if their predator cue detection, recognition, and/or anti-predator responses are absent, inappropriate, ineffective, or excessive, some species or populations may be fire naïve. Importantly, prey naivety is particularly prevalent when prey and predator lack a shared evolutionary history (Anton et al., 2020) and has been implicated in numerous extinctions worldwide (Doherty et al., 2016). This parallel between prey naivety and fire naivety is important because fire naïve populations may be similarly vulnerable to changes in the distribution and frequency of fires.

Rather than a simple all-or-nothing state of predator wariness or naivety, Banks and Dickman (Banks & Dickman, 2007) and Carthey and Banks (Carthey & Banks, 2014) proposed multiple levels of predator naivety, from (i) an inability to detect predator cues, precluding any anti-predator response (level 1 naivety), (ii) deploying inappropriate defences such as hiding from an olfactory hunter (level 2), through to (iii) appropriate anti-predator responses but being outgunned by a superior hunter (level 3). A final possibility is over-responding to a predator, and incurring excessive energetic or missed opportunity costs, for example by hiding long after the predation risk abates (level 4).

Applying this framework to predatory fire, fire naivety can also be viewed as a spectrum, ranging from (i) animals that lack the capacity to detect fires cues, most likely for animals that have evolved in regions where fire is absent, suppressed or infrequent (level 1 naivety); (ii) animals that detect and recognise fire cues, but respond inappropriately (level 2); and (iii) animals that detect fire cues and respond in a generally appropriate manner (i.e. one that would normally reduce mortality risk), but are nonetheless consumed by fire, perhaps due to uncharacteristic fire behaviour (relative to that usually experienced in the ecosystem).

If fire occurrence or behaviour changes suddenly—due to more extreme fire weather, higher fuel loads, or uncharacteristically low fuel moisture (or combinations thereof)—we expect a mismatch between the historical association of risk with a particular fire cue and its current associated risk. In this scenario, animals may misinterpret the danger implied by fire cues, and make maladaptive decisions (Figure 3). In some instances, this mismatch could result in evolutionary traps that drive a population or even a species towards extinction. For example, Australian frilled lizards *Chlamydosaurus kingii* in the fire-prone savannas of northern Australia respond to fire by maintaining their position in the canopy of trees (i.e. remaining in place; Figure 2), well out of reach of cool, early dry season burns. However, this response results in increased mortality when fires scorch the canopy in late dry season fires (Griffiths & Christian, 1996). Changes to the characteristics of fire in this landscape, due to the spread of invasive grasses (Setterfield et al., 2010), climate change, and altered fire regimes, may trap some species into responding inappropriately to intense fires whose threat they misunderstand. Where animals are trapped by evolved anti-fire responses to historic fire conditions, we may require evolutionary tools to help them escape.

A large body of work has shown how antipredator responses are evolutionarily plastic. Retaining anti-predator responses after a predator has been extirpated is likely to be costly because individuals forego opportunities without the benefit of reduced mortality risk (Lahti et al., 2009). Hence, anti-predator behaviours can be lost rapidly (e.g. in as few as 13 generations(Jolly et al., 2018)) when they are no longer under strong selection (Blumstein et al., 2004; Lahti et al., 2009) or when selection removes them(Jolly & Phillips, 2020). It is an empirical questions if and how quickly strong selection may generate anti-predator responses, but in some instances, they have been gained rapidly, presumably due to strong selection (Carthey & Blumstein, 2018; Jolly et al., 2019).

Could the capacity to detect, recognise, and appropriately respond to fire be similarly labile? This question is vital in terms of how rapidly appropriate anti-fire behaviours can be lost from populations—for instance following prolonged fire suppression—or gained, as fire behaviour and regimes shift. If anti-fire behaviours have a genetic basis, then it suggests that evolutionary tools, such as assisted or targeted gene flow—which has been suggested as a means of preadapting vulnerable populations to of fire-impacted plants (Kelly et al., 2020)—may also be used to preadapt animal populations to altered fire behaviour and regimes.

While our focus is on responses to the cues of fire, surviving the fire event is just part of the challenge. Post-fire environments are particularly dangerous for survivors exposed to elevated risk of predation in barren landscapes (Doherty et al., 2015a). This “pyric carnivory” is a rapid and global phenomenon (Bonta et al., 2017). One U.S study showed a seven-fold increase in raptor activity during fire (Hovick et al., 2017), and an Australian study even suggests raptors intentionally spread fire by transporting burning sticks in their talons or beaks (Bonta et al., 2017). Raptors and other predators can exert mass mortality on survivors of the fire event. Hence, in the immediate aftermath of fire, animals again make high stakes decisions under extreme risk. Research suggests some animals can read ‘post-fire cues’, such as the presence of ash beds and charcoal, as a sign of danger. For example, yellow-footed antechinus (*Antechinus flavipes*) enter torpor when exposed to smoke, ash, and charcoal (Stawski et al., 2017). Both the yellow-footed and brown antechinus (*Antechinus stuartii*) use torpor to avoid daytime movements after fire, perhaps to avoid diurnal predators and food shortages (Matthews et al., 2017a; Stawski, Körtner, et al., 2015). Animals that have co-evolved with pyric carnivory may have adaptations to increase the odds of surviving the post-fire gauntlet, whereas animals without evolutionary exposure to fire could again be exposed to heightened mortality risk, further reinforcing selection for fire savvy animals.

5. RESEARCH PRIORITIES

While there is a growing list of anti-fire responses in a variety of animals, we need to better understand the diversity of adaptations and fire-associated assessment abilities animals may possess. This is likely to vary by species. However, insights from anti-predator theory permit us to make a variety of predictions.

First, we expect that animals from fire-prone environments will be more responsive to fire cues than will animals from environments that never or infrequently experience fire. We therefore expect gradients of fire-proneness to predict animal responsiveness to fire cues, and the type of anti-fire behaviours deployed. This variability should be evident at both the species- and population-level. We need to better understand how widespread, taxonomically and ecologically, the behavioural responses to fire cues are, and whether different cues elicit different behavioural responses.

Second, we expect habitat structure to influence the cues animals use to detect fire. We expect that animals in structurally sparse environments would be more responsive to the visual cues of fire than animals in dense vegetation, due to differences in visibility, and that animals at more imminent threat from fire—for instance, those that occupy flammable retreat sites in high fuel ecosystems—should be more responsive to fire cues and able to detect them at lower concentrations.

Third, the antipredator literature illustrates the widespread sensitivity to costs and benefits of responding to predator cues and we expect that this will also be applicable to fire cues. Thus, we expect responses to potentially vary with cue intensity (indicative of fire intensity or distance to potential fires).

Fourth, we expect that increased energetic demands will increase the relative cost of responding to fire cues, as is predicted for anti-predator responses (Trimmer et al., 2017). Hungry and subordinate animals take greater predatory risks (Hayes et al., 2020) and, because of widespread condition dependence seen in many behavioural decisions (Schmitz & Trussell, 2016), we expect that body condition will influence the response to fire cues.

Fifth, many studies have shown that there is substantial individual variation and population variation in antipredator traits in a variety of taxa (Ibáñez et al., 2014), that these may have fitness consequences (Smith & Blumstein, 2008), that they may be heritable (Petelle et al., 2015), and that individual variation has ecological consequences (Des Roches et al., 2018). For some time, we have known that individuals may have different temperaments, coping styles or personalities (Réale et al., 2010). Additionally, the more recent literature on behavioural syndromes emphasizes that the response to threats may be associated with other traits in predictable ways (Sih et al., 2004). Thus, we expect to find some degree of individual variation in those species that have the ability to respond to fire related cues and that this may be associated with the well-studied shyness-boldness or proactive-reactive continua (Wilson et al., 1994). More importantly, at the population-level, we expect that recent fires will reduce the variation in behavioural types by potentially eliminating bold individuals in a way similar to that seen by predators (Jolly et al., 2019). These effects should be most evident in landscapes recently affected by mega-fires, due to their scale and intensity leading to heightened mortality.

While we cannot make concrete predictions, it will be important to understand the spatial scales of fire cue detection and whether and how the value of using specific cues varies by the environment. For instance, are animals more reliant on olfactory than visual cues in complex landscapes? Additionally, can animals incorporate additional information indicative of fire risk (e.g. wind speed, air temperature) into decisions regarding at what stage in the fire sequence anti-fire behaviours should be deployed?

While we expect, given the variety of antipredator responses seen, many species living in fire-prone regions to have the ability to detect cues associated with fires, not all species will likely be able to respond to fire-related cues. Why? What are the constraints that prevent effective responses? It will be important to study how these traits are acquired and quantify their heritability. Insights into the genetic basis of fire cue response abilities is essential if we wish to understand the impact of increased and changed fire regimes as well as possible conservation interventions, such as targeted gene flow.

6. CONCLUDING REMARKS

Fire threatens >1,000 animal species with extinction (Kelly et al., 2020), yet we have limited understanding of how it shapes the behaviour and evolution of animals. We've touched only on the most immediate impacts of fire: there is also much to be learned about the behavioural adaptations that allow animals to persist in the immediate aftermath of fire, where the risks of dehydration, starvation, and predation often peak (Doherty et al., 2015b). Nonetheless, we have outlined a series of predictions that we formulated by applying the lens of anti-predator behavioural responses onto fire. The insights gained by such research will be essential to manage animal populations in the Pyrocene. Importantly, we note that understanding the dynamics of fire naivety is essential to identify species and populations at risk. There are also potential novel interventions (e.g. targeted gene flow) to increase the persistence of animal populations during abrupt changes in fire behaviour and regimes. We will require all the tools at our disposal to secure Earth’s biodiversity as we enter an increasingly flammable future.

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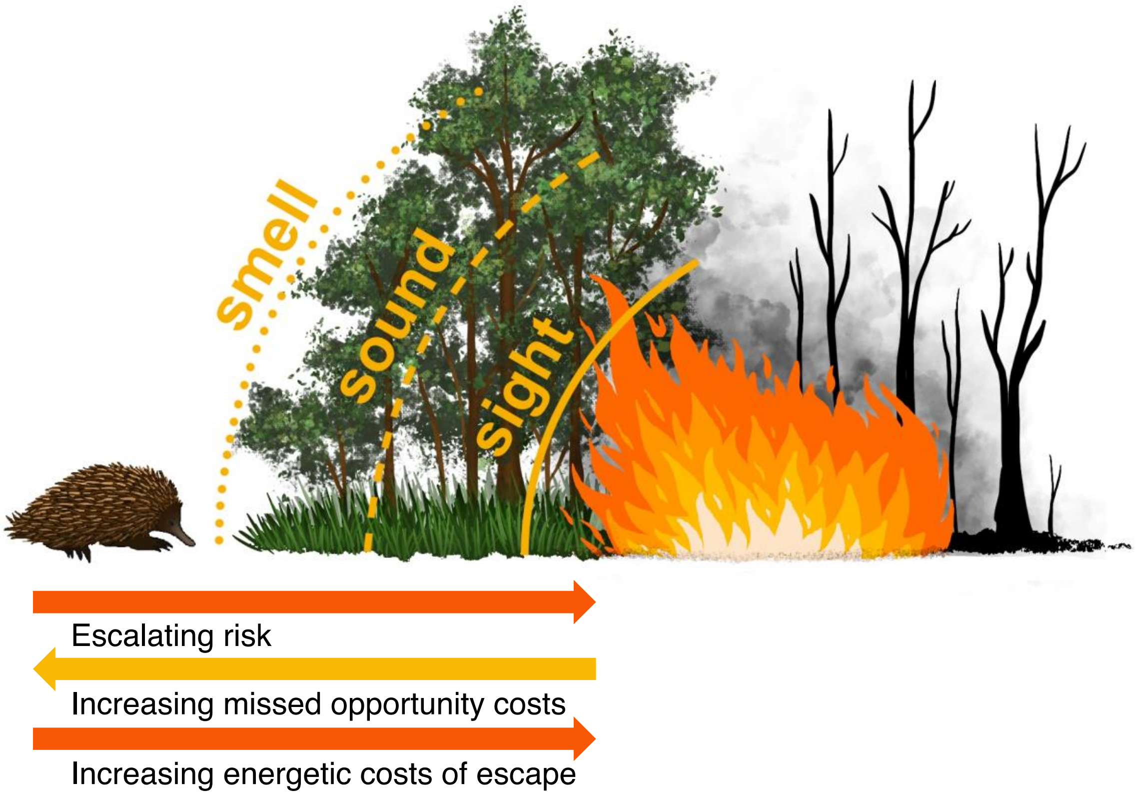

Figure 1. Different fire cue modalities and their association with risk (mortality by fire) and missed opportunity costs. Fires emit olfactory (smell), auditory (sound), and visual (sight) cues, each or all of which might be used by animals to reduce their risk of mortality in a fire. Yet animals must trade-off the risk of death by fire against a need to perform other fitness-enhancing behaviours such as foraging. Olfactory cues travel the furthest from a fire, and hence, would provide the earliest warning of a fire's approach. Animals that choose to evacuate at this stage may have the best chance of surviving the fire but will incur missed opportunity costs. Sounds of a fire herald its imminent approach, while sighting the fire means it has arrived. Waiting to respond until fire is sighted is likely to be the riskiest strategy (although some species may have defences—such as retreating to a local burrow—that only take seconds to enact) but would incur minimal missed opportunity costs. Responding to the sound of a fire should fall somewhere in between these two extremes. Note that different cue types may travel at different speeds in different environments, due to abiotic variables such as weather and climate, structural complexity, and other factors.

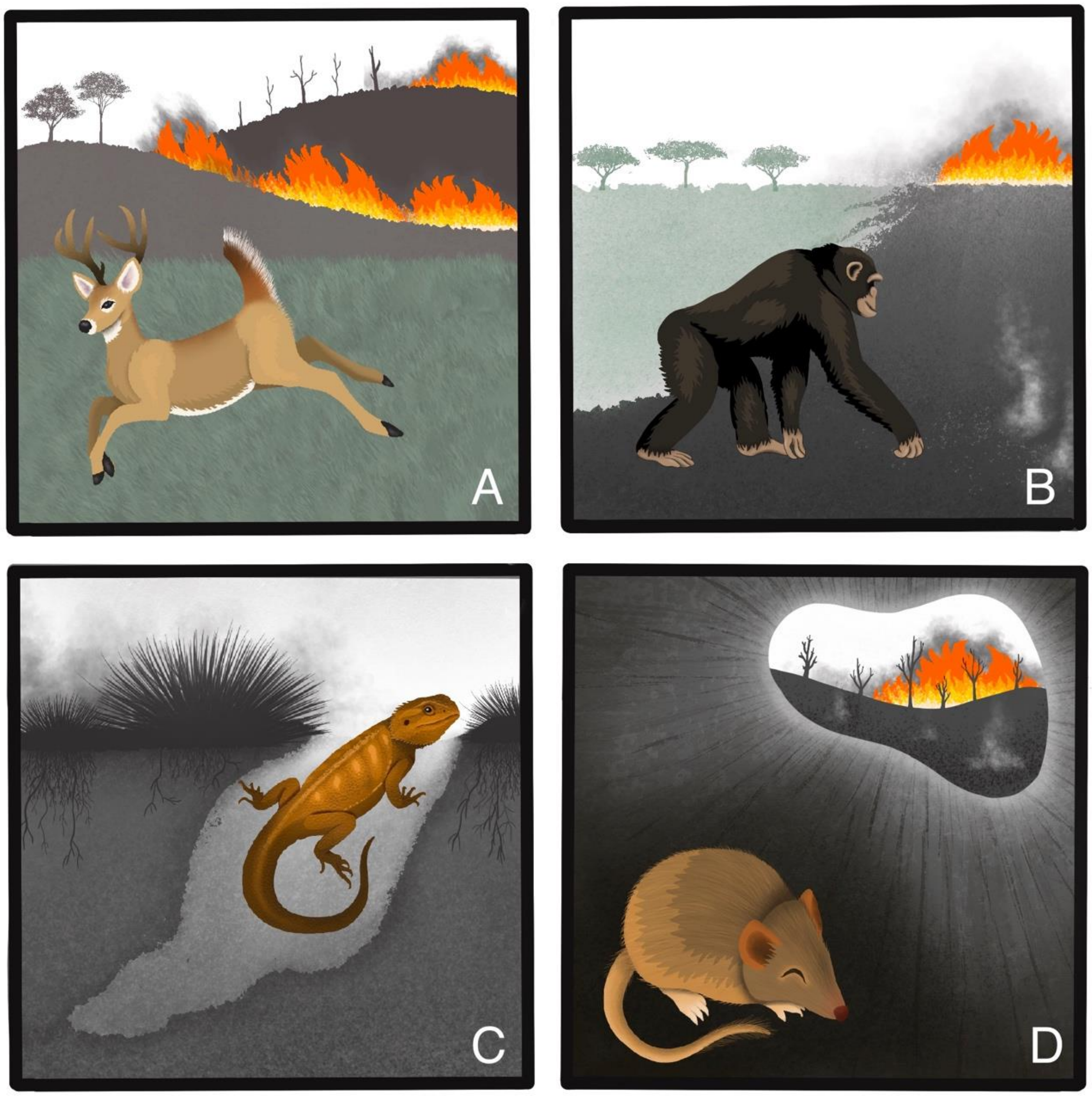

Figure 2. **Anti-fire responses**. Fire in the landscape triggers a range of anti-fire responses in animals. A) white-tailed deer (*Odocoileus virginianus*) employ *immediate evacuation* to rapidly flee approaching fire, anticipating its likely direction(Ivey & Causey, 1984). B) By *doubling back,* savanna chimpanzees (*Pan troglodytes verus*) reduce their risk of encountering intense, late dry season fires by selectively travelling via recently burnt fire scars (Pruetz & Herzog, 2017). C) central bearded dragons (*Pogona vitticeps*) use *delayed evacuation*—they seek refuge until the fire has passed then seek unburnt habitat(Swan & Wilson, 2015). D) Many animals choose to *shelter in place* until an approaching fire has passed. Antechinus (*Antechinus* spp.) have evolved the added ability to shelter in place for prolonged periods by entering torpor to avoid dehydration, starvation, or predation risk in simplified post-fire landscapes (Matthews et al., 2017b; Stawski, Körtner, et al., 2015).

Level 1 fire naivety

Level 2 fire naivety

Level 3 fire naivety

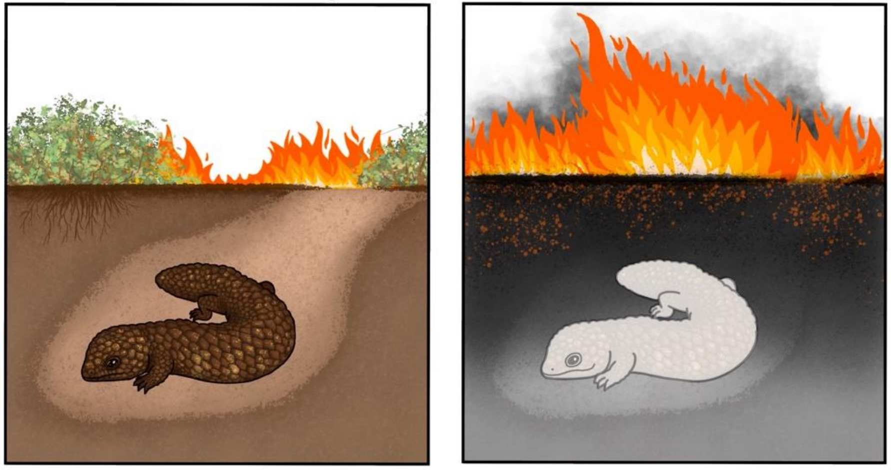

Figure 3. ***Multiple levels of fire naivety.*** Prey that inhabit ecosystems that have historically never burnt, such as rainforests, may be entirely naive to fire (level 1). They would have had no selective pressure to develop the ability to detect and recognise fire cues. Should these ecosystems burn, we would expect that prey who do not detect fire cues will be precluded from responding to them—resulting in high mortality. We expect level 1 fire naivety to be widespread in ecosystems where fire is absent or infrequent, such as ecosystems that are typically too wet (e.g. rainforest, Arctic tundra) or too fuel limited to carry fire (e.g. Sahara Desert). Prey from ecosystems that do burn will have experienced selection pressure to adapt to those particular fire regimes. Therefore, when fire regimes rapidly shift, the behavioural responses of animals to fire could become maladapted. They might be expected to detect and recognise fire cues, but to respond inappropriately (level 2 fire naivety) or ineffectively (level 3 fire naivety). For example, a level 2 fire naive animal may recognise that smoke indicates an approaching fire, but choose to move to the canopy, where it has historically been able to wait out lower intensity fires (e.g. see frill-necked lizard example in Box 1). However, increased fuel loads, reduced fuel moisture, and/or more extreme fire weather can create more intense fires, leading to crown fires that consume the canopy. In such an instance, a different response might be more effective at reducing mortality risk —such as fleeing or accessing animal burrows. Level 2 naivety would be expected in ecosystems that experience fire semi-regularly (i.e., on decadal to centurial timescales), such as temperate and boreal forests. Depending on the generation time of the organism, the period between fires may be too long for fire to act as a consistent selection pressure, so that while fire cues do register as indicators of a threat, the anti-fire response is not particularly fine-tuned. In a level 3 fire naivety scenario, an animal might flee fire but not be able to escape more severe and rapidly spreading fire than it is used to. Or it might burrow in response to the smell of smoke, to a depth that was sufficient for past fires but causes mortality during more intense fire. Level 3 naivety is likely to be common in fire-prone landscapes (e.g. such as semi-arid shrubland, tropical savanna) undergoing shifts in fire regimes towards more extreme fire behaviour. Here, although animals might have evolved finely tuned anti-fire behaviours that increase survivorship, drying conditions or heightened fuel loads (e.g. due to invasive grasses(Rossiter et al., 2003)) result in new environmental conditions, where previously adaptive anti-fire responses become ineffective.