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 fire avoidance behaviours that maximise survival probability. If fire defences are costly, it follows that intraspecific variation in fire avoidance behaviours should correspond with variation in fire behaviour and regimes. Species and populations inhabiting ecosystems that rarely experience fire may lack these traits, placing 'fire naive' 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 (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 altering the nature of global fire activity (Bowman et al., 2020). In many regions, fire is expanding its distribution into landscapes long considered fire-free (Bowman et al., 2020). The centrepiece of Earth's fiery transition are the megafires, characterised by their scale, intensity, and severity (Boer et al., 2020; Collins et al., 2021), and often propelled by unprecedented climatic conditions (Abram et al., 2021; Higuera & Abatzoglou, 2021). While a clear trend in global burned area is yet to emerge (Bowman et al., 2020), predictions are that continued climatic warming will drive an increase in global fire activity in the coming decades (Wu et al., 2021). Indeed, some argue that recent megafires in Australia, California, Siberia, and the Amazon herald the potential emergence of a new epoch, the 'Pyrocene' (Pyne, 2020).

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). Fire incinerates vegetation, exposing some animals to enhanced predation risk in landscapes devoid of protective shelter, in which starvation and dehydration pose potentially lethal threats (Doherty et al., 2015). The impacts of fire can continue to shape species' distribution for decades or even centuries (Haslem et al., 2011). A primary mechanism by which fire is thought to affect animals is mortality during the fire event (Whelan et al., 2002), yet we understand very little of how fire acts as an evolutionary force on animals (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.

1. 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 (Álvarez-Ruiz et al., 2021; Geiser et al., 2018; Stawski et al., 2015a). This capacity to detect, recognise, and respond to olfactory cues raises obvious parallels with another widespread and lethal selective force—predation.

2. 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 et al., 2015a). 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 et al., 2015a).

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 antipredator 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 fire avoidance 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). Fire avoidance 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 (Endler, 1991). Acting earlier (e.g. entering a burrow upon detecting a distant fire cue) means missing opportunities to engage in fitness-enhancing activities such as gathering resources or mating, but improves immediate survival probability. Choosing to act late (i.e. when fire is in the immediate vicinity of an animal) results in fewer missed opportunity costs, but can require higher energetic costs (e.g. fleeing a fire front), and likely comes with a lower survival probability should the fire reach the individual (Figure 1). The deployment of fire avoidance 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.

Individual variation in response to perceived risk of predation has been documented in the predator-prey literature (López et al., 2005). The “bold–shy continuum” describes the willingness of animals to take risks when faced with potential danger (Wilson et al., 1993). This continuum could map onto fire avoidance behaviours. Fires may act as selection events against “bold” individuals that delay fire avoidance, but the patchy and stochastic nature of fire and the costs of fire avoidance could maintain bold behaviours at the population level. Variability in behavioural types allows populations to adapt when confronted with sudden environmental change (i.e., insurance effects; Wolf & Weissing, 2012), and may well provide the evolutionary capital needed for populations to adapt to rapidly changing fire regimes.

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.

3. FIRE NAIVETY

Because not all populations live in areas that burn, there may have been no historic selection driving fire avoidance responses. This may be the case both within regions that rarely burn, and within vegetation types in otherwise fire-prone regions that usually escape fire, for instance due to high fuel moisture (e.g. wet gullies) or low fuel loads (e.g. rocky outcrops). In the same way that animals are considered predator naive if their predator cue detection, recognition, and/or antipredator responses are absent, inappropriate, ineffective, or excessive, some species or populations may be fire naive. 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 naive populations may be similarly vulnerable to changes in the distribution, intensity, and frequency of fires. For instance, an expanding footprint of fire could threaten the persistence of fire naive species associated with vegetation types that rarely burn, in the same way that rapid range expansions of an invasive predator imperils native wildlife (Savidge, 1987).

Rather than a simple all-or-nothing state of predator wariness or naivety, Banks & Dickman (2007) and Carthey & Banks (2014) proposed multiple levels of predator naivety, from (i) an inability to detect predator cues, precluding any antipredator response (level 1 naivety), (ii) deploying inappropriate defences such as hiding from an olfactory hunter (level 2), through to (iii) appropriate antipredator 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 benign 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, because they suffer increased mortality when fires scorch the canopy in late dry season fires, some lizards choose to shelter in fire-resistant termite mounds—a behaviour not enacted during early 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. Gamba grass (*Andropogon gayanus*) is rapidly spreading across the savannas of northern Australia (Petty et al., 2012). Even during cool fire conditions in the early dry season, gamba grass burns at far greater heights into the canopy and at substantially higher temperatures than native grasses (Rossiter et al., 2003; Setterfield et al., 2010). If frilled lizards are relying on environmental cues to predict fire behaviour, they may not anticipate such extreme fires when prevailing conditions would suggest them to be benign. Where animals are trapped by evolved fire avoidance 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 both evolutionarily and phenotypically plastic. Retaining antipredator 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, antipredator 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, 2021). It is an empirical question if and how quickly strong selection may generate antipredator responses, but in some instances, they have been gained rapidly, presumably due to strong selection (Carthey & Blumstein, 2018; Jolly et al., 2021) and/or behavioural adjustments by individuals (Berger et al., 2001; Cunningham et al., 2019).

Could the capacity to detect, recognise, and appropriately respond to fire be similarly labile (Pausas & Parr, 2018)? This question is vital in terms of how rapidly appropriate fire avoidance behaviours can be lost from populations—for instance following prolonged fire suppression—or gained, as fire behaviour and regimes shift. If fire avoidance 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 of fire-impacted plants (Kelly et al., 2020)—may also be used to preadapt animal populations to altered fire behaviour and regimes. Targeted gene flow involves moving pre-adapted individuals with favourable traits to areas in which the traits could confer a conservation benefit (Kelly & Phillips, 2016). In this case, targeted gene flow could involve moving individuals with fire avoidance behaviours into populations that lack such behaviours in order to spread this favourable trait throughout a fire naive population.

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., 2015). This "pyric carnivory" is a rapid and global phenomenon (Bonta et al., 2017), and highlights that fire cues can signal opportunity to some species, with flow-on effects for others (Geary et al., 2018). 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., 2017; Stawski et al., 2015b). 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.

4. RESEARCH PRIORITIES

While there is a growing list of fire avoidance behaviours in a variety of animals, we need to better understand the diversity of adaptations and fire-associated assessment abilities animals may possess. We also need to better understand how behavioural responses to fire cues vary among individuals, populations, species, the drivers of this variability, and whether different cues elicit different behavioural responses. Insights from fire ecology and predator-prey theory permit us to make a variety of predictions.

- 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 fire avoidance behaviours deployed. A recent study of Mediterranean lizards (*Psammodromus algirus*) in Spain showed evidence for this hypothesis: animals from fire-prone vegetation types were more responsive to smoke than animals from non-fire-prone vegetation (Álvarez-Ruiz et al., 2021). In terms of the characteristics of the fire regime (i.e., frequency, intensity, severity, seasonality, size; Gill, 1975), we predict that the frequency of large, high intensity fire will be the best predictor of responsiveness to fire cues, owing to the greater potential for lethal conditions leading to frequent selection events across large areas. Variability in responsiveness to fire cues across such gradients should be evident at both the species- and population-level.

- We predict that species with traits that make them vulnerable to fire—such as low mobility or associations with highly flammable shelter sites—should be able to detect fire cues at lower concentrations and from greater distances to facilitate early deployment of fire avoidance behaviours.

- In terms of cue modalities, we expect habitat structure to influence which cues animals rely on 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. Whereas animals in structurally complex habitats (e.g. heathlands), where vision is often obstructed, will be more reliant on olfactory than visual cues.

- 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).

- We expect that increased energetic demands will increase the relative cost of responding to fire cues, as is predicted for antipredator 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. If true, fires that follow prolonged periods of drought and/or anomalous heat may further enhance the vulnerability of individuals to lethal fire.

- 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) or plastic (Berger et al., 2001), 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). At the population-level, we expect that recent fires will reduce the variation in behavioural types by potentially favouring shy individuals in a way similar to that seen by predators (Jolly et al., 2021). These effects should be most evident in landscapes recently affected by megafires, due to their scale and intensity leading to heightened mortality.

- While we cannot make concrete predictions, research could ask whether animals can incorporate additional information indicative of fire risk (e.g. wind speed, air temperature) into decisions regarding at what stage in the fire sequence fire avoidance 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 plasticity and 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.

5. 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 survive in the immediate aftermath of fire, where the risks of dehydration, starvation, and predation often peak (Doherty et al., 2015). Nonetheless, we have outlined a series of predictions that we formulated by applying the lens of antipredator 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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References

Abram, N. J., Henley, B. J., Sen Gupta, A., Lippmann, T. J. R., Clarke, H., Dowdy, A. J., Sharples, J. J., Nolan, R. H., Zhang, T., Wooster, M. J., Wurtzel, J. B., Meissner, K. J., Pitman, A. J., Ukkola, A. M., Murphy, B. P., Tapper, N. J., & Boer, M. M. (2021). Connections of climate change and variability to large and extreme forest fires in southeast Australia. *Communications Earth & Environment*, *2*(1), 1–17. https://doi.org/10.1038/s43247-020-00065-8

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

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, J. T. A. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1928), 20192978. https://doi.org/10.1098/rspb.2019.2978

Arteaga-Torres, J. D., Wijmenga, J. J., & Mathot, K. J. (2020). Visual cues of predation risk outweigh acoustic cues: A field experiment in black-capped chickadees. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936), 20202002. https://doi.org/10.1098/rspb.2020.2002

Atherton, J. A., & McCormick, M. I. (2020). Parents know best: Transgenerational predator recognition through parental effects. *PeerJ*, *8*, e9340. https://doi.org/10.7717/peerj.9340

Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution*, *22*(5), 229–230. https://doi.org/10.1016/j.tree.2007.02.006

Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: Conservation lessons from pleistocene extinctions. *Science*, *291*, 1036–1039.

Blumstein, D. T., Daniel, J. C., & Springett, B. P. (2004). A test of the multi-predator hypothesis: Rapid loss of antipredator behavior after 130 years of Isolation. *Ethology*, *110*(11), 919–934. https://doi.org/10.1111/j.1439-0310.2004.01033.x

Blumstein, D. T., & Pelletier, D. (2005). Yellow-bellied marmot hiding time is sensitive to variation in costs. *Canadian Journal of Zoology*, *83*(2), 363–367. https://doi.org/10.1139/z05-020

Boer, M. M., Resco de Dios, V., & Bradstock, R. A. (2020). Unprecedented burn area of Australian mega forest fires. *Nature Climate Change*, *10*(3), 171–172. https://doi.org/10.1038/s41558-020-0716-1

Bonta, M., Gosford, R., Eussen, D., Ferguson, N., Loveless, E., & Witwer, M. (2017). Intentional fire-spreading by "firehawk" raptors in northern Australia. *Journal of Ethnobiology*, *37*(4), 700–718. https://doi.org/10.2993/0278-0771-37.4.700

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., Swetnam, T. W., van der Werf, G. R., & 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

Caro, T. (2005). *Antipredator defenses in birds and mammals.* University of Chicago Press.

Carrascal, L. M., & Alonso, C. L. (2006). Habitat use under latent predation risk. A case study with wintering forest birds. *Oikos*, *112*(1), 51–62. https://doi.org/10.1111/j.0030-1299.2006.13787.x

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*(4), 932–949. https://doi.org/10.1111/brv.12087

Carthey, A. J. R., & Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends in Ecology & Evolution*, *33*(2), 106–115. https://doi.org/10.1016/j.tree.2017.10.009

Collins, L., Bradstock, R. A., Clarke, H., Clarke, M. F., Nolan, R. H., & Penman, T. D. (2021). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters*, *16*(4), 044029. https://doi.org/10.1088/1748-9326/abeb9e

Cunningham, C. X., Johnson, C. N., Hollings, T., Kreger, K., & Jones, M. E. (2019). Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. *Ecography*, *42*(12), 2053–2059. https://doi.org/10.1111/ecog.04635

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*(1), 57–64. https://doi.org/10.1038/s41559-017-0402-5

Doherty, T. S., Dickman, C. R., Nimmo, D. G., & Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, *190*, 60–68. https://doi.org/10.1016/j.biocon.2015.05.013

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*(40), 11261–11265. https://doi.org/10.1073/pnas.1602480113

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

Endler, J. A. (1991). Interactions between predators and prey. J.R. Krebs, N.B. Davies (Eds.). In *Behavioural Ecology* (3rd edn., pp. 169–196). Blackwell Scientific Publishing.

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

Friend, G. R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: A review. *Biological Conservation*, *65*(2), 9–114.

Garvey, P. M., Glen, A. S., & Pech, R. P. (2016). Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator. *Behavioral Ecology and Sociobiology*, *70*(4), 481–492. https://doi.org/10.1007/s00265-016-2063-9

Geary, W. L., Ritchie, E. G., Lawton, J. A., Healey, T. R., & Nimmo, D. G. (2018). Incorporating disturbance into trophic ecology: Fire history shapes mesopredator suppression by an apex predator. *Journal of Applied Ecology*, *55*(4), 1594–1603. https://doi.org/10.1111/1365-2664.13125

Geiser, F., Stawski, C., Doty, A. C., Cooper, C. E., & Nowack, J. (2018). A burning question: What are the risks and benefits of mammalian torpor during and after fires? *Conservation Physiology*, *6*(1), coy057. https://doi.org/10.1093/conphys/coy057

Gill, A. M. (1975). Fire and The Australian Flora: A Review. *Australian Forestry*, *38*(1), 4–25. https://doi.org/10.1080/00049158.1975.10675618

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

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

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*, 386–398.

Haslem, A., Kelly, L. T., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., Avitabile, S. C., Callister, K. E., Spence-Bailey, L. M., Clarke, M. F., & Bennett, A. F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire: Habitat or fuel? Post-fire resource dynamics. *Journal of Applied Ecology*, *48*(1), 247–256. https://doi.org/10.1111/j.1365-2664.2010.01906.x

Hayes, H. G., Hollander, E. N. R., Vydro, S. A., Williams, D. M., & Blumstein, D. T. (2020). Cautious clams? Energetic state modifies risk assessment in giant clams. *Journal of Zoology*, jzo.12853. https://doi.org/10.1111/jzo.12853

Hettena, A. M., Munoz, N., & Blumstein, D. T. (2014). Prey responses to predator's sounds: A review and empirical study. *Ethology*, *120*(5), 427–452. https://doi.org/10.1111/eth.12219

Higuera, P. E., & Abatzoglou, J. T. (2021). Record-setting climate enabled the extraordinary 2020 fire season in the western United States. *Global Change Biology*, *27*(1), 1–2. https://doi.org/10.1111/gcb.15388

Hovick, T. J., McGranahan, D. A., Elmore, R. D., Weir, J. R., & Fuhlendorf, S. D. (2017). Pyric-carnivory: Raptor use of prescribed fires. *Ecology and Evolution*, *7*(21), 9144–9150. https://doi.org/10.1002/ece3.3401

Ibáñez, A., López, P., & Martín, J. (2014). Inter-individual variation in antipredator hiding behavior of Spanish terrapins depends on sex, size, and coloration. *Ethology*, *120*(8), 742–752. https://doi.org/10.1111/eth.12245

Ito, R., & Mori, A. (2010). Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). *Proceedings of the Royal Society B: Biological Sciences*, *277*(1685), 1275–1280. https://doi.org/10.1098/rspb.2009.2047

Ivey, T. L., & Causey, M. K. (1984). Response of white-tailed deer to prescribed fire. *Wildlife Society Bulletin*, *12*(2), 138–141.

Jolly, C. J., & Phillips, B. L. (2021). Rapid evolution in predator-free conservation havens and its effects on endangered species recovery. *Conservation Biology*, *35*(1), 383–385. https://doi.org/10.1111/cobi.13521

Jolly, C. J., Smart, A. S., Moreen, J., Webb, J. K., Gillespie, G. R., & Phillips, B. L. (2021). Trophic cascade driven by behavioral fine-tuning as naïve prey rapidly adjust to a novel predator. *Ecology*. https://doi.org/10.1002/ecy.3363

Jolly, C. J., Webb, J. K., & Phillips, B. L. (2018). The perils of paradise: An endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biology Letters*, *14*(6), 20180222. https://doi.org/10.1098/rsbl.2018.0222

Kelly, E., & Phillips, B. L. (2016). Targeted gene flow for conservation. *Conservation Biology*, *30*(2), 259–267. https://doi.org/10.1111/cobi.12623

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., Penman, T. D., Regos, A., Rumpff, L., Santos, J. L., Smith, A. L., Syphard, A. D., Tingley, M. W., & Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science*, *370*(6519), eabb0355. https://doi.org/DOI: 10.1126/science.abb0355

Komarek, E. V. (1969). Fire and animal Behavior. In *Proceedings Tall Timbers Fire Ecology Conference: No. 9.* (pp. 160-207.). Tall Timbers Research Station, Tallahassee, Florida.

Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., Coss, R. G., Donohue, K., & Foster, S. A. (2009). Relaxed selection in the wild. *Trends in Ecology & Evolution*, *24*(9), 487–496. https://doi.org/10.1016/j.tree.2009.03.010

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, *48*(1), 25–34. https://doi.org/10.2307/1313225

López, P., Hawlena, D., Polo, V., Amo, L., & Martín, J. (2005). Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour*, *69*(1), 1–9. https://doi.org/10.1016/j.anbehav.2004.05.010

Matthews, J. K., Stawski, C., Körtner, G., Parker, C. A., & Geiser, F. (2017). Torpor and basking after a severe wildfire: Mammalian survival strategies in a scorched landscape. *Journal of Comparative Physiology B*, *187*(2), 385–393. https://doi.org/10.1007/s00360-016-1039-4

Mendyk, R. W., Weisse, A., & Fullerton, W. (2020). A wake-up call for sleepy lizards: The olfactory-driven response of *Tiliqua rugosa* (Reptilia: Squamata: Sauria) to smoke and its implications for fire avoidance behavior. *Journal of Ethology*, *38*(2), 161–166. https://doi.org/10.1007/s10164-019-00628-z

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology*, *23*(3), 457–462. https://doi.org/10.1093/beheco/arr220

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., Ritchie, E. G., Schneider, K., Turner, J. M., Watson, S., Westbrooke, M., Wouter, M., White, A., & Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, *94*(3), 981–998. https://doi.org/10.1111/brv.12486

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

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

Petelle, M. B., Martin, J. G. A., & Blumstein, D. T. (2015). Heritability and genetic correlations of personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Evolutionary Biology*, *28*(10), 1840–1848. https://doi.org/10.1111/jeb.12700

Petty, A. M., Setterfield, S. A., Ferdinands, K. B., & Barrow, P. (2012). Inferring habitat suitability and spread patterns from large-scale distributions of an exotic invasive pasture grass in north Australia: Gamba grass spread patterns. *Journal of Applied Ecology*, *49*, 742–752. https://doi.org/10.1111/j.1365-2664.2012.02128.x

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

Pyne, S. J. (2020). From Pleistocene to Pyrocene: Fire replaces ice. *Earth's Future*, *7*(11), e2020EF001722. https://doi.org/10.1029/2020EF001722

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Rossiter, N. A., Setterfield, S. A., Douglas, M. M., & Hutley, L. B. (2003). Testing the grass-fire cycle: Alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions*, *9*(3), 169–176. https://doi.org/10.1046/j.1472-4642.2003.00020.x

Savidge, J. A. (1987). Extinction of an Island Forest Avifauna by an Introduced Snake. *Ecology*, *68*(3), 660–668. https://doi.org/10.2307/1938471

Scesny, A. A. (2006). *Detection of fire by eastern red bats (*Lasiurus borealis*): Arousal from torpor*. Master's Thesis, Missouri State University.

Schmitz, O. J., & Trussell, G. C. (2016). Multiple stressors, state-dependence and predation risk—Foraging trade-offs: Toward a modern concept of trait-mediated indirect effects in communities and ecosystems. *Current Opinion in Behavioral Sciences*, *12*, 6–11. https://doi.org/10.1016/j.cobeha.2016.08.003

Setterfield, S. A., Rossiter-Rachor, N. A., Hutley, L. B., Douglas, M. M., & Williams, R. J. (2010). Turning up the heat: The impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. *Diversity and Distributions*, *16*, 854–861.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Stawski, C., Matthews, J. K., Körtner, G., & Geiser, F. (2015a). 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

Stawski, C., Körtner, G., Nowack, J., & Geiser, F. (2015b). 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

Stawski, C., Nowack, J., Körtner, G., & Geiser, F. (2017). A new cue for torpor induction: Charcoal, ash and smoke. *The Journal of Experimental Biology*, *220*(2), 220–226. https://doi.org/10.1242/jeb.146548

Swan, G., & Wilson, S. (2015). Where do they all come from? Animal movement immediately following a hummock grassland fire. *Australian Zoologist*, *37*(4), 485–491. https://doi.org/10.7882/AZ.2015.012

Trimmer, P. C., Ehlman, S. M., & Sih, A. (2017). Predicting behavioural responses to novel organisms: State-dependent detection theory. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1847), 20162108. https://doi.org/10.1098/rspb.2016.2108

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.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, *9*(11), 442-446.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (Lepomis gibbosus): An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*(3), 250–260. https://doi.org/10.1037//0735-7036.107.3.250

Wisenden, B. D. (2000). Olfactory assessment of predation risk in the aquatic environment. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *355*(1401), 1205–1208. https://doi.org/10.1098/rstb.2000.0668

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

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

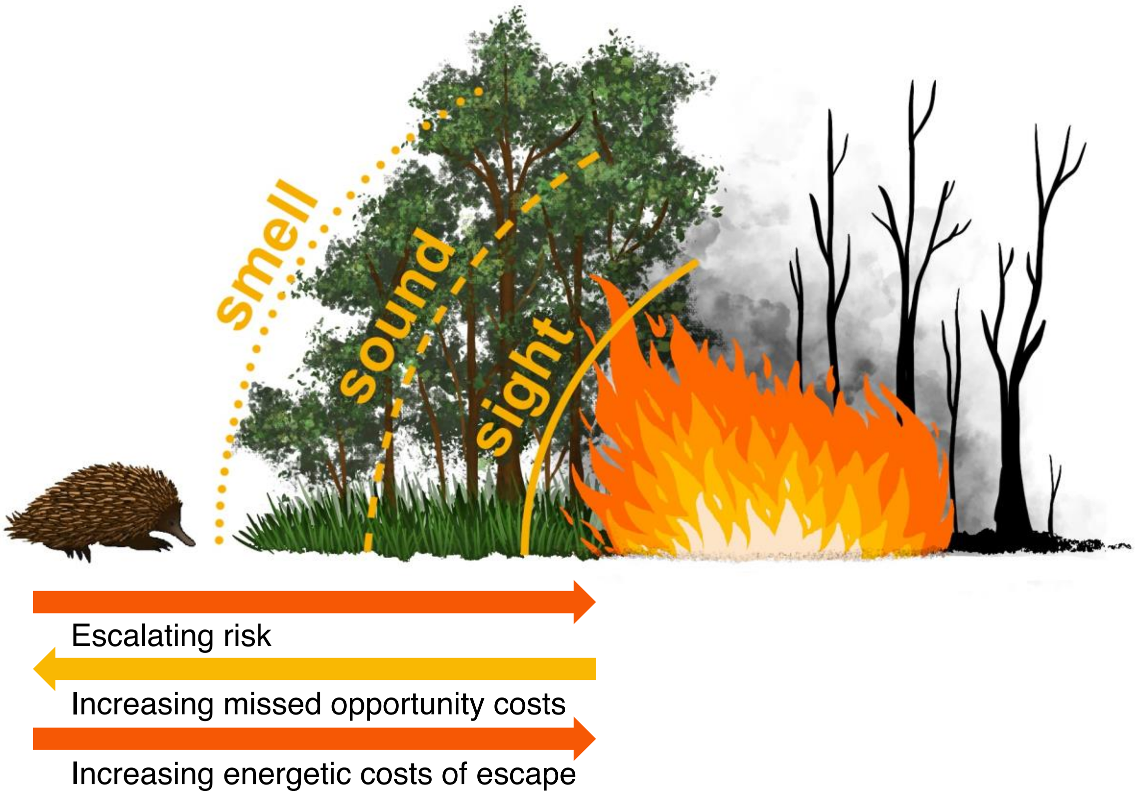

Figure 1. Different fire cue modalities and their association with risk (mortality by fire) and missed opportunity costs. Fires emit olfactory (smell), auditory (sound), and visual (sight) cues, each or all of which might be used by animals to reduce their risk of mortality in a fire. Yet animals must 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.

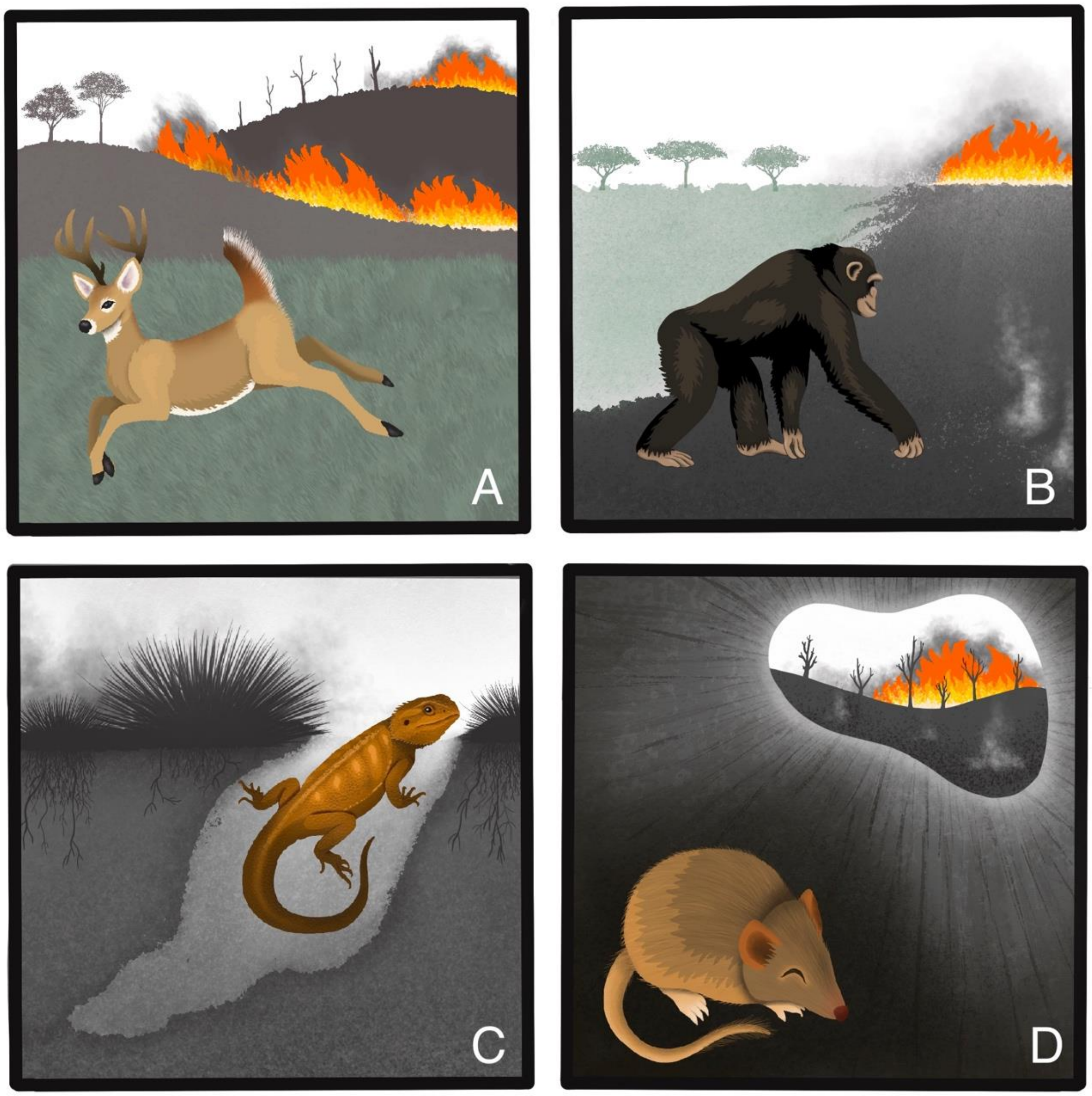

Figure 2. **Fire avoidance behaviours**. Fire in the landscape triggers a range of fire avoidance responses in animals. A) white-tailed deer (*Odocoileus virginianus*) employ *immediate evacuation* to rapidly flee approaching fire, anticipating its likely direction (Ivey & Causey, 1984). B) By *doubling 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., 2017; Stawski et al., 2015b).

Level 1 fire naivety

Level 2 fire naivety

Level 3 fire naivety

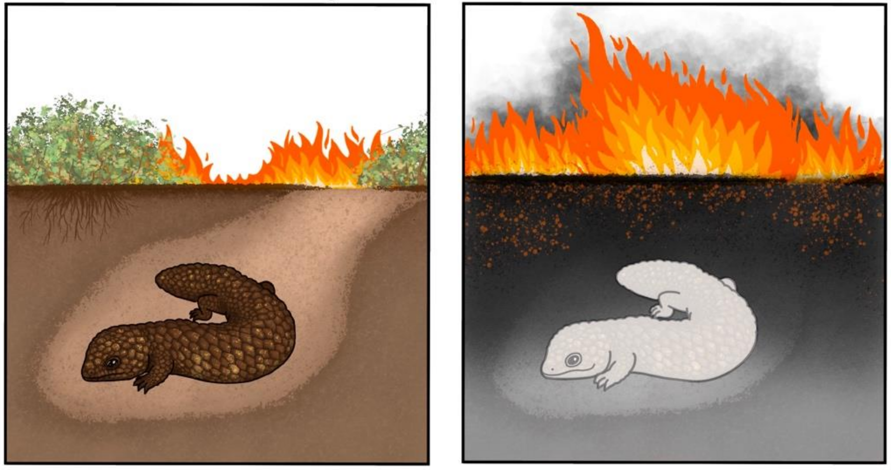

Figure 3. Multiple levels of fire naivety. Prey that inhabit ecosystems that have historically never burnt, such as rainforests, may be entirely naive to fire (level 1). They would have had no selective pressure to develop the ability to detect and recognise fire cues. Should these ecosystems burn, we 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. 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 fire avoidance 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 fire avoidance 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 fire avoidance responses become ineffective.