

## PERSPECTIVE

# Integrating sensory ecology and predator-prey theory to understand animal responses to fire

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**Abstract**

Fire regimes are changing dramatically worldwide due to climate change, habitat conversion, and the suppression of Indigenous landscape management. Although there has been extensive work on plant responses to fire, including their adaptations to withstand fire and long-term effects of fire on plant communities, less is known about animal responses to fire. Ecologists lack a conceptual framework for understanding behavioural responses to fire, which can hinder wildlife conservation and management. Here, we integrate cue-response sensory ecology and predator-prey theory to predict and explain variation in if, when and how animals react to approaching fire. Inspired by the literature on prey responses to predation risk, this framework considers both fire-naïve and fire-adapted animals and follows three key steps: vigilance, cue detection and response. We draw from theory on vigilance tradeoffs, signal detection, speed-accuracy tradeoffs, fear generalization, neophobia and adaptive dispersal. We discuss how evolutionary history with fire, but also other selective pressures, such as predation risk, should influence animal behavioural responses to fire. We conclude by providing guidance for empiricists and outlining potential conservation applications.

**KEYWORDS**

animal behaviour, climate change, ecological disturbance, fear, fire, movement ecology, neophobia, signal detection, wildlife conservation

## INTRODUCTION

Fire can have major impacts on ecosystems (Abatzoglou & Williams, 2016; He et al., 2019; Kelley et al., 2019; Kelly et al., 2020). Now, in the ‘Pyrocene’, we are experiencing unprecedented fire regimes worldwide (Pyne, 2020). In some ‘fire-prone’ environments, fire was historically relatively regular and carefully managed (Mariani et al., 2022). In other habitats, fire was previously less frequent, or negligible relative to the life cycle of resident, ‘fire-naïve’ species. Yet today, due to both altered management and climate change, fire regimes are changing temporally and spatially. In fire-prone environments, fire now often occurs over a longer season (Safford

et al., 2022). Moreover, across the globe, large and intense fires are now remarkably common in dry forests in North America, Australia and the Mediterranean, rainforests in the Amazon and Congo Basins, Siberian tundra and even deserts (e.g. California, Nevada) (Abatzoglou et al., 2019; Hugelius et al., 2020; Kelly et al., 2020). Importantly, most of our understanding of fire ecology comes from the study of plants (Bond & Keeley, 2005). However, a growing literature is beginning to shed light on the complex relationships between fire, plants and also animals (Banks et al., 2017; Doherty et al., 2022; Engstrom, 2010; Foster et al., 2020; Geary et al., 2020; He et al., 2019; Nimmo et al., 2019, 2021; Pausas, 2019; Pausas & Parr, 2018; Sergio et al., 2018; van Mantgem et al., 2015).

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Like plants, animals can respond adaptively to fire, avoiding or taking advantage of it. While plants rely on physiological, morphological or life history adaptations to survive fire, animals can also use behavioural responses (Geary et al., 2020; Nimmo et al., 2021; Pausas, 2019). Although some animals living under long-term, regular, predictable fire regimes might have evolved fixed, preemptive adaptive behaviours to fire (e.g. constructing nests out of mud rather than flammable material; Bignell et al., 2011; Hölldobler & Wilson, 1990; Peterson, 2010), our focus is on immediate, flexible behavioural reactions to fire. How animals respond behaviourally (e.g. fleeing versus seeking refuge) and how quickly—can have major impacts on individual survival and, ultimately, on entire ecosystems. If animals survive, then subsequent post-fire behaviours are also important and indeed, relatively well studied (see Nimmo et al., 2019); accordingly, we focus here on behavioural responses to approaching fire. While animals exhibit a range of behavioural responses, the explanations and mechanisms behind this variation remain under-studied and poorly understood. This limits our ability to understand and predict the impacts of fire on evolution, and on populations, communities and ecosystems, which impedes proactive conservation and management interventions. To help fill this important knowledge gap, we describe here a novel framework for predicting and understanding variation in behavioural responses to fire.

Our proposed framework is built around the fundamental concept that animal responses to dangers are governed by cue-response systems. An organism's ability to detect, assess and respond to stimuli released by a threat is determined by its sensory and cognitive capacities (Evans et al., 2019). Although animals are faced with numerous challenges to survival, from starvation to disease to competition, one of the most salient and well-studied threats is predation (Sih, 1992; Sih et al., 1998, 2010; Wirsing et al., 2021). Most animals, even large apex predators (Suraci et al., 2019), face predation and have adaptations to detect risk and respond appropriately.

Accordingly, Nimmo et al. (2021) recently suggested using prey responses to predation risk as a framework for understanding animal responses to fire. Just as naïve prey respond poorly to predators (Carthey et al., 2017), species that lack evolutionary history with fire might be 'unable to recognize fire cues as a sign of impending danger until it's too late' (Nimmo et al., 2021). For animal species that evolved with fire, the authors predict adaptive use of fire cues to assess risk (e.g. rely on visual cues in open habitats, but olfactory cues in visually obstructed habitats). Following the theory on antipredator behaviour, they further predict that responses to fire should depend on the individual's energetic and opportunity costs of responding, its state and personality. They emphasize, however, that even fire-adapted animals might exhibit maladaptive responses to novel fire regimes. Here, we build upon the 'fire ecology meets predator-prey ecology' approach of Nimmo et al. (2021) in several ways to generate a series of novel predictions on: (1)

why animals that evolved with fire respond the way they do; (2) if and how that might change as fire regimes change; (3) how animals that were previously naïve to fire might respond through generalized fear responses.

The heart of the 'fire ecology meets predator-prey ecology' view is the hypothesis that many animals respond to fire cues using shared or analogous mechanisms to those they use to respond to predation risk. This is particularly likely to be true for animals that have adaptations for coping with predators, but that are fire naïve or only rarely exposed to fire. We hypothesize, for example, that whether these animals use visual versus olfactory cues to detect fire might not reflect what is optimal for collecting useful information about fire, but might instead reflect how they detect predators. Then, when animals perceive fire as potentially dangerous, their basic response (e.g. to flee versus hide in a bush versus climb a tree) might depend largely on their primary response to predation risk, even if that response is not effective against fire. We further posit that the strength of their response might reflect a generalized level of fear or neophobia (fear of novel stimuli) shaped not by fire *per se*, but more by their evolutionary history with predation risk or other dangers. This idea is an example of *fear generalization* (see Box 1), a concept that is well-studied in humans and is gaining attention in non-human animals. The concept emphasizes that various cognitive, physiological or hormonal mechanisms underlie a tendency for animals to exhibit correlated consistent individual differences in their fear of multiple threats. Fearful animals that respond more strongly (than other conspecifics) to predation risk are also more fearful than others of various other threats (e.g. predators, parasites, pathogens, humans, moving vehicles, roads, chemical stressors and fire; Sih et al., 2023).

Animals with an evolutionary history with fire might fine-tune those responses, deciding the optimal moment to flee or what type of shelter to use based on their assessment of fire cues and levels of risk. Even fire-adapted animals, however, often have imprecise information on fire risk and the benefits versus costs of different responses, especially in the context of modern fire regimes. Thus, rather than assume a well-adapted response, we use theory on prey behaviour when faced with uncertain cues about risks (e.g. signal detection theory and the 'smoke detector principle') to generate more nuanced predictions on behavioural responses to fire cues. Below, we develop and describe our framework and predictions in detail, review relevant theoretical and empirical literature, provide suggestions for empiricists, conservationists and managers and discuss future directions.

## VARIATION IN BEHAVIOURAL RESPONSES TO FIRE

Behavioural responses to fire fall into two broad categories: stay (refugia/resistance) versus leave

### BOX 1 Fear generalization

When organisms detect a stimulus, they need to evaluate whether it should be approached, avoided or ignored. Rather than treat every situation as unique, organisms typically generalize. If prey avoid a given predator, they often generalize to avoid similar predators, but not very different ones (Anton et al., 2020; Carthey et al., 2017; Carthey & Banks, 2014). Fear generalization can be especially important if it allows prey to adaptively avoid novel predators that resemble a familiar predator. However, over-generalizing can be costly if it results in over-avoidance of safe situations; for example, avoidance of humans (e.g. ecotourists) that pose no risk (Trimmer, Ehlman, McNamara, et al., 2017). Cognitive neuroscientists have studied behavioural and neurological aspects of fear generalization; in particular, over-generalization in the context of post-traumatic stress disorder, PTSD (Asok et al., 2019; Dunsmoor & Murphy, 2015; Dunsmoor & Paz, 2015).

For ecologists, the study of fear generalization has largely focused on generalization from cues of familiar to novel predators (Carthey & Blumstein, 2018; Sih et al., 2010). Empirical studies have quantified variation in the degree of generalization (Anton et al., 2020; Carthey & Banks, 2014), and signal detection models have analyzed factors that might explain variation in generalization (Ehlman et al., 2019; Trimmer, Ehlman, McNamara, et al., 2017; Trimmer, Ehlman, & Sih, 2017). Far less studied is the possibility that fear of predators increases fear of other biotic dangers (parasites, aggressive competitors, pathogens), or avoidance of abiotic stressors (e.g. moving vehicles, chemical pollutants, noise or heat stress). If fear of predators generalizes to other very different stressors (Sih et al., 2023), does fear generalization depend on a shared sensory modality for cue detection? If predators were detected largely via olfactory cues, does that increase the animal's sensitivity, in particular, to olfactory-based stressors, even ones that are very different from predation risk? How much does novelty per se (neophobia, Box 2) enhance fear generalization? Does individual variation in the breadth of fear generalization reflect the animal's personality (i.e. boldness) as measured by standardized assays (e.g. latency to leave refuge)?

Here, we apply the concept of fear generalization to fear of fire cues. Particularly intriguing are situations when fire cues overlap in sensory modality or even cue specific with cues associated with other dangers. As an example at the molecular level, rats exhibit a fear response to 2-phenylethylamine (PEA), a compound found in high concentrations in carnivore urine. Interestingly, 2-PEA shares a similar chemical structure to compounds found in smoke. Because its odour receptor is highly conserved in mammals, it is plausible that there is sufficient overlap that smoke would elicit the same behavioural response pathway in these mammals as a carnivore. Smoke could also trigger a generalized fear response due to the presence of particulate organic carbon and polycyclic aromatic hydrocarbons, compounds with genotoxic and mutagenic effects (Nephew et al., 2020).

Visual cues such as smoke plumes, and an advancing flame front or auditory cues like the high-intensity, low-frequency (400 Hz) roar emitted by crowning fires (Zhang et al., 2019) may not have much cue overlap with predator signals (except to the degree that they are large and loud and could thus evoke fear; Hein et al., 2018; Peek & Card, 2016), but animals tuned in to these sensory modalities may avoid these cues simply because they reduce their ability to detect threats.

Beyond the role of shared cue modalities, plausible, but untested hypotheses are that previous exposure to predators, or other stressors, or novel situations enhances fear that spills over to fear of fire. Conversely, might prior exposure to industrial pollutants or distant low-intensity burns desensitize animals to fire? Or, might prior habituation to humans reduce responses to real dangers, both predators (Geffroy et al., 2015) and fire? Of interest also is whether these earlier exposures are personal (learned fear that carries over to fear of fire), transgenerational (parental priming of fear that carries over to fear of fire) or over an evolutionary time scale.

(dispersal, movement out of the individual's home range) (Booyesen & Tainton, 1984; Pausas, 2019; van Mantgem et al., 2015). Large mammals can sometimes outrun even widespread fires (Garvey et al., 2010); small mammals (Geluso et al., 1986; Koprowski et al., 2006), lizards and amphibians may 'outrun' smaller fires (Rochester et al., 2010), and insects and birds can fly rapidly and over large distances to avoid fire (Nimmo et al., 2019; Overton

et al., 2022). Yet the ability to flee fire does not guarantee survival. The efficacy of dispersal depends on an animal's speed relative to the fire, the timing of when they initiate their escape attempt and their ability to navigate a safe path away from an often unpredictably-spreading and disorientating blaze (Jolly et al., 2022; Quintiere, 2016).

Small to medium-sized mammals, reptiles, flight-limited birds and amphibians with limited dispersal

ability tend to stay, relying on refugia, such as tree hollows, burrows, leaf litter, boulder piles or crevices, moist riverbeds, caves, etc. (Chia et al., 2016; Robinson et al., 2013; van Mantgem et al., 2015). Some fire-adapted small marsupials like the yellow-footed antechinus (*Antechinus flavipes*) respond to a combination of smoke exposure and nutritional stress by hiding and going into torpor (Stawski et al., 2017). Shelled animals like armadillos and tortoises may have some degree of morphological resilience to fire (Catano & Stout, 2015), but animal resistance to fire is not as effective as for plants (Pausas, 2019). More mobile species can either disperse, or seek local refuge during fires. Wallabies (*Wallabia bicolor*) and chimpanzees (*Pan troglodytes*) combine the two, fleeing a limited distance, then doubling back into safe, already-burnt patches (Garvey et al., 2010; Pruetz & LaDuke, 2010).

Intriguingly, some animals are attracted to fire. Birds of prey and mammalian carnivores including feral cats (*Felis catus*) have been drawn from over 10 kilometres away to capitalize on fleeing and burned prey (Foster et al., 2020; Hovick et al., 2017; McGregor, Cliff, & Kanowski, 2016). Others require fire to reproduce, like pyrophilous beetles that breed only in freshly burnt, still-smoking trees (Schmitz, Schneider, et al., 2015). Since fire-attracted species often stay near fires, they may have adaptations to avoid burning and asphyxiation; for example, the thoracic infrared-sensing organ of pyrophilous beetles is hypothesized to enable both navigation to fire and also avoidance of hotspots upon arrival (Schmitz, Schneider, et al., 2015). For predatory mammals, relevant adaptations could simply be their high mobility and cognitive navigation capabilities, though these might not be sufficient to escape unscathed; after recent wildfires in California, mountain lions (*Puma concolor*) required treatment for severely burned paws (Dr. J. Peyton, pers. comm.).

## PROPOSED FRAMEWORK: THE PARALLELS BETWEEN FEAR OF FIRE AND FEAR OF PREDATION

Parallel to how prey responds to predators (Figure 1; Lima & Dill, 1990), animal responses to fire involve three key steps: cue perception, assessment and response. For animals to adequately respond to a potential threat—be it a predator or approaching wildfire—they must first perceive cues emitted by the threat before it is too late to react effectively. Upon perception of a cue, animals can then assess the cue's strength relative to an internal threshold (Trimmer, Ehlman, McNamara, et al., 2017). If a cue surpasses that threshold, animals initiate an evasive response (e.g. disperse or seek refuge).

Species with an evolutionary history with fire might have evolved cue-response systems that result in adaptive responses to fire. Crucially, however, the adaptive

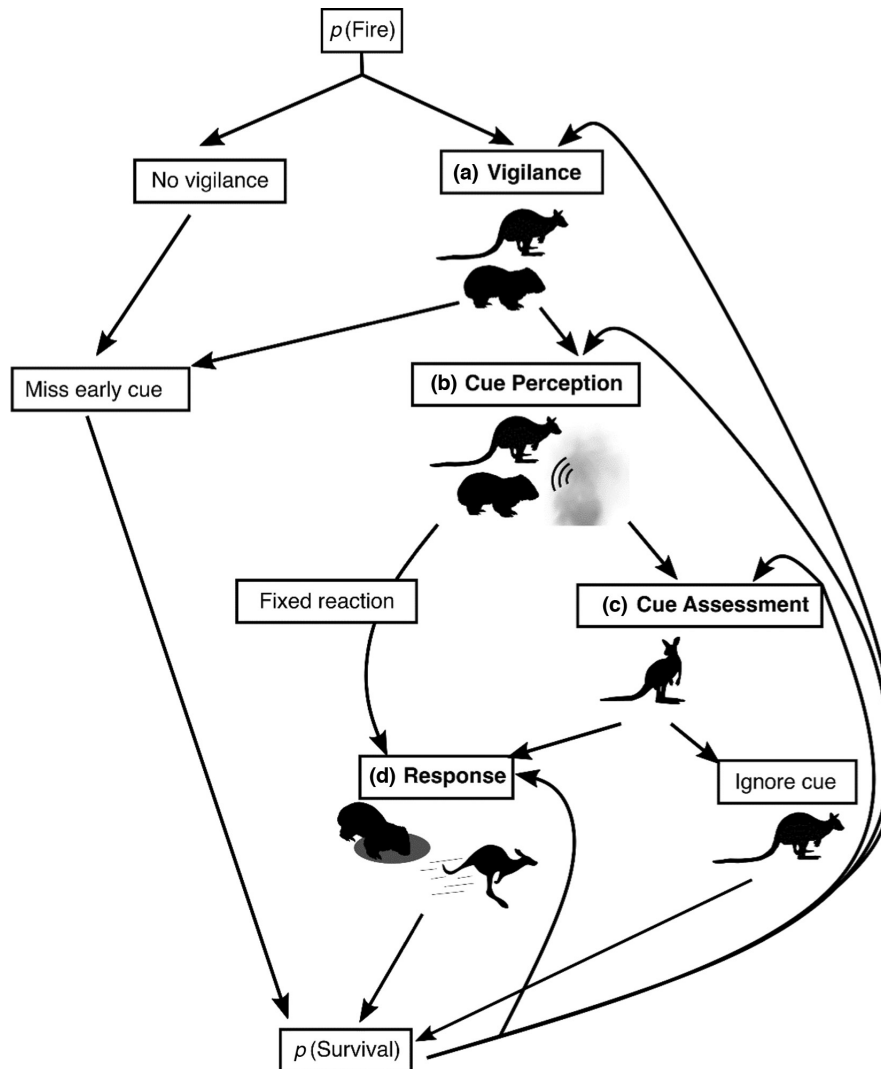
precision of their response is likely limited by lack of precise information about the intensity, spatial extent and future spread of a fire. Even humans with technologically advanced information availability fall well short of perfection in predicting fires and responding appropriately (Das, 2018; Wong et al., 2020). Our framework thus draws heavily from the literature that predicts how imperfect information and the potential value of collecting more information should affect behaviour (Brown & Kotler, 2004; Ehlman et al., 2019; Sih, 1992; Sutton & O'Dwyer, 2018; Trimmer, Ehlman, McNamara, et al., 2017). Imperfect information causes errors: either over- or under-responding to risk. Animals tend to 'choose' the type of error that is perceived to be less costly. Decision-making under uncertainty affects each step in a fire response: investment in vigilance, when to respond and how to respond.

Some populations are likely experiencing fire for the first time in recent history. Even in locations where fires have historically occurred, if fire has been infrequent, many individuals are effectively fire-naïve. Like prey naïve to exotic predators, these animals might exhibit little or no adaptive response to fire (Nimmo et al., 2021). However, just as some naïve prey respond appropriately to exotic predators (Carthey & Blumstein, 2018; Ehlman et al., 2019), some animals with little or no evolutionary history with fire might still exhibit suitable behaviours. We posit that variation in responses of naïve animals to fire can be explained by generalized fear responses (Box 1) or responses to novel stimuli (neophobia, Box 2). A general prediction is thus that animal responses to fire will often depend on their level of fear of other dangers, especially predators. Prey that have evolved with higher predation risk will often exhibit greater vigilance and stronger responses to cues associated with risk; however, this prediction is mediated by tradeoffs—by the cost of responding to risk.

Importantly, the idea that fear of predators explains responses to fire depends on whether fear is 'specialized' to predation risk versus 'generalized' to carryover to fear of fire. This concept applies to the various stages in the overall response to fire. If vigilance or fear are specialized to predation risk, without carryover to fire, then fire naïve animals will be less likely to respond to fire. In contrast, while fire naïve animals might not be vigilant to fire *per se*, if vigilance is general, then vigilance relative to other common threats (predators, competitors, inclement weather) may carry over to enhance detection of fire cues. In addition, even if these fire-naïve animals do not 'understand' the danger from fire, their generalized fear or fear of novel stimuli can cause them to readily flee or hide from fire.

In the following sections, we discuss each stage of the fire cue-response system through a sensory ecology framework, taking into account the costs and benefits of each step (*sensu* Bonte et al., 2012; Figure 1) in the context of generalized threat cue-response mechanisms derived from antipredator behaviour.





**FIGURE 1** A sequential framework illustrating the sensory ecology of responses to fire. Animals are more likely to detect fire if they are (a) vigilant. A major question is whether vigilance is ‘multi-purpose’. If so, vigilance towards predation risk could increase the probability of detection of other threats, like fire, permitting cue perception (arrow to (b)). If, on the other hand, vigilance is specific, where vigilance towards one threat decreases vigilance towards another, fire detection could be suppressed by increased predation pressure (arrow to left, miss early cue). With adequate vigilance, animals can (b) perceive fire cues, but only if such cues fall within their sensory capabilities. For example, an approaching fire could emit strong olfactory cues and weak auditory cues, but these will only be perceived by animals that have sensory attunement within the proper range. An animal's range of sensory detection is often shaped by cues associated with resources and predators (in their developmental, parental and evolutionary environments), which may or may not overlap with fire cues. Upon perceiving a novel cue, animals can employ an immediate ‘fear’ response (arrow to left to (d)) or not (arrow to right), and, if so, how, which may include additional cue sampling. Responses fall into two broad categories: dispersal and refuge-seeking. Highly mobile animals have the option to disperse (e.g. the wallaby shown), but whether they do so can depend on historical costs and benefits of dispersal. Refuge-seeking should be particularly likely in animals that commonly seek refuge to avoid predation risk or other dangers (e.g. the wombat). The efficacy of a response is likely reduced with intensifying fire regimes, though animals that tend to avoid novel threats are still likely to fare better than those that do not. Through each step in this process, the new Pyrocene-epoch fire regimes create mismatches that decrease the chance of animals responding appropriately to fire: (a) Vigilance can be reduced if drought increases the need to focus on foraging as opposed to avoiding threats. (b) Fire cues may be obscured by background noise (e.g. pollution, campfires, other novel stimuli). (c) Assessment and adaptive response may be impaired when fires behave differently from historical fires that animals evolved under. Finally, even the strongest responses may be insufficient in extremely widespread, high-energy fires (e.g. fleeing during Australian Megafires of 2020).

## Vigilance and perception

As noted above, if antipredator vigilance carries over to detection of fire then many animals have some degree of vigilance to fire even if fire is novel. In that case, detection

of fire should depend on the animals' level of overall vigilance. Animals tend to increase vigilance when risk is high (Beauchamp, 2015; Unck et al., 2009), but decrease vigilance in larger groups (see Box 4). Even when asleep, many animals retain some antipredator vigilance

## BOX 2 Neophobia and responses to fire

Neophobia is the fear of novel stimuli or situations, where novelty can reflect either individual or evolutionary history. It has been documented in a range of contexts including novel predators, foods, social partners, environments and objects (Crane et al., 2020; Crane & Ferrari, 2017; Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2009). Neophobia can enhance survival when it causes animals to avoid novel predators or other novel dangers without the need to learn from experience with those dangers (Crane et al., 2020; Greenberg, 2003). For many animals, fire and fire cues are novel, either evolutionarily or individually. We thus hypothesize that, like generalized fear (Box 1), neophobia can cause animals to respond (or respond more quickly) to fire and potentially increase survival.

Numerous studies show that individuals and species differ in their level of neophobia (Brown & Jones, 2016; Elvidge et al., 2016; Moretti et al., 2015). A cost-benefit approach to explaining variation in neophobia emphasizes factors including: (1) the diversity of previous experience that affects how often situations are perceived as novel and uncertain; (2) whether in the past, novel situations tended to be dangerous versus rewarding; (3) the relative costs of under-avoiding novel dangerous situations versus over-avoiding novel rewarding ones (Crane et al., 2020).

These factors predict some general trends. Migratory species (or those that disperse readily) might generally experience a greater diversity of situations than sedentary ones and thus tend to be less neophobic (Mettke-Hofmann, 2014). Animals that have been exposed to high predation risk should be more neophobic, particularly if they live in areas with higher risk from novel predators (Elvidge et al., 2016). Lower trophic levels typically experience higher predation risk than upper trophic levels, and should thus be not just more fearful, but also more neophobic (Crane et al., 2020). Experiments manipulating animals' past experiences show that prey exposed to predation risk are indeed more neophobic not just to novel predator cues, but to novel objects and stimuli more generally (Brown et al., 2014; Ferrari et al., 2007). Conversely, hungry animals that have more to lose from over-avoiding non-dangerous novel situations may be less neophobic. Hence, neophobia would be less important when food is scarce.

If neophobia carries over to fear of fire, the above predictions should explain some variation in behavioural response to fire, particularly for fire-naïve animals. Many of the predictions about neophobia overlap with those on responses to fear generalization—both are reasons why even fire-naïve animals might respond to fire cues. Indeed, if predation risk is a main cost of ignoring novel cues, then the level of neophobia should be correlated to the level of generalized fear. However, neophobia and generalized fear might differ in the strength of fear and the type and, ultimately, effectiveness of the response to fire. It can be maladaptive to freeze (or perhaps freeze and assess for too long) when an intense fire is approaching rapidly. Since neophobia is a response to uncertainty that can often be resolved by some avoidance along with monitoring and assessment, it might often cause animals to 'freeze and assess'. While some animals also respond to predator cues by freezing in place, when refuge is available, generalized fear should often induce fleeing to refuge. We thus predict that, all else the same, animals that perceive fire as a direct danger will respond more strongly and potentially more effectively than animals that treat fire as an uncertain stimulus.

(Lima & Rattenborg, 2007; Mathews et al., 2006). Vigilance, however, exacts costs in energy, time and lost opportunities relative to other needs, necessitating tradeoffs (Bednekoff & Lima, 2005). Animals thus tend to be less vigilant when their energy state is low (so the need to forage is high; Beauchamp, 2015), when they are engaged in contest competition with conspecifics (Hess et al., 2016; Yee et al., 2013) or when performing complex tasks (Dukas & Kamil, 2000). Habitat conditions also influence vigilance levels (Costelloe & Rubenstein, 2018; Favreau et al., 2018; Kotier et al., 2010). For example, Bennett's wallabies (*Macropus rufogriseus*) increased vigilance during windy conditions, probably because wind obscures visual and auditory predator cues (Blumstein & Daniel, 2003).

Alternatively, vigilance may be specialized (Leavell & Bernal, 2019) where focused vigilance for predators reduces detection of fire. A key issue then is, when do we expect antipredator vigilance to carryover to enhance vs reduce detection of fire? A simple idea is that vigilance for predators is more likely to generalize to vigilance for fire if the sensory mechanisms used to detect predators are also effective at perceiving fire amid background noise (Leavell & Bernal, 2019; Weissburg et al., 2014). Animals can potentially detect fire using visual, olfactory, auditory, thermal or mechanosensory stimuli (Table 1) deriving from flame propagation, smoke or ashes or other factors more loosely tied to conditions associated with fire. In fire-prone regions, evidence exists for adaptive fire-recognition sensory mechanisms where

**TABLE 1** Cues and sensory mechanisms for perception of approaching fire.

Fire stimulus	Cue type	Sensory mechanism	Species	Reference
Flame	Visual Spectra	Sight		
		Heat		
		Infrared (IR) sensors	Pyrophilous insects: <i>Melanophila</i> spp. <i>Aradus</i> spp. <i>Acanthocnemus nigricans</i> <i>Merimna atrata</i>	Kreiss et al. (2005); Schmitz, Schneider, et al. (2015); Schmitz, Schmitz, et al. (2015); Schneider et al. (2015)
			[IR sensors, but not for fire in Crotalinae, <i>Desmodus rotundus</i> ]	
		Olfactory—terpenes of heated eucalypts	<i>Merimna atrata</i>	Schmitz, Schneider, et al. (2015); Schmitz, Schmitz, et al. (2015)
	Sound	Auditory	<i>Hyperolius nitidulus</i> <i>Lasiurus borealis</i>	Grafe et al. (2002); Scesny and Robbins (2006)
Smoke	Vibrations	Somatosensory		
	Gas i.e., CO, CO <sub>2</sub>	Broadband IR sensors?		
	Visual—cloud	Sight	Pyrophilous insects	Schmitz, Schneider, et al. (2015); Schmitz, Schmitz, et al. (2015)
		Smell	Olfactory	<i>Tiliqua rugosa</i> <i>Cercartetus nanus</i> <i>Sminthopsis crassicaudata</i> <i>Nyctophilus gouldi</i> <i>Antechinus flavipes</i> <i>Lasiurus borealis</i>
	Particulates (ash)	Respiratory/ Somatosensory		
Weather	Humidity	Mechanical		
	Pressure			
	Wind			

the specific sensory mode used to detect fire appears to depend on their broader sensory experience with the world—their ‘umwelt’ (Van Dyck, 2012). Animals that use olfaction to detect predators (e.g. small mammals, lizards and various insects) also use olfaction to detect smoke (Álvarez-Ruiz et al., 2021; Doty et al., 2018; Lyon et al., 2000; Mendyk et al., 2020; Nowack et al., 2016; Sanderfoot et al., 2021; Scesny & Robbins, 2006; Simons, 1991; Stawski et al., 2017). Some animals in fire-prone areas even wake up from sleep when exposed to smoke (e.g. pygmy-possums (*Cercartetus nanus*; Nowack et al., 2016), and sleepy lizards (*Tiliqua rugosa*; Mendyk et al., 2020)). In contrast, acoustically-oriented bats (*Nyctophilus gouldi*, *Lasiurus borealis*; Doty et al., 2018; Scesny & Robbins, 2006) and frogs (*Hyperolius nitidulus*; Grafe et al., 2002) respond to the sound of fire. Visual stimuli, such as the glow of a night-time blaze, or large smoke plumes, may cue visually-oriented animals to the presence of fire; however, to our knowledge, these possibilities remain to be investigated.

Since both fires and smoke tend to move downwind, olfactory cues like smoke can provide valuable advance notice of an approaching fire. In contrast, in visually obstructed habitats, visual stimuli like flames might be more

indicative of imminent danger. Nimmo et al. (2021) thus suggested that animals that rely heavily on vision may be more prone to missing early fire cues. However, swirling winds can obscure olfactory signals. For predation risk, animals that use multiple cues involving multiple sensory modes likely respond better to novel predators than those that rely heavily on one type of cue (Munoz & Blumstein, 2012; Sih et al., 2010; Weissburg et al., 2014). We thus posit that species that commonly rely on multiple sensory modes will, all else being equal, be more sensitive to approaching fires. For example, red bats responded most strongly when exposed to both the sound of fire and the smell of smoke (Scesny & Robbins, 2006). Since animals that have experienced multiple predators in their evolutionary history appear more likely to use multiple cues to assess danger (Blumstein, 2006; Ehlman et al., 2019), we posit that even if animals are fire naïve, if they have evolved with a greater diversity of predator archetypes, they might be more likely to use multiple cues to perceive fire. Conversely, if fire perception parallels perception of predation risk, then island species that lack extensive predation histories and often fare poorly with invasive predators (Cox & Lima, 2006) might also fare poorly with fire. Of course, even if the taxonomic

diversity of predators was historically relatively low, in places like Australia where animals have a long history of exposure to fire, they should still respond well to fire (Hradsky, 2020; Pausas & Parr, 2018).

Finally, social animals often respond if they observe conspecifics, or even heterospecifics, fleeing (Gil et al., 2018; Magrath et al., 2015). Intriguingly, in that case, individuals or species that are particularly sensitive to fire risk might, by fleeing or seeking refuge, be 'keystone information providers' for less sensitive or fire-naïve animals (Box 4).

### Signal detection thresholds and cue assessment: The 'smoke detector principle' for actual smoke

Once an animal senses a fire cue, the decision to react versus ignore depends on the cue's strength relative to an internal threshold. If the cue is strong enough, animals respond, whereas if a cue falls below the threshold, animals can either continue assessing the situation or ignore it. Cue strength depends on the potency of the cue at the source and the distance to it (Sutton & O'Dwyer, 2018).

Signal detection theory (SDT) provides predictions on factors affecting the cue threshold, and thus the relative likelihood that animals will respond to fire cues. SDT has been used to explain variation in mate or food choice (Holen & Sherratt, 2021; Pearse et al., 2013), evolutionary traps involving habitat choice (Pollack et al., 2021; Robertson et al., 2013) and the decision to ignore versus respond to predators or other potential threats (Ehlman et al., 2019; Trimmer, Ehlman, McNamara, et al., 2017; Trimmer, Ehlman, & Sih, 2017). For simplicity, SDT typically assumes that animals choose between two actions (e.g. ignore versus flee) in two possible scenarios (e.g. safe versus dangerous) given one cue. In this case, the optimal solution is to flee when the scenario is dangerous, and to 'ignore' when conditions are safe.

For predation risk, numerous studies show that well-adapted prey respond to even low levels of predator-specific cues that reliably indicate an impending attack (Weissburg et al., 2014). For example, prey are often highly sensitive to the smell of a dangerous predator. However, even naïve prey commonly respond to general stimuli such as the rapid approach of a large object even if the object does not resemble an actual predator (e.g. a featureless circle). Larger objects approaching more rapidly are more likely to induce an escape response. Although response thresholds tend to be lower for threat-specific as compared to general cues, the generality is that cue strength must exceed a threshold to generate a response.

For fire-adapted animals, SDT predicts that response thresholds should depend on both: (1) cue reliability—the probability that fire cues reliably indicate danger and (2) the relative costs of not responding to true danger versus responding unnecessarily to false alarms. Adding state-dependence to SDT further predicts that

the response threshold (which is inversely related to readiness to flee) should be higher if animals are energy stressed (i.e. higher cost of 'false alarms') and that the threshold can depend in complex ways on the timing of the event relative to the organism's life cycle demands (Ehlman et al., 2019; Trimmer, Ehlman, McNamara, et al., 2017; Trimmer, Ehlman, & Sih, 2017).

With regard to cue reliability in the context of fire, false alarms may include cues like drought and heat, barometric pressure changes, storm or dust clouds, signals produced by other animals or plants and particularly anthropogenic signals, such as industrial or vehicular exhaust and sound or even barbecues, campfires or humans smoking. 'True' fire cues may also be unreliable if they derive from fires that are distant or burn out before they reach the animal. Cue reliability for fire is high only if the fire spreads in a spatially and temporally predictable way, and if the cues that animals detect accurately reflect the predictable aspects of a fire's future spread. Wind that blows both smoke and fire towards an animal might make smoke a reasonably accurate cue, but less so if the wind changes direction after the animal has committed to a response.

Conversely, false negatives that result in under-responding to fire produce substantial fitness costs. The main source of mortality due to wildfires is often the long-term change in vegetation after a burn, which can limit shelter and foraging opportunities (Puig-Gironè et al., 2018). Still, there are numerous reports of death and injury due to direct fire effects (e.g. burning, asphyxiation from smoke), especially for small, relatively immobile species (Abom et al., 2016; Abom & Schwarzkopf, 2016; Namukonde et al., 2017). Fire is intuitively highly costly if evasive action such as burrowing or fleeing is not taken. Due to the asymmetry in potential costs of under vs over-responding, as long as evasion costs are not extremely high (and particularly if evasion costs can be later offset by compensatory behaviour), the optimal threshold should be low (Ehlman et al., 2019). Thus, in many circumstances, upon detecting a fire cue, animals should respond, even when the threat is not real; in evolutionary psychology, this is known as the 'smoke detector principle' (Nesse, 2001).

However, fire avoidance may in fact be extremely costly if it necessitates long-distance dispersal or re-fuging with energy conservation tactics such as torpor (Geiser et al., 2018). Even if a fire response is not particularly costly, if false alarms are common, cumulative overexpression of avoidance behaviours can exact a significant cost in terms of energy, time, lost mating opportunities or territory, etc. (Trimmer, Ehlman, & Sih, 2017). Hence, if fire is extremely rare and background factors frequently generate 'false alarms', natural selection should favour animals that only respond to very strong fire cues. Unfortunately, by that time, it might be too late to escape. In contrast, animals whose evolutionary or recent histories have driven them to



use ‘smoke detector’-style tactics might respond more readily and appropriately.

Having perceived fire cues, animals can immediately respond or assess further before responding (Blumstein, 2003; Figure 1). Repeated sampling can provide additional information (e.g. about the fire's rate of spread, intensity and danger level) (Greggor et al., 2019). However, the benefit of additional assessment either by using multiple cues or repeated sampling is weighed against the time, energy and opportunity costs of collecting information. Hence, animals assessing fire risk face a speed-accuracy tradeoff (Chittka et al., 2009; Sih & Del Giudice, 2012; Trimmer et al., 2008).

The benefits of additional sampling include fewer ‘false alarms’. Therefore, sampling is more beneficial if the response to fire cues involves substantial time and energy commitments (e.g. long-distance dispersal or persistent hiding in burrows). Perhaps obviously, the cost of a delayed response to approaching fire can be deadly. The relative ability to escape even when the fire is close should thus affect the animal's tendency towards speed versus accuracy. Smaller, slower-moving organisms with few natural defences against heat should tend to be ‘fast responders’ since waiting too long can be deadly and ‘too long’ comes sooner. In contrast, larger, fast-moving organisms can assess longer, as their ability to outpace an encroaching fire is much greater (Pruetz & LaDuke, 2010; Udvardy, 1969). Organisms that can fly, such as birds and bats, may be more likely to thoroughly assess the risk of fire relative to similar-sized earth-bound animals, as they have a particularly rapid means of escape. This may explain, in part, why red bats respond strongly only when exposed to multiple sensory cues, while anecdotal evidence suggests small rodents and insects respond to a single cue (Engstrom, 2010; Lyon et al., 1978).

## Fear generalization, neophobia and animal personalities

Although fire-naïve animals are expected to show poor responses to fire (Nimmo et al., 2021), anecdotes suggest that many do flee or hide from fires (Bendell, 1974; Udvardy, 1969). We posit that these responses reflect generalized fear (Box 1) where experiences with other dangers generate fear that spills over to increase sensitivity to and avoidance of cues including novel cues. While this hypothesis fits the literature on post-traumatic stress disorder (PTSD) in humans (and lab rodents) where fear generalizes across *very different dangers*, it has received relatively little attention from behavioural ecologists (Sih et al., 2023). Here, the testable hypothesis is that greater experience with predation risk might increase general fear that carries over to produce a stronger response to fire cues. In that case, the key factors explaining variation in response to fire are not the reliability of fire cues or cost asymmetries for speed vs accuracy in assessment,

or for over vs under-responding to fire, but instead are cue reliabilities and cost asymmetries relative to predation risk.

Variation in antipredator response is often quantified by measuring flight initiation distances (FIDs)—the distance that an animal allows a predator (often, a human) to approach before initiating an escape response (Møller, 2010; Ortiz-Jimenez et al., 2022; Stankowich & Blumstein, 2005). Factors that affect FIDs include: predator traits (perceived capture ability, speed of approach), prey traits (escape ability, hunger level, personality) and environmental characteristics (distance to refuge, presence of conspecifics). FIDs are larger when situations are more dangerous and prey are more fearful. An intriguing, untested prediction is that animals that have lower FIDs in response to predation risk (often, simulated by the approach of a human) will also allow fires to come closer before responding. If animals that are faster (or otherwise better able to escape predators) are also better at escaping from approaching fires, then, in some cases, the carryover from predation risk can result in animals exhibiting adaptive balancing of tradeoffs in responding to fire. However, assessment mismatches could occur, for example, when the speed and spatial extent of spreading fire far exceeds that of potential predators (Phillips et al., 2021; Ward et al., 2020), or if habituation to humans and persistent burning, from crop fields to industrial, fire-like emissions, results in bold animals that are too cavalier about approaching fire.

In parallel with our earlier prediction that animals that evolved with multiple predators might be more vigilant and respond to a greater variety of predator cues, those animals might also be more responsive to fire cues. This overall conceptual approach, however, hinges on the strength of fear generalization, a topic that deserves more study. For fire naïve animals, the response to fire cues might also depend on a general fear of novel stimuli (neophobia, Box 2). While neophobia relative to novel objects, predators, habitats and foods have received substantial attention (Crane et al., 2020; Greggor et al., 2015; Mettke-Hofmann et al., 2009), we know of no studies that have examined the connection between neophobia and responses to novel fire cues. Nonetheless, we suggest that animals that are generally more neophobic should be more likely to respond to novel fire cues. Factors that explain variation in neophobia should then also explain some of the variation in behavioural response to fires.

Individual differences in fear and neophobia are aspects of an animal's personality (Réale et al., 2007). The idea that fear might carry over across contexts, novel or not, from predation risk to fires is related to the concept of a behavioural syndrome (Sih et al., 2004). An intriguing extension is that individual differences in fear of fires might be correlated to other ecologically-important traits including other behavioural tendencies (e.g. aggressiveness, exploratory tendency), aspects of cognition (e.g. learning, speed-accuracy tendencies;

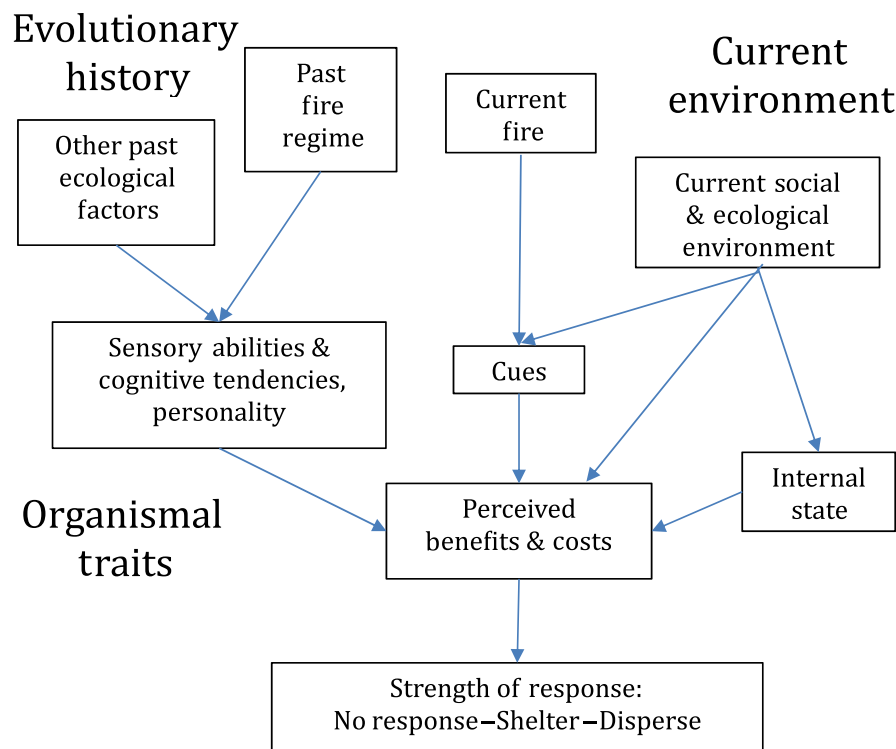
Sih & Del Giudice, 2012), physiology (Stamps & Biro, 2016) and life history (Réale et al., 2010), all of which are thought to be connected to consistent-individual differences in boldness/fearfulness. Thus, the broad range of selection pressures that affect this overall suite of traits (Sih et al., 2012; Wolf & Weissing, 2012) could indirectly affect individual differences in responses to fire.

### The response: Dispersal, dormancy and refuge use

If fire cues trigger a response, the nature of the response, from enhanced stress to refuge-seeking to dispersal, should depend on how the organism's evolutionary history has shaped its morphology, mobility, sensory and cognitive machinery, personality and life history (Figure 2). Fire-adapted animals with good information can plausibly fine-tune their response (discussed in the next section), but for fire naïve animals, or those with only imprecise information about the fire's characteristics, we suggest that their response mirrors their response to predation risk.

When fires are large, intense and spreading rapidly, the best option for mobile animals to survive should

often be to disperse soon after they detect an approaching fire. However, simply because animals have the locomotor ability to disperse does not mean that they will do so, and even if they ultimately disperse, they can either flee immediately, or delay, possibly until it is too late. All else being equal, the relative tendency of animals to disperse from fire should obviously be higher for animals that have greater dispersal abilities (Abrahms et al., 2017; Clobert et al., 2012; Hansson & Åkesson, 2014). For a given species, dispersal tendency also varies with life history stage, sex, social status and personality (Bonte & Dähirel, 2017; Clobert et al., 2012; Cote et al., 2010; Stevens et al., 2014). Populations at the centre of a species' range have often evolved behaviour or even morphology that makes them less prone to disperse (Duckworth, 2008; Phillips et al., 2006; Stevens et al., 2014). Instead, animals located along the periphery of a population's range tend to exhibit higher dispersal tendency, including adaptations that enhance dispersal success (Clobert et al., 2012). If dispersers survive better than refuge-seekers, the behavioural and morphological composition of the population might shift post-fire. Notably, after a fire, the sprinting speed of a population of eastern fence lizards (*Sceloporus undulatus*) was relatively faster in burned versus unburned areas, suggesting



**FIGURE 2** An overview of factors affecting animal responses to fire. Animal responses to fire depend on their perceived costs and benefits of responding (dispersing vs. sheltering in place, Box 3) versus continuing to assess the situation. Those perceived costs and benefits depend on the fire's cues, and how they are interpreted in the context of the organism's internal state and its social/ecological environment. The social and ecological environment can also either provide cues or disrupt sensory perception of the fire (Box 4). How the organism perceives and assesses these multiple cues (about the fire, and the organism's external and internal environment) depends on the organism's sensory capacities, cognitive tendencies and personality (e.g. fearfulness (Box 1) and neophobia (Box 2)), all of which are shaped by its past evolutionary history both with fire, and with other ecological factors (e.g. other risks and resources).

that mainly faster dispersers survived the fire (Wild & Gienger, 2018).

Beyond those factors, dispersal should depend on the individual's assessment of the costs and benefits of

moving away relative to the option to stay and seek refuge (Box 3). Importantly, for fire-naïve animals, and even for fire-adapted ones, many likely have only imprecise information on these relative costs and benefits. If

### BOX 3 Previously adaptive dispersal, a trap in the Anthropocene?

Theory predicts that animals disperse when dispersing yields higher fitness than staying (Clobert et al., 2012). Potential benefits of leaving include gaining better access to resources (e.g. water, food or space) or unrelated mates, or reducing exposure to stressors—either biotic (competition, predation or parasite/pathogen risk) or abiotic. High costs, however, can make it maladaptive to disperse. The process of dispersing is often dangerous, and for active dispersers, is energetically expensive, especially if suitable habitat patches are separated by barriers or large distances relative to dispersal capacity. In addition, the potential benefits of dispersal to a new home are reduced if newcomers face high competition, or high settlement costs (e.g. a high cost of learning to effectively use a new habitat). In social species, dispersers must either integrate with a new group (often initially as a low-ranked subordinate) or wander alone, vulnerable to various dangers. Even if resources are present and competition is weak, low population density can produce Allee effects (e.g. via loss of safety in numbers, reduced social information sharing or difficulty in finding mates). Finally, even if dispersers reproduce, outbreeding depression can reduce offspring fitness.

Adaptive dispersal is facilitated if organisms 'prospect' to collect information about habitat suitability over a broad area beyond the animal's home range (Delgado et al., 2014). This can be particularly important if animals experience sudden, unpredictable drivers of dispersal, such as fires or other environmental disturbances. Many if not most animals, however, cannot or do not prospect and thus must make dispersal decisions based on little or no precise, direct information about the costs and benefits discussed in the above paragraph. For those animals, the expectation is that their dispersal tendencies will depend on their cue-based assessment of current conditions balanced against their evolutionary history of costs and benefits of dispersal.

For some animals, dispersal to escape from a disturbance is temporary. After a fire abates, animals often return home. In that case, dispersing to a barely suitable location may be temporarily adaptive, but it is only functionally adaptive if the animal can later return to its original home or move on to more suitable habitat. If the original habitat does not recover quickly, other territorial individuals prevent return and/or return becomes impossible (e.g. due to barriers or energy depletion) or difficult (e.g. because landmark cues are altered or smoke is disorienting), dispersal is maladaptive.

Habitat loss or fragmentation often increases the costs of dispersal; for example, via reduced habitat connectivity where patches are separated by substantially larger distances or human-associated barriers (fences (McInturff et al., 2020) or walls (Fowler et al., 2018)) that effectively removing access to other habitat. Urban and peri-urban developments, roads and highways, farmland, campsites and hunting and hiking trails slice through habitat and dispersal corridors (Coffin, 2007). In these situations, animals might still attempt to disperse because it used to be adaptive even if it is now futile. The cues that trigger dispersal are then an evolutionary trap (Pollack et al., 2021; Robertson et al., 2013), where previously adaptive cue-response systems now produce a maladaptive response.

In the context of mega-fires, the opposite problem may be common. Animals that evolved in conditions where dispersal is very dangerous, or where high-quality patches are rare, might be loath to disperse even when they should initiate escape as soon as they detect fire cues. This problem can be further exacerbated if the lack of evolutionary history with mega-fires results in mis-assessment of fire cues that produces an under-estimate of the danger associated with not dispersing. Interestingly, even if animals correctly assess the danger associated with an approaching mega-fire, this can still result in a maladaptive response if staying in the original habitat, perhaps in a burrow refuge or riverine safe haven, would yield higher survival than attempting to escape.

Overall, we suggest that regardless of whether animals are fire naïve or fire-adapted, their tendency to disperse to escape fire will depend on the intensity of the fire cues, their locomotor abilities and most interestingly, on their general dispersal tendency shaped by past costs and benefits of dispersal not so much for escaping fire, but for other selective pressures. With mega-fires in the Anthropocene that differ from past fire regimes, the potential for evolutionary mismatches resulting in maladaptive behaviour is high even for fire-adapted animals.

animals stay and seek refuge, their immediate survival and longer-term fitness depend on numerous factors, many of which animals can only roughly assess even if they have an evolutionary history with fire. A simple prediction is that if fire cues are very strong and the quality of potential refuge is poor (i.e. the benefit of staying is low), then animals should be more likely to disperse. However, this should still be weighed against the costs and benefits of leaving. The costs of dispersal can be high in terms of energy expenditure, risk and opportunities lost (Bonte et al., 2012). In particular, mortality risk (e.g. from predation) can be very high while in

transit (McGregor, Legge, et al., 2016; Payne et al., 2014). The benefit of dispersing depends on the likelihood of finding better habitat elsewhere—which historically depended on the availability of good habitat elsewhere often mediated by density-dependent competition and Allee effects (see Box 3). Because dispersal often means moving into unfamiliar territory, both fire-adapted and fire-naïve animals might typically have little information on actual costs and benefits of leaving, but must rely on estimates based on their evolutionary history, or their personal experience if they have previously dispersed. Thus, animals that evolved in environments with high

#### BOX 4 Social effects on responses to threats

Social systems range across a continuum from temporary, loose aggregations to long-term hierarchical societies (Ward & Webster, 2016). For social animals, information about resources and threats can be gleaned through social cues, instead of, or in addition to, direct signals from environmental stimuli (Gil et al., 2018). Furthermore, for these animals, the response to social information can be influenced by collective action dynamics (Couzin, 2018; Couzin et al., 2005; Kao et al., 2014; Miller et al., 2013).

Social cues can be ‘intentional’, such as alarm calling between conspecifics or hetero-specifics, or ‘passive’. Passive social cues include observing other individuals fleeing, detecting their fear metabolites or via other inadvertent transmissions of direct danger cues (e.g. threat odours lingering on the fur, skin or feathers of a prey animal). Social information transfer via any of these mechanisms can enable threat detection via group vigilance, reducing the required level of individual vigilance and facilitating foraging, mating and other activities (Elgar, 1989; Rubenstein, 1978; Treves, 2000). By relying on keystone information providers, individuals can enhance their ability to reliably detect environmental stimuli (Gil et al., 2018).

Social dynamics can also impact individual animal responses to socially-transmitted environmental stimuli. Response initiation will depend on the individuals that receive the direct cue first and transmit (intentionally or passively) social cues to the rest of the group. Their ability to detect cues and propensity to respond to them matters and might relate to variations in their behavioural type, or social status. These ‘leaders’ or keystone decision makers might have assumed this role through their ability to confer adequate group-wide responses to typical threats. Thus, a key issue for fire detection is whether keystone decision makers have generalized threat responses (Box 1), and, if so, whether their level of ‘flightiness’ is appropriate in the face of novel stimuli. There is also a spatial aspect, as individuals or species at the group periphery should be more likely to first detect an approaching threat. At the group level, this might mean that peripheral individuals that tend to be exploratory and bold (Breck et al., 2019; Fraser et al., 2001; Sih et al., 2004; Sutrisno et al., 2011) are effectively the keystone decision makers. The collective-action decision-making dynamics of the response itself (e.g. the pattern of fleeing) likely depend on species-specific attributes and the density and composition of the animal species assemblage (Gil et al., 2018). Notably, having only a small proportion of directly-informed individuals can be sufficient to guide a collective group response (Couzin et al., 2005).

While social cues add information, too much imperfect information may in some cases degrade the appropriate responses of animals to environmental stimuli, particularly novel stimuli (Barrett et al., 2019). Animals moving or seeking refuge as a group likely encounter elevated resistance to change, even as new details about environmental threats emerge, due to social inertia. Models reveal that relying on ‘telephone’—type information cascades as cues rather than direct threat cues can cause critical delays in response, due to mismatches between individual and group optima—a collective inertia problem akin to the tragedy of the commons (Torney et al., 2015). Moreover, if and when individuals do respond, in groups, they often do so without specific threat information because social cues are often an imprecise reflection of the initial environmental stimulus. This means that the response to a novel stimulus will in effect be a generalized social response, possibly inhibiting fine-tuned responses to highly spatiotemporally variable novel stimuli. However, the degree to which animals rely on social vs. direct cues for decision-making at the initiation and propagation of a response to a novel environmental stimulus like a wildfire remains to be investigated.



dispersal costs, or low or highly variable and unpredictable benefits of dispersal should be less likely to flee a fire (or might delay fleeing until it is too late) even when it is beneficial to do so.

The possibility that misleading information about actual costs and benefits results in poor dispersal decisions relative to fire can be further exacerbated by changing fire regimes in the Anthropocene. With mega-fires that spread more rapidly, are more intense or greater in spatial extent or temporal duration relative to historical norms, even fire-adapted animals may delay dispersal until too late or exhibit ineffective escape behaviours. Conversely, animals may make futile attempts to outrun mega-fires when hunkering down in local refuges is their best strategy. In recent Australian megafires, animals that are morphologically capable of dispersal, yet chose not to, managed to survive by seeking refuge in wombat (*Vombatus ursinus*) burrows (Lewis, 2020). Similarly, wallabies (*Wallabia bicolor*) that are quite mobile, may actually fare better if they seek refuge on nearby, rocky outcrops or riverine refugia, rather than fleeing (Garvey et al., 2010; Recher et al., 1975; Thornett et al., 2016). For animals that dispersed when they should have sought local refuge, the cues that triggered dispersal could be considered a form of evolutionary trap (Pollack et al., 2021; Robertson et al., 2013; Sih et al., 2020) where previously adaptive cue-response systems now result in maladaptive behaviours (Box 3).

If animals seek local refuge, key questions include what type of refuge do they use and how effective is that refuge likely to be? Some animals from fire-prone areas use specific fire refuges. For example, during prescribed burns, many small animals increased their use of gopher tortoise burrows (Catano & Stout, 2015; Knapp et al., 2018). For fire-naïve animals, anecdotes suggest that the choice of refuge type (e.g. burrowing versus climbing versus squeezing into crevices) often mirrors their refuge use in response to predation risk, which in turn, depends on their size, morphology and general habitat use (Kaliontzopoulou et al., 2010; Krause et al., 1998; Sundell & Ylönen, 2004).

The relative efficacy of these alternative refuge types likely depends on fire characteristics. Low-intensity fires char the surface with little damage to the tree canopy, though underground soil temperatures can actually be hotter during heterogeneous, smouldering fires than intense, hot fires (Iverson & Hutchinson, 2002; Stoof et al., 2013). For a smaller, cooler fire that does not penetrate far below or aboveground, using dens, burrows or trees while waiting for the fire to pass can be effective (Durigan et al., 2020), while hiding in a bush or under leaf litter is more likely lethal. For a larger, more intense crown fire, climbing to escape is deadly, but fleeing an area (Boer, 1989) or finding a refuge (Banks et al., 2011; Robinson et al., 2013) moderately deep underground (e.g. in a wombat or gopher tortoise, *Gopherus polyphemus*, burrow) can be safe even during severe fires (Knapp

et al., 2018; Lewis, 2020; Thornett et al., 2016). That said, if a predator has also chosen the burrow, predation may be a risk once the fire has passed.

### Fine-scale behavioural responses to fire

Animals can exhibit a more fine-tuned adaptive response to fire if their cue assessment provides accurate information on the fire's directionality, speed of approach, extent and overall risk. Assuming that environmental cues like the wind, fuel load, dryness and topography provide reliable information that can help predict a fire's spread, fire-adapted animals should use those cues to guide their escape or refuging responses. The speed and direction of escape should depend on whether the animal is at the leading edge, periphery or back edge of a fire's spread. Escape routes should also depend on the animal's knowledge of the landscape—barriers that block escape and corridors that facilitate it. If the fire spreads patchily, leaving 'islands' of safety (e.g. in areas with low fuel load), or if some sites inherently provide refuge (e.g. water sources, burrows), fire-adapted animals can move to those safe sites. To date, information on these fine-scale responses is fascinating but largely anecdotal. For example, swamp wallaby (*Wallabia bicolor*) behaviour during prescribed burns and wildfires ranged from dispersal to refuge-seeking in streambeds depending on the individual's location relative to the fire (Garvey et al., 2010). One wallaby moved north, but when the fire moved in that direction, the animal moved south along a creek line where it safely remained throughout the burn. Another wallaby moved west ahead of the fire front to safety in the same creek, and a third moved through the fire front to again shelter in a creek. Similarly, individual black-tailed deer (*Odocoileus hemionus columbianus*) dispersed different distances from a recent megafire in California, depending on their habitat type, proximity of their home range to the fire, and, possibly, individual factors (Kreling et al., 2021). By taking advantage of the many animals fitted with tracking devices in fire-prone areas, it should be possible to combine empirically-derived movement models with landscape analyses of fire risk and signal diffusion to identify how critical habitats and corridors affect animal movements and success during and after fires (e.g. Khosravi et al., 2022; see Box 5).

For social animals that often escape as a group (Box 4), since the cues of an approaching fire would likely first arrive at the periphery of the group, the spatial distribution of behavioural types can affect how social species move to avoid fire. Studies on group responses to predators have found that peripheral animals are often more bold and exploratory (Breck et al., 2019; Fraser et al., 2001; Sih et al., 2004; Sutrisno et al., 2011). Depending on personality-based leader-follower effects, the response of the leaders (that might

### BOX 5 Advice for empiricists

While there is great interest in the details of both adaptive and maladaptive behavioural responses to fire by both fire-adapted and fire-naive animals, few studies have tracked these responses in much detail. An obvious logistical issue is the unpredictability of fires in space and time. Here, we suggest several pathways to gaining insight despite this unpredictability.

*Leveraging existing research infrastructure and knowledge:* In some cases, animals threatened by fires were already being tracked (e.g. via biologgers) for other studies. Alternatively, radar can detect large movements of animals in response to a fire (Supp et al., 2021). Comparing animal movements before, during and after the fire, ideally coupled with satellite monitoring of the fire's spread, could provide detailed information on the animal's fire responses. For example, Kreling et al. (2021) tracked GPS-collared deer following a severe wildfire, observing substantial changes in movement behaviour and space use. Even the behaviour of animals that only experienced smoke and not the fire *per se* can be insightful. Air quality indices taken from monitoring stations could be paired with movement data to assess smoke detection and tolerance thresholds, helping analyze the importance of cue intensity in governing movement decisions. With data on multiple individuals, it may be possible to assess social influences on responses (Box 4). With data on multiple species, one could examine how community composition mediates behavioural responses, such as the effect of predator diversity on FIDs from fire, or the possibility of mixed species information transfer on responses.

*Planned field experiments:* Another underused opportunity involves working more closely with managers of prescribed burns on public or private property (Braun de Torrez et al., 2018). When planned in advance, baseline surveys of wildlife community composition and behaviour before and after the fire could be conducted (Taillie et al., 2018). In some cases, even direct observations of animal behaviour during a management fire may be possible. Establishing a standardized set of data that could be easily and consistently collected near fire fronts could yield large behavioural datasets that allow for cross-system and temporal analyses. Basic information to collect could include the species observed, its behaviour (seeking refuge vs fleeing from a fire front or back through a fire front), group size and composition (e.g. age composition, mixed species groups), etc. While studying prescribed burns is typically logistically feasible and safe, a limitation is that they are usually far less intense and smaller in spatial and temporal extent than natural wildfires (Hiers et al., 2020); thus, the power of inference and generalization is somewhat constrained.

*Laboratory experiments:* For smaller, less mobile animals, laboratory studies offer the opportunity for direct experimental observation of behavioural responses to fire cues. Dispersing smoke into a testing chamber (Doty et al., 2018), broadcasting the sounds of fire (Grafe et al., 2002), or displaying images of fire should help researchers isolate and understand what cues elicit greater or lesser responses, and under what environmental contexts. Testing for changes in cue preference, signal detection thresholds and response variability as a function of organismal traits (e.g. personality) or states (e.g. condition or reproductive status), will be useful in predicting responses to fire in scenarios where other stressors are in play. Including physiological and molecular techniques (Kay et al., 2021; Williams et al., 2013) may provide valuable insight for management by, for instance, uncovering relationships between cortisol levels and response thresholds, or epigenetic patterns that emerge in offspring after parental exposure to a major fire. By simulating a species' natural habitat in a laboratory setting, researchers may even determine cue thresholds which facilitate switching to a different behavioural strategy (i.e. an animal retreating under a burrow in the case of low-intensity cues but attempting to flee the testing area during higher-intensity cues). Comparing responses of solitary individuals versus those in groups should elucidate social influences on responses.

By synthesizing the study of fire via the above approaches, empiricists may be better able to predict animal behaviour in the wake of a naturally unpredictable event. For each of the above, it will be useful to compare individuals, populations or related species that have a history of more versus less exposure to fire. To further study contemporary evolution, one can contrast behavioural responses in areas that burned recently versus those that remain unburned, and one can, in principle, transplant fire-adapted individuals into unburned but vulnerable areas to study the possibility of priming fire-naive animals to be more ready for fires when they arrive.

## BOX 6 Conservation implications

An increased understanding of the capacity of species to perceive and respond to fire, and hence prediction of the likely impacts on biodiversity and ecosystems, has important potential conservation applications.

### *A priori identification of species most at risk and in what ecological contexts*

By combining biogeographical, evolutionary (e.g. species' history with fire and predation risk to identify naive and non-naive species or populations) and traits-based data (e.g. solitary or group living, fossorial, terrestrial or arboreal species), it should be possible to assess, for numerous species, at least roughly, their sensory capabilities to perceive fire and the relative risk posed by fires. This information could be secondarily examined to see how variations in habitat type (e.g. open grassland vs. a topographically complex narrow gorge) modulate the effectiveness of such capabilities. A risk score could then be assigned to species, which would be further contingent on a species' ability to respond (e.g. low vs. high mobility, able to use refuges or not) and barriers to response (dispersal constraints). This would enable managers to estimate, in advance, which species, in what habitats and under what local or regional conditions, are most likely to be at greatest risk due to fire, and hence when active intervention may be needed. In particular, mismatches that result in deleterious responses could be identified. If a species' response to a predator is generally to bunker down in leaf litter, this is unlikely to be successful in the face of a fire, but likewise attempting to flee could be maladaptive for some species if a fire is too fast and large, such as the megafires that occurred in Australia in 2019–2020. Such spatially, taxonomically and temporally explicit information would further enable the implementation of formal decision theory (Possingham et al., 2000), to decide, in advance, which taxa (e.g. range-restricted and/or threatened species) to prioritize for assistance.

### *Conservation interventions*

Following risk identification, managers could decide which conservation actions are most suitable for which species. *In-situ* responses could include identifying and spatially mapping areas of critical refuge for species, and ensuring these are conserved from other threats (e.g. invasive predator control, grazing management to protect vegetation cover). In some cases, adding artificial refuges (Cowan et al., 2021) such as wire netting, rockpiles and chain-sawed tree hollows, can allow animals to either escape from the immediate threats posed by fire (which is especially important for species with low dispersal capacity) or return to and persist in more open, burnt landscapes where in the absence of such refuges they may face elevated predation risk (Geary et al., 2020). Using metapopulation theory, potential dispersal pathways and linkages between species' subpopulations could be identified. If such linkages are assessed as inadequate to allow animals to escape from fire, or repopulate areas following fire, wildlife corridors could be created, enhanced or restored. Ensuring wildlife have multiple corridors to escape from fire or repopulate areas after fire would be a key requirement, but we note such corridors also come with inherent risks, including potential aiding the spread of fire from one region to another and/or acting as pathways for invasive species. In some cases, strategic fire breaks that reduce the risk of fire spreading from one area to key subpopulations and habitat refuges might also be used, but this poses the risk of inhibiting the movement of smaller and/or less mobile species. The ability to appropriately manage these complex landscape-scale considerations and conserve species' populations and ecosystems will likely be contingent on access to both high-resolution topographic information and fire history and modelling data, as well as accurate wildlife population information.

In other cases, *ex situ* responses may be needed, including emergency evacuation of individuals or populations (especially range-restricted and/or endangered species) into captive husbandry, or species translocations. An intriguing dimension to consider in this context is using the reintroduction of one species to potentially aid the survival of others during a fire. For example, Australia's northern hairy-nosed wombat has declined over much of its former geographic range. As these animals are known to dig large, extensive burrow systems and species have been observed sharing wombat burrows during fires, it begs the question of what the consequence of their loss has meant for the ability of some species to respond to and survive fire events. Are species such as wombats akin to 'keystone' in this regard? If so, identifying such species that might be missing from landscapes and reinstating their ecological function(s) might help others to survive fire.

be ill-informed) could cascade to the entire group (Box 4).

## HOW PREDATORS AND FIRE DIFFER

In this penultimate section, we note several ways that fires can differ from predators, each of which produces mismatch errors in animal responses to fire. With regard to the detection of danger, a *sensory mode mismatch* occurs when the most informative type of stimulus emanating from fires does not match the type that familiar predators produce and prey detect. If the odour of smoke is the best indicator of approaching fire, then animals whose predators exude volatile odours that prey detect in the wind should respond better to fire than animals that primarily detect predators visually (Nimmo et al., 2021). With regard to risk assessment and fear generalization, *risk mismatches* occur when, for example, fires are deadly, but familiar predators are ineffective so the focal animals are not fearful enough. Finally, several differences between fires and predators can generate *response mismatches* where prey respond, but inappropriately. First, whereas predators are often only dangerous when they come very close, fires can approach more rapidly and be deadly over a larger spatial scale. Prey often respond to predator attacks with last second escape decisions, but by the time a fire is close, it may be too late to escape. For mobile prey, dispersal initiated immediately upon detecting a fire could allow effective escape, but animals with slow-moving predators will likely wait too long to disperse. Fires also do not typically ambush prey. Prey faced with ambush predators often respond by moving less and by avoiding habitats or times of the day when ambush predators are particularly dangerous; however, these behaviours are unlikely to be effective against fires. Finally, fires do not tend to satiate after consuming one or a few animals. Thus, prey that rely heavily on group-based safety to reduce predation risk will fare poorly with fires. This brief discussion covers only a few of the ways that predators and fires can differ. Our general suggestion is that, particularly for fire naïve animals, understanding differences between characteristics of an animal's familiar predators and specific fires will help identify mismatches that potentially explain poor animal responses to fire.

## CONCLUSIONS AND FUTURE DIRECTIONS

Predator-prey theory provides a framework for understanding behavioural responses when faced with fire, especially for fire naïve animals and for animals facing novel fire regimes that are becoming increasingly common. One important need is for further work applying existing animal decision theory (signal detection theory,

and theory on adaptive dispersal versus use of refugia) to develop a more quantitative, theory-based set of predictions on variation in fire-related behaviours. Empirically, basic information on cues that animals use to detect and gauge fire risk is sorely needed. At the cognitive level, the predator-prey-based framework would also benefit from deeper investigation into the role of fear generalization and neophobia in explaining responses to fire. The use of modern technologies (e.g. biologging, remote sensing, drones) holds promise for better understanding behavioural responses to fire in the wild (see Box 5). Promising avenues for future research include: (1) comparing animal behaviour in populations of the same or closely related species living at different levels of fire risk and predation risk; (2) examining the effects of fire cues on diverse animals—especially compared to the background noise of pollution; (3) comparing behavioural responses to fire cues in populations before and after fire events. A deeper understanding of animal behavioural responses to fire should allow for improved conservation and management in the Pyrocene (see Box 6).

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## AUTHOR CONTRIBUTIONS

Alice Michel, Euan G. Ritchie, and Andrew Sih formulated original ideas, and Alice Michel wrote the first draft. All authors further developed ideas, added sections, and extensively revised the paper.

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No data were used.

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