

FIRES IN NATURE: A REVIEW OF THE CHALLENGES FOR WILD ANIMALS

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Abstract.

Animals living in the wild are exposed to numerous challenges, such as fires. Depending on the characteristics of fire, habitat and taxa affected, fires can cause pain, negative experiences, suffering, and death in individual animals. The impacts of fire have been studied in different branches of ecology, but studies of its effects on the welfare of individual animals remain scarce. The current review aims to synthesize a sample of relevant aspects regarding fire's negative effects on wild animals. We mainly focus on the immediate impacts of fire on individuals. How animals respond to fire depends on many factors including their life history, evolutionary adaptations to fire, and individual stress coping styles, in addition to the characteristics of the fire.

The fundamentals of carrying out future work for animal rescue and prevention of animal harms in fires were also explored. Fires may increase the risk of injury, disease, stress, and mortality for animals living in the wild. Although animal taxa differ significantly from each other, a wide variety of vertebrate species (and perhaps some invertebrates) are capable of experiencing both physical and emotional pain, engaging in substantive relationships, and executing cognitively complex tasks. The consequences of fires can involve suffering, psychological damage, negative experiences, discomfort and pain, and long-term detrimental consequences.

Wild animals can benefit from effective rescue, rehabilitation, and release during fires, and post-release monitoring must accurately evaluate their outcome success. The resulting information can be used to educate veterinarians, rehabilitators, and the public in the prevention of the poor welfare and deaths of as many animals as possible in future fire events, which ultimately benefits animal welfare. This review provides a better understanding of how fire compromises animal welfare, providing an example of how to use the knowledge gathered in animal ecology to examine the welfare of wild animals. It can help raise concern for the situation of wild animals as individuals, and to develop the field of welfare biology, by identifying promising future lines of research.

Key words: wild animals, animal welfare, animal harms, animal suffering, fires

INTRODUCTION

In the coming years, wildfires will burn larger areas (Doerr and Santín 2016; Westerling 2016; Rodrigues *et al.* 2020), and become more frequent and intense (Cochrane and Barber 2009; Flannigan *et al.* 2009; Jolly *et al.* 2015), partly as a result of global increases in invasive grasses (D'Antonio and Vitousek 1992), as well as the impact of climate change on fire regimes (Keeley and Syphard 2016; Parks *et al.* 2016; Michetti and Pinar 2019; Turco *et al.* 2019; Krikken *et al.* 2019). Although approximately 4% of the earth's surface is burned per year (Randerson *et al.* 2012), most attention is paid to fires which impact humans (Yell 2010).

The characteristics and environmental context of fires, together with life-history differences between species, determine the degree of harm to animals (Whelan *et al.* 2002; Geary *et al.* 2019). While exten-

sive research has been done on the ecological consequences of fires (Kauffman 2004; Keeley *et al.* 2005; Andersen *et al.* 2005; Parr and Andersen 2006; Claridge *et al.* 2009), the animal welfare impact has not been extensively studied, and has mainly focused on domesticated and companion animals (Irvine 2007; Edmonds and Cutter 2008), because of affection (Heath *et al.* 2000) or economic interest (Fayt *et al.* 2005). Recently, a review of existing knowledge on fire management concluded that further investigation about species responses, including examination of occupancy, life history, dispersal, demographics and behavioural responses (Driscoll *et al.* 2010; Conner *et al.* 2011; Stawski *et al.* 2015b; Day 2017) is needed.

Fires have been found to affect the distribution, abundance, and genetic diversity of populations, as they are life-threatening (Kauffman 2004; Yoder 2004; Turner 2010; Banks *et al.* 2013; Griffiths and Brook 2014). Both anthropogenic and natural fires, including local deliberate uses for hunting (Bouaket 1999; Daltry and Momberg 2000), may harm animals (Karki 2002). In fact, as a result of Australian mega-fires, very recent studies in ecology have been carried out on the effects on wild Australian fauna (Wintle *et al.* 2020).

Scientific evidence has established that some animal species have the ability to experience negative psychological stress, suffering, or even chronic stress, due to their cognitive development (DeGrazia and Rowan 1991; Duncan and Petherick 1991; Sherwin 2001; Griffin and Speck 2004). For this reason, it is expected that some taxa perceive fires as stressful events, and consequently trigger physiological and behavioural responses as an evolutionary adaptation to survival (McEwen 2005). While a state of stress can allow glucocorticoids to mobilize energy to positively modify behaviour (Korte et al. 1993; Lee et al. 2015), excessive amounts of perceived stress can lead to negative physiological and psychological consequences for the individual (Anderson 1998), such as fear, anxiety, despair and disorientation, and increased risk of death. The most immediate effects of fire on individual animals include risk of injury and death during flight to unburned areas (Whelan et al. 2002), and second order effects include starvation, dehydration, predation and migration (Silveira et al. 1999a; Whelan et al. 2002).

Numerous studies have evaluated post-disturbance population recovery patterns and processes (Smith and Lyon 2000; Griffiths *et al.* 2015; Davies *et al.* 2016; Banks *et al.* 2017). However, there is a lack of studies on the immediate experienced damage and short-term responses of wild animals during fires (Vernes 2000; Smith and Lyon 2000; Bury *et al.* 2002; Penn *et al.* 2003; Banks *et al.* 2017), including physiological and behavioural adaptations (Stawski *et al.* 2015b).

AIMS AND METHODOLOGY

The current review aims to summarize the main negative effects of fires on wild animals on an immediate timescale (from seconds or minutes to several days). The main objective of this work is to gather the essential knowledge for an updated understanding of the threats and poor welfare experienced by wild animals as a result of fires.

The fundamentals for further investigation and promising future lines of research related to the sub-

ject are proposed. In the same way, the design of future damage harm prevention and animal rescue protocols are laid out. In summary, the eventual objective is the growth of welfare biology, both in its practical and theoretical perspective, along with the identification of promising future lines of research related to the subject.

The methodology of the present study consists of the evaluation of the most relevant scientific articles and reviews related to the main significant negative effects of fires on animals living in the wild. The search criteria prioritized those scientific articles that evaluated fire effects from the perspective of the individual. We focused our search on articles published in the last two decades. All the selected literature was read by a first observer, and reviewed posterior by the rest of the authors.

The bibliographic search process excluded research only focused on the effect of fire in humans, plant communities and fungi. Scientific articles about long-term fire effects on animals, or positive effects of fires on biodiversity were not of high interest to this review. Nonetheless, we would like to mention that the text includes a short summary of the importance of fire and its potential positive effects on the habitat.

RESULTS

Injuries and mortality

Physical damage like burns to the face and limbs are quite common for animals after fires (Rethorst et al. 2018). Rescue actions should include veterinary check-ups assessing burns and other damages incurred from smoke poisoning and traumatic injuries. Research on pathophysiology and burns treatment in animals has generated sustained interest over the past few decades. The first barrier of the animal's body is the skin. Burned skin traps heat inside, spreading the burn to the subcutaneous layer. Initial treatment in mammals often consists of warm water washes to stop the 'microwave' effect and remove traces of soot and plant material(Fowler 2010). The infusion of saline solution and the injection of different drugs are common in the treatment of burns during the first days in rescued animals. Ointments such as silver sulphadiazine and chlorhexidine bandage are also used on burnt skin (Prasad et al. 2016).

The first assessment of burns includes a study of the depth, extent and location (Fowler 2010): (1) most superficial burns (which can generate bleeding and tissue damage) are more painful than thick burns (which cause severe skin damage, and a loss of hair, nerves and blood vessels), (2) burns of more than 50% of the body surface have only the prognosis of death or euthanasia; and (3) wounds located near the joints can lead to scarring that prevents movement and feeding, as occur in arboreal animals as koala (*Phascolarctos cinereus*). Nail damage can make it difficult for some mammals to climb, feed, escape, fight, and breed. Injuries located on facial structures can hinder functions such as chewing (Fowler 2010).

Rehabilitation is complicated if the animal suffers from long-term stress. For example, stress syndrome is common in koalas, which easily lose their appetite. Lack of food intake can lead to dehydration and can delay or prevent wound healing. If appropriate, the use of analgesic and anxiolytic drugs may minimize the pain and stress (Kirkwood and Sainsbury 1996). Although some research has been done on survival in rehabilitated koalas versus uninjured individuals (Lunney et al. 2004a), further research on the relationship between fire-related injuries and physical condition or premature mortality is still needed (Ernst et al. 1999; Engstrom 2010), as well as replication of studies in other affected taxa. For instance, koalas initially require intensive care and continuous dressing changes, often accompanied by sedation or general anaesthesia (Fowler 2010). Then, they go to moderate-intensity care in small groups in which they are frequently observed. They finally finish their rehabilitation in wide enclosures in which individuals can express their natural behaviours and develop strength.

Collisions with vehicles also increase as animals fleeing from fire, usually disoriented (Quinn 1979). Intensive care of animals often includes wounds from vehicle collisions that can generate soft tissue and skeletal injuries, mainly affecting the extremities, as reported for New Zealand pigeons (*Hemiphaga novaeseelandiae*) (Cousins *et al.* 2012).

Most animals die from asphyxiation during fires (Lawrence 1966), while many more are burnt alive and killed(e.g. deer in Australia;Forsyth *et al.* 2012). Breathlessness is a negative experience in terms of animal welfare that may involve respiratory effort, chest tightness, and air hunger, the latter being reported to be the most unpleasant (Beausoleil and Mellor 2015).

Although some animals can maintain their body temperature by evaporative cooling (King and Farner 1961), such mechanisms become impossible when water vapour pressure and temperature exceed lethal limits, so deaths from heat damage can occur (Kozlowski 1974). Direct animal mortality from fires has been reviewed (Koprowski *et al.* 2006) and fire has been reported to induce mortality in mammals, birds, insects, fish, reptiles and amphibians. The risk of mortality depends on characteristics of the species such as mobility (Peres 1999; Silveira *et al.* 1999a; Barlow and Peres 2004), shelter use (Williams *et al.* 2010), dietary flexibility (Isaac *et al.* 2008; Banks *et al.* 2011b), body size (Cardillo 2003; Griffiths and Brook 2014), etc.

Regarding mammals, while a general decline in population abundance was reported for small mammal species following fire (Keith and Surrendi 1971; Erwin and Stasiak 1979; Geluso and Bragg 1986; Kaufman *et al.* 1988; Simons 1989; Friend 1993; Fisher and Wilkinson 2005; Banks *et al.* 2011a; Banks *et al.* 2017), larger mammals appear to be less prone to mortality due to their increased ability to flee from affected areas (Cardillo 2003; Griffiths and Brook 2014), although at least 10 species of large mammals also exhibited increases in fire-related mortality (Brynard 1972; Gasaway *et al.* 1989; Oliver *et al.* 1997; Peres 1999; Silveira *et al.* 1999b; Barlow and Peres 2004; Williams *et al.* 2010; Griffiths and Brook 2014).

As for birds, individuals that fly at lower altitudes have been reported to die from smoke inhalation or exhaustion (Campbell 2016). Feeding, cover and nesting habitat changes can negatively impact cavity-nesting populations (Erwin and Stasiak 1979; Horton and Mannan 1988; Lnions *et al.* 1989; Smith and Lyon 2000) such as grouses and northern harriers(Kruse and Piehl 1984). Chicks and eggs are affected too (Palmisiano 2014), and nest parasitism may increase as a result of females ranging more widely in search of nest building materials (Best 1979).

Fires can also damage aquatic animals. Increases in water temperature and toxic chemicals, variations in pH (Gresswell 1999), turbidity (Gill and Allan 2008) and stream sedimentation (Bozek and Young 1994; Lyon and O'Connor 2008)have detrimental effects on fish, macroinvertebrates and emergent insects and amphibians in aquatic phases(Fish and Rucker 1945; Dunham *et al.* 2007). Excess sediment may crush or dislodge fish eggs, preventing the emergence of fry (Cooper 1965; Bjornn *et al.* 1977). This can induce physiological stress and growth reduction for fish (Newcombe and Macdonald 1991; Bozek and Young 1994). A cumulative impact from successive fires will affect the watershed's morphology in the long term (Moody and Martin 2001). Fish populations may be unable to recolonize fire-affected streams, as seen for salmonids one year after a fire (Rinne 1996). Post-fire sediments can be beneficial or detrimental to fish and aquatic macroinvertebrates by either providing resources or polluting habitat. Some fish species exhibit accelerated maturity rates by rapidly recolonizing post-fire channels along debris-flow runout paths (Goode et al. 2012). Further research is advisable on developing effective options to prevent potential damage that aquatic fauna may experience in post-fire conditions. Eventually, fires can impact marine animals as well. Post-fire heavy rains near the coast can causeashes to quickly reach the sea, wherein an increased mortality has been reported for shellfish, waders that feed on insects near the sea, river mussels and Kentish plover (Europa-Press 2016).

Although literature reports little or no direct postfire mortality for reptiles (Scott 1996; Russell *et al.* 1999; Smith and Lyon 2000), probably because mesic habitats tend to burn infrequently (Ford *et al.* 1999), some studies have found reductions in population density post-fire for five common species (Hossack 2006; Costa *et al.* 2013).

Arthropods can perish in the heat of the flames, and fire destroys their shelters and food. Eggs, nymphs, and adult stages may be affected, and fires can cause a long-term depression effect on populations (Lyon 1978). Decreases in soil fauna populations after a fire have been reported (Rickard 1970; Metz and Farrier 1973; Harris and Whitcomb 1974; Rinne 1996; Fellin and Kennedy 2014), including ticks not attached to a host animal, beetles, mites, aquatic macroinvertebrates, etc. Even after 2-6 years post-fire, invertebrate populations density may not reach pre-fire levels (Huhta et al. 1967; Vlug and Borden 1973). A significant decline in pollinators has been reported, concluding that future research on fire effects on plant-pollinator interactions are necessary (Brown et al. 2017).

There are currently no accurate estimates of the number of animals that die each year in fires. Quantifying exact post-fire mortality is practically impossible because bodies are often charred, some species are too small to be counted, and monitoring individuals for years until a fire occurs is tremendously complicated (Sutherland and Dickman 1999a). Moreover, mortality cannot be quantified by comparing population densities before and after a fire event, since a distinction would not be made between mortality and migration (Whelan 1995). In future, mortality quantification could make it possible to assess which areas have been most damaged and require wild animal welfare intervention, as well as raising public awareness. Post-fire immediate mortality is quantified by direct estimates, either through software (Jeffers *et al.* 1982; Silveira *et al.* 1999b), or relying on recent reports estimating animal populations sizes and excluding those species with the ability to flee (Dickman 2020).

Acute heat stress response

Animals' responses to fire depend on the particular characteristics of the fire itself, their habitat, their life history traits, how they manage their daily energy budget (Letnic 2001; Letnic *et al.* 2004; McGregor *et al.* 2014; Stawski *et al.* 2015a), and their individual 'stress coping styles' (Koolhaas *et al.* 1999)(the latter related to the individual's predisposition to frustration(Dawkins 1988)), and the animals' temperaments (Martin and Réale 2008) and personalities (Carere and Eens 2005).

Although the immediate physiological effects of fire exposure are poorly understood in animals, inferences can be drawn from studies of the effects of exposure to high environmental temperature(Engstrom 2010). Generally, cellular protein denaturation occurs from 50 °C (Schmidt-Nielsen 1964), and temperatures higher than 63 °C are usually lethal (Howard *et al.* 1959; Smith and Lyon 2000). High environmental temperatures predispose animals to heat stress, which includes physiological and behavioural disturbances such as hyperventilation or loss of coordination (Radford *et al.* 2006). Heat stress effects are aggravated when accompanied by burns on limbs, feet and paws caused by the hot surfaces (Klein 1960; Lyon 1978).

Different consequences of acute heat stress previously reported in animals have included decreased food intake (Marai *et al.* 2007; Xing *et al.* 2019), hormonal, metabolic, hypothalamic and circadian alterations (Marai *et al.* 2007), epinephrine and norepinephrine increases (Johnson and Vanjonack 1976), tissue stress (Islam *et al.* 2013), respiratory rate and skin temperature increases, gonadal deleterious effects with litter size diminution (Askar and Ismail 2012), and stress-related behaviours (Debut *et al.* 2005).

Since wildfires frequently occur at the end of spring or during the summer, stress also hinders population recovery, reproduction and breeding (Koprowski 2005). Reduced forest cover may lead to higher temperatures that can affect cavity-nesting species, hindering incubation and nest survival (Neal *et al.* 1993; Wachob 1996; Conway 2000). Dead trees generate extreme temperatures inside nest cavities (Wiebe 2001), and both eggs and young birds are susceptible to heat stress. The survival of cavity-nesting birds is threatened in fires followed by rain since the activity of flying arthropods on which they feed decreases (Murphy and Lehnhausen 1998; Covert-Bratland*et al.* 2006; Hutto 2006; Koivula and Schmiegelow 2007; Saab *et al.* 2007). Difficulty in acquiring food can increase the risk of nest abandonment (Neal *et al.* 1993; Conway 2000; Wiebe 2001; Jehle *et al.* 2004) and offspring mortality.

Heat stress impact can be reduced. For example, supplementation with olive oil in chickens alleviates superoxide anion production in the skeletal muscle (Mujahid *et al.* 2009). During prolonged dry periods and fires, drinking fountains can be placed in trees. Arboreal animals that are on the ground, and animals that show loss of balance, convulsions or confusion can be rescued with a towel, a well-ventilated box, or by offering them water (AWARE 2019).

Flight from the fire

The immediate post-fire environment generates a sudden drastic alteration of habitat structure and local microclimate that affects all terrestrial fauna (Lyon 1978). The consequent habitat simplification, including loss of vegetation cover and soil layer, may result in a reduction of the number of species after fire, as reported for rodents (Sutherland and Dickman 1999a). Likewise, aspects such as increased levels of sunlight penetrating the forest canopy and loss of food resources can affect behavioural search patterns (Barlow *et al.* 2002). As a result, many animals frequently move to fire-free areas (Brynard 1972; Recher and Christensen 1981), unburnt islands or surrounding unburnt vegetation (Begg 1981; Quinn 1979).

Moving to other places allows animals to access new resources, maintain homeostasis, find mates, and respond to predators, parasites and competitors. These functions eventually allow growth, survival and reproduction, which define fitness (Nathan *et al.* 2008; Weinstein *et al.* 2018). Movement is critical for species living in environments characterised by periodic change (Hanski 1999; Roshier *et al.* 2008), and regular fires (Nimmo *et al.* 2019). Low mobility animals will be more affected by smoke, high temperatures and oxygen shortage. For instance, while amphibians usually have limited migration abilities (Sinsch 1990), larger reptiles normally disperse skillfully from fire (Komarek 1969; Patterson 1984). Movement in vertebrates ranges from attraction (Komarek 1969) to avoidance (Nimmo *et al.* 2019) responses, ranging from calm escape to a state of panic and anxious movements (Komarek 1969; Lyon 1978). Tendency to flee depends on animal adaptations to high temperatures, like mud baths and burrowing (Quinn 1979). Moreover, some species have fire detection mechanisms even functional during torpor (Grafe *et al.* 2002; Scesny and Robbins 2006; Schmitz *et al.* 2008; Stawski *et al.* 2015a; Doty *et al.* 2018; Mendyk *et al.* 2019).

The study of post-fire movement patterns is crucial to understanding refuge seeking behaviour. Moving towards open areas can be especially favourable in fires accompanied by wind, since wind increases heat loss particularly if the animal is wet (Hart et al. 1961). However, other species (Rosenzweig et al. 1975; Price 1978; Price and Waser 1984) prefer foraging near cover and avoid approaching open areas (Glass 1969; Miller et al. 1972). Among the animals that decide to escape the flames (Geluso and Bragg 1986; Grafe et al. 2002), some small mammals species (Vacanti and Geluso 1985) have been found running from the fire, most commonly in groups in small clearings, depressions, road cuts and hiking trails (Quinn 1979), indicating specific flight patterns with preference for clear paths. Other mammals have been seen swimming along rivers to avoid the flames (Kozlowski 1974). While some of them may return within hours or days, others migrate because the food (King et al. 1997) and cover (Lyon and Marzluff 1985) they require are no longer available in the burnt area (Bradstock et al. 2005; Parr and Andersen 2006; Nimmo et al. 2013; Nimmo et al. 2019). Some radio-tracked individuals were transient and travelled 10 km or more to find patches with available resources in both burned and unburned areas (Letnic 2001). Large mammals tend to move calmly and act indifferently towards the fires near the fire borders (Phillips 1965; Sunquist 1967; Komarek 1969; Vogl 1973; Lyon 1978; Smith and Lyon 2000; Barkley 2019).

Moving to unburned areas is not the only way to survive a fire. Some species have beneficial adaptations such as torpor (Stawski *et al.* 2015b; Nowack *et al.* 2016; Matthews *et al.* 2017; Doty *et al.* 2018) and burrowing (Grafe *et al.* 2002; Garvey *et al.* 2010; Pike and Mitchell 2013), even occupying burrows made by another animal (Bradstock and Auld 1995). Lizards (Kahn 1960; Lillywhite and North 1974), frogs (Vogl 1973), turtles (Fenner and Bull 2007) and insects in mobile stages (Lyon 1978) have been seen burrowed during fires.

Hiding in burrows is not always a successful strategy. As the soil heats up, the air in the burrow becomes hotter and more humid (Kozlowski 1974). Burrow characteristics may expose animals to life-threatening challenges. Good ventilation (Bendell 1974; Hedlund and Rickard 1981), closeness to the surface, or multiple entries (Geluso and Bragg 1986) potentially reduce mortality risk of some species such as Lepidoptera and other univoltine pollinators (Carbone et al. 2019). The construction material is also relevant. Small rodents that build close-surface nests made of flammable materials have a higher vulnerability than species that nest deeper (Kaufman et al. 1988; Simons 1991; Quinn 1979). Survival chances in burrows will also depend on behaviour. Some rodents (Neotoma sp.) have been seen to refuse to leave the burrow during active burning fires (Simons 1991), whereas others (Sigmodon sp.) have been seen carrying young individuals with eyes still closed out of the burrows while fire approached (Komarek 1969).

The decision to move to another area is often accompanied by an inspection of the environment to identify settle options. If the fire has severely damaged the habitat, animals must face the difficulty of becoming oriented. They face increased risk of being preyed on (Johnson et al. 2009), and approaching urban areas, vehicles, and harmful chemicals. In fact, research on road ecology has recently been proposed to mitigate negative roadside behaviours (Proppe et al. 2017). Due to altered vegetation or resource provisioning, roads can serve as attractants to animals. For this reason, a recent review concluded that road use contributes to the risk of collisions with vehicles (Hill et al. 2020). Furthermore, animal migration may also lead to the dispersal of infectious agents, which can have unpredictable effects and cause difficult-to-control diseases (Kirkwood and Sainsbury 1996). New infections can also occur in rescue veterinary hospitals (Kirkwood and Sainsbury 1996).

As a consequence of trophic relationships and resource distribution changes after migration, intraspecific and interspecific competition conflicts may determine post-fire colonisation success (Sutherland and Dickman 1999a) as reported for different species of rodents (Catling 1986; Higgs and Fox 1993), and animal community reorganization (Smith and Lyon 2000). Dominance in competition can be influenced by individual body size (Thompson and Fox 1993; Higgs and Fox 1993) and sex (Monamy and Fox 1999).

In view of the challenge of escaping from fire, some key aspects of management can be highlighted. First, unburnt patches and fire borders -frequented for example by ungulates in search of forage, bedding, cover, and thermal protection (Smith and Lyon 2000)- could be proposed as primary key areas for monitoring, rescue and supplementation. Second, further studies modelling the fluid dynamic processes of gases in burrows could facilitate understanding the challenges faced by burrowing animals (Engstrom 2010). Third, proper human behaviour towards animals is a crucial factor to prevent harm to animals that approach urban spaces, as found for five songbird species (Clucas and Marzluff 2012). Therefore, it is important to inform society on what actions can help or may further harm wild animals during fires. Finally, any accidental introduction of diseases in veterinary hospitals and rescue centres after a fire must be prevented by strict medical management protocols.

Habitat modification

Surviving a fire does not guarantee survival in the post-fire environment, which is characterised by habitat alteration, reduction in shelter and resource availability, competition changes, and increased predation risk (Sutherland and Dickman 1999b; Nimmo *et al.* 2014; Valentine *et al.* 2014; van Mantgem *et al.* 2015).

Fire generates extreme edaphic conditions and the drying of the soil alters bacterial and fungal activity, altering key biological processes. Since burned areas constitute their own local climate, specific behavioural responses within faunal populations occur (Lyon 1978). Specifically, fires cause light, temperature, soil heating and wind increases; humidity decrease; loss of nitrogen and carbon to the atmosphere; charcoal and ash depositions and physicochemical alterations in soil (Callaham *et al.* 2003; Certini 2005). Other specific alterations include increases in canopy fracture, higher rates of tree fall, a downward shift in the vertical stratification of foliage density, a marked increase in the amount of light reaching the understorey and forest floor (Peres *et al.* 2003), and increased solar heat input as a result of the low albedo of black charred soil and vegetation (Klein 1960).

Post-fire environmental alterations can often affect animal distribution and behaviour, eventually affecting welfare. For example, light and temperature excesses together with lack of humidity alter the distribution of different species of birds and small mammals (Ahlgren 1960; Gashwiler 1970; Beck and Vogl 1972), even causing mortality increases (Curry-Lindahl and Marcstrom 1961; Ritcey and Edwards 1963). Both shelter and movement are also reduced in mice and birds due to ash, burned soil, and removal of stem and fallen leaves (Cook 1959; Gashwiler 1970; Sims and Buckner 1973).

Species' environmental requirements determine their post-fire survival. For instance, populations requiring elevated perching sites on shrubs and logs and low vegetation for cover may noticeably decline(-Friend 1993). Specialists and frugivores in need of canopy and other highly specific microhabitat may be restricted to narrow areas (such as moist, shaded understorey). Local extinctions and marked declines are frequent, as reported for antbirds (Barlow et al. 2002), army-ant swarms, pitheciine primates, and large psittacids (Peres et al. 2003). Furthermore, habitat changes are more damaging to highly sensitive species. For instance, amphibians, in addition to having restricted home ranges, have permeable skin vulnerable to flames. Unburned riparian areas likely buffer the stream immediately after the fire (Bury et al. 2002), being main zones to be protected following the fire.

Additionally, food seems to be an important postfire resource selection driver. In fact, time since fire significantly influences food resources (Valentine et al. 2014), and species can modify their diet to survive after a fire, especially in the early stages (Sutherland and Dickman 1999b). For instance, in a study on small mammals' diet, fungus, which is normally an insignificant component of their diet, became dominant after fire (Johnson 1996). Once fire eliminates resources such as nectar, fruits, seeds (Valentine et al. 2012; Valentine et al. 2014), lichens and cottongrass, forage behaviour in species is reduced (Jandt et al. 2008). In fact, some forages take years to recover (Bret-Harte et al. 2013; Zouaoui et al. 2014). As snags fall, foraging options decrease for many beetle-foraging species as well (Morissette et al. 2002). At the same time, fire is beneficial in some contexts for foraging and nesting behaviors of some species. For example, fire provides beneficial resources such as snags for bark forager and cavity-nesting birds (Hutto 1995; Lindenmayer *et al.* 2004; Saab *et al.* 2011). Although higher post-fire foraging and food-seeking behaviours are reported for some species (Begg 1981), the difficulty in finding food generated body condition reduction in some such as bush rats (*Rattus fuscipes*) (Fordyce *et al.* 2016).

Sometimes the post-fire practices of humans cause habitat disturbances that affect animals. For instance, post-fire salvage logging negatively affects deadwood-dependent species like beetles (Villard 1994; Murphy and Lehnhausen 1998; Nappi *et al.* 2003), and forest birds (Haggard and Gaines 2001; Kotliar *et al.* 2002; Morissette *et al.* 2002).

In this section it is relevant to mention that literature also shows numerous examples of the benefits of fire in habitats. There are numerous scientific studies emphasizing that fires are a key agent for the persistence of many ecosystems, such as savannahs, prairies, pine forests or Mediterranean scrublands (Whelan 1995, Orgeas & Andersen 2001, Panzer 2002, Kauffman 2004, Keeley et al. 2005). Fires have been reported to benefit sometimes the regeneration of plant development and succession, the increase of biomass, the irregularity of the habitat, the diversity of food cover, the production of seeds of grasses and legumes, and even the increase in nutritional content and digestibility of plants (Smith & Lyon 2000).

In addition, there is an extended evidence on the assumption that meeting needs of plant communities will automatically meet the needs of animal species (Clarke 2008). Previous research has reported that landscapes exposed to greater diversity of fire regimes generate greater diversity in the long term (Parr and Andersen 2006), stimulating very relevant organisms such as hypogenic fungi (Claridge *et al.* 2009); and that organisms can survive fire disturbances through evolutionary adaptations (Clarke 2008).

Predation risk

Predation is another significant risk that wild animals face due to fires. After a fire, many animals are visually more exposed to their predators, thus having greater vulnerability to being preyed on (Rickbeil *et al.* 2017), as reported for amphibians (Daly 2019), lizards (Shepard 2007) and termites (Prada and Marinho-Filho 2004). For some birds, nests placed in the post fire environment are closer to the ground due to the loss of taller stems, making hatchlings and adult birds more vulnerable to predation (Best 1979). Fires make animals more vulnerable to predators in other ways as well. Energy lost during flight from the fire makes prey animals weaker, increasing predation risk (Johnson *et al.* 2009). This is exacerbated by the increase in predation activity reported after a fire (Sutherland and Dickman 1999b; McGregor *et al.* 2014). Affinity for burned areas has been reported for wolves (*Canis lupus*) (Robinson *et al.* 2012), red foxes (*Vulpes vulpes*), feral cats (*Feliscatus*) (McGregor *et al.* 2016; Geary *et al.* 2019) and raptors (F. Falconidae) (Barnard 1987; Hovick *et al.* 2017).

Post-fire predation increases native mammal mortality and limits population recovery (Hradsky 2020). Some native species may not be accustomed to cope with invasive predators, so they might ignore cues indicating their presence. For instance, native rodents were 21 times more likely to die in areas exposed to intense fire compared to unburned areas, mostly due to predation by feral cats (Leahy *et al.* 2015).

Predation activity after a fire usually increases at the edges of the burned area, and some prey species remained less active in the edges until cover restoration (Parkins *et al.* 2019). Edge zones could be potentially more dangerous for many animals and rescue efforts could begin on the borders of the burn area.

However, there is a lack of research on the influence of flammable ecosystems' dynamics on animal activity patterns (Penn *et al.* 2003; Parkins *et al.* 2019). Mechanisms through which fire could create predation pinch points have been recently reviewed, and key questions about how to increase the resilience of native animals to fire in predator-invaded landscapes have been addressed (Hradsky 2020).

Both predation and competition have a central role in ecosystems, thus conservation science cannot always avoid challenging decisions regarding animal welfare (Sekar and Shiller 2020). Scientific evidence on post-fire predator activity needs to be increased. Understanding how ecosystem context and fire factors affect predator-predator and predator-prey relationships could prevent predation from exceeding adequate levels to maintain the ecosystem balance.

Overview of wild animal management challenges

Interventions on behalf of animals during fires face two main challenges. First, the evaluation of the behavioural responses of wild animals to identify key intervention points still needs to be expanded. This evaluation should consider influencing factors such as fire characteristics, environmental context (Whelan et al. 2002; Andersen et al. 2005; Geary et al.2019), habitat characteristics (Sutherland and Dickman 1999b), and individual stress coping styles (Koolhaas et al. 1999). Second, management of fire-affected animals must guarantee an overall evaluation and clinical assistance. The global state of the individual should be constantly evaluated, including burns, injuries, pre-existing diseases, mental and breathing status, dehydration level, level of shock, and stress due to handling and human proximity, (Fowler 2010). For instance, elderly koalas with advanced tooth wear will be unable to gain sufficient nutrition for the metabolic rate increase that burns require. Since they normally lose weight and starve during the rehabilitation process, veterinary protocol usually determines their euthanasia to avoid poor welfare (Fowler 2010).

Similarly, veterinarians should identify if infections arise during rehabilitation. For example, captive stress can aggravate chlamydiosis in koalas, and contagious individuals must be isolated. Moreover, adult individuals that are next to their dead calves when rescued should be separated to prevent the adult from contracting infection(Fowler 2010).

In the case of koalas, they are especially susceptible to "koala stress syndrome", characterized by lassitude, depression, anorexia and abrupt metabolic function decline. Koalas suffering from this syndrome are frequently found wandering aimlessly, or prostrate and comatose, with no evidence of trauma or overt illness. Captivity, surgeries, anaesthesia, and medical handling can provoke this syndrome (Obendorf 1983). Disorientation and weakness can enhance the probability of road approaches and vehicle collision, and consequent injuries (such as blindness, broken jaws, spines, and legs) that delay their rehabilitation.

Proper management of emergencies such as fires requires not waiting for the fire to occur, but developing pre-disaster efforts and well-organized protocols. In fact, the emergency management lifecycle has been thoroughly described (Heath and Linnabary 2015). For instance, pre-disaster planning can focus on increasing the commitment of the groups involved and improving community preparedness. Moreover, associations specialized in fire evacuations have already been developed and some of them include protocols focused on animals (Marsella and Sciarretta 2018). Animals can benefit from multidisciplinary efforts such as those carried out in the Australian fires in 2020, in which animals obtained the food that they otherwise could only have obtained with great difficulty from the infertile post-fire soils with irregular production and poorly digestible vegetation (Morton *et al.* 2011). The importance of providing food to starving individuals and medical assistance to injured or sick animals has been recently underlined (Faria 2015). Metabolic requirement varies when sick or hurt; therefore, once under rehabilitation, specific nutritional supplementation can be provided (Saito *et al.* 1987).

Feeding and water areas, easily arranged along the natural transects can supply many different species (Mella *et al.* 2019). Unless the rescuer is a veterinarian it is not recommended to provide water to animals before they arrive at the rescue center. Excessive rehydration can lead to subsequent kidney damage problems, and animals should never be bathed. For example, in the case of koalas it is recommended that the environment remain dark, quiet, warm and with an optimal humidity of 10% (Fowler 2010).

Once in the rescue centre, the new environment in captivity can be a harmful factor for wild animals (Kleiman 1989; Biggins *et al.* 1999). Animals deprived of stimuli and space for a long time can display atypical behaviours and natural crucial skills such as anti-predator behaviour and food finding abilities can be compromised, especially for newborn individuals (Shier 2016). Anti-predator training, environmental enrichment, and soft release as pre-release conditioning tactics improved adaptive behaviour and post-release survival for fish, mammals, and reptiles (Tetzlaff *et al.* 2019).

In order for rescue centre environments to ensure similarity to natural habitat and interaction with co-specifics, environmental enrichment (Coleman and Novak 2017) must be considered. Simple initiatives like branch gum-feeders to simulate gum-foraging behaviour are inexpensive, low-maintenance methods that can be applied to various animals (Kreger 1999). New technologies such as Wi-Fi, LED projectors, and cameras can be used to give cognitive and visual enrichment, and monitor physiological variables (Coleman and Novak 2017). Exposure to natural scenes showing the species-typical environment caused beneficial psychological effects (Kahn et al. 2008; Mayer et al. 2009), such as decreased aggression (Kuo and Sullivan 2001), reduced autonomic activity (Parsons et al. 1998), and better surgical recovery along with reduced pain in a hospital setting (Ulrich 1984).

Finally, reintroduction is the ultimate goal for rescued animals and it can prevent long-term population decline, especially in isolated areas likely to be destroyed in subsequent fires (Lunney et al. 2004a), as well as can restore individual animals' welfare (Mathews et al. 2006; Gelling et al. 2012; Harrington et al. 2013; Berg 2018). Reintroduction has been revised in recent years (Kolter and van Dijk 2005; Taggart et al. 2015; Harding et al. 2016; Taylor et al. 2017; Zamboni et al. 2017; Arumugam and Annavi 2019; Jourdan et al. 2019), including the assessment of potential health risks during translocation such as contagious diseases (Leighton 2002). The release should carefully follow re-introduction guidelines available for the species to minimize negative effects. Some aspects considered to assess reintroduction success are the individual's ability to avoid human activities, the minimization of a potential negative effect on the animal host population, and the survival and reproductive success of the individual herself (Kolter and van Dijk 2005). Generally, survival success of released animals is greater for individuals with better development (Muths et al. 2014), as well as in individuals released at their birthplace when compared to translocated ones (Fischer and Lindenmayer 2000).

Monitoring released individuals can be helpful to improve interventions (Muths et al. 2014), and examine fire effects (Engstrom 2010). Individual tagging can provide relevant information on how life history stage and season of fire influence fire-related mortality risk (Griffiths and Christian 1996). Further studies are needed regarding: (1) post-release success measurement in rehabilitated animals following fire and comparing information between individuals within the same population (Goldsworthy et al. 2000; Lunney et al. 2004a; Lunney et al. 2004b), and (2) sophistication and complexity of modern tracking methodologies (Griffiths and Pavajeau 2008). As an example, post-fire rehabilitated koalas were released and monitored for >3 months (NSW Government 2018). Koalas with limbs injuries received minimal intervention and high-quality nutrition, staying away from human contact to heal themselves. Results revealed that koalas healed better than if they had received regular treatments (Daniels 2018). Further investigation into animals' ability to recover from environmental disturbances and injuries may promote minimization of invasiveness.

CONCLUSIONS

Considering that fires are expected to be more frequent and intense in the coming years, wild animals could be exposed to drastic modifications of their natural environment to which they are not adapted to flee and survive. Fires may increase the risk of injury, disease, stress, and mortality for animals living in the wild.

The consequences of fires can result in physiological and psychological damages, experiences of suffering, discomfort and pain, and long-term detrimental consequences.

There are substantial differences between different animal taxa. However, a wide variety of vertebrate species (and perhaps some invertebrates) are capable of experiencing physical and emotional pain, engaging in substantive relationships, and executing cognitively complex tasks (Clayton and Dickinson 1998; Braithwaite and Boulcott 2007; Bartal et al. 2011). This emphasizes that animal welfare is morally significant and policy-relevant (Sekar and Shiller 2020). The effects of fire on wild animals should be considered carefully. Individuals' responses depend on fire characteristics, habitat, life history traits, management of the daily energy budget of the species, and individual stress coping styles. Both active flight and remaining in burrows can severely compromise animal welfare.

Wild animals, especially more vulnerable ones can benefit from effective interventions in fires. All potential suffering, invasiveness, and discomfort during human proximity and handling should be avoided. Further efforts are necessary to expand scientific knowledge, develop multidisciplinary actions and increase social awareness.

FUTURE PERSPECTIVES

The knowledge of the challenges and suffering to which wild animals are exposed in fires can facilitate interventions. In addition to the damage caused by the fire, research has shown that animals are vulnerable to the perceived stress of handling and captures (Obendorf 1983), which may add psychological and physiological damage. In fact, the faster the recovery and the greater the tolerance of an animal to a stressful event are, the lower the likelihood of such an event causing poor welfare (Morton 2007).

To overcome the current challenge that animal rescue actions in fires are focused on domestic animals (Linnabary 1993), awareness campaigns, roundtable events, and multidisciplinary approaches through technological advances are highly recommended.

The use of drones combined with automatic object recognition techniques to manual animal counting (van Gemert *et al.* 2015), centralized public telephone numbers and phone apps can facilitate interventions (White 2014). Media participation and information dissemination (Kolter and van Dijk 2005) may accelerate social interest and public awareness. In fire prone regions, community groups may be involved in interventions, raising awareness of their local environment (Lunney *et al.* 2004a).

Filling the current gaps in research can reveal new ways to help animals. As far as we know, the following list summarizes a sample of aspects that require further investigation.

• Behavioural responses (Smith and Lyon 2000; Penn *et al.* 2003; Banks *et al.* 2017) and physiological effects of fire for a large number of taxa.

• Modelling of gas fluid dynamics within burrows (Engstrom 2010).

• Replication of studies on the influence of morphological factors on the probability of success after a fire (Griffiths and Brook 2014).

• Monitoring the activity of pollinators after fires in different ecosystems (Carbone *et al.* 2019).

• Long-term stress after a fire in wild animals.

• Relationship between fire-related injuries and physical condition or premature post-fire mortality (Engstrom 2010).

• Population studies of tagged individuals before, during and after the fire to distinguish between mortality and migration (Driscoll *et al.* 2010; Conner *et al.* 2011).

• R&D in effective options to prevent potential damage that aquatic fauna may experience in the harsh post-fire conditions .

• Relationship between post-fire food resource changes and diet modification (Begg 1981; Johnson 1996; Sutherland and Dickman 1999b) considering a review of nutrition requirements of fire-affected animals.

• Influence of post-fire activities such as logging on animal welfare (Koivula and Schmiegelow 2007), as evaluated for birds (Haggard and Gaines 2001; Kotliar *et al.* 2002; Morissette *et al.* 2002) and beetles (Villard 1994; Murphy and Lehnhausen 1998; Nappi *et al.* 2003). • Monitoring and management experiments understanding the mechanisms driving predator responses to fire, and potential broader effects (Hradsky *et al.* 2017; Geary *et al.* 2019). Multiple approaches measuring predator abundance, movement and diet are advisable.

• Self-healing ability to minimize invasiveness during interventions.

• New technologies developing environmental enrichment strategies for animals affected by fires (Tetzlaff *et al.* 2019). The consideration of animal temperaments to cover individualized needs during captivity (Coleman and Novak 2017) is recommended.

• Post-release success measurement in rehabilitated animals (Lunney *et al.* 2004b) and comparing information between individuals within the same population (Goldsworthy *et al.* 2000; Lunney *et al.* 2004a).

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