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Fire-induced mortality and associated pathologies across functional reptile groups in relation to fire behaviour

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Abstract. Variation in fire behaviour has been suggested to affect faunal species differently depending on their physical condition and functional traits. Following a management burn in the Munywana Conservancy, KwaZulu-Natal province, South Africa, post-fire mortality surveys produced unique reptile fatality profiles corresponding to variations in fire behaviour and associated pathologies. Mortality due to thermal injury was sustained by epigeic snakes in the headfire, while pulmonary oedema was prevalent in fatalities collected following backburns for a viperid and a fossorial skink. Fat reserves and ecdysis are likely to affect survivorship through these factors placing constraints on locomotion. These results suggest that specific traits and physical condition may make certain reptile functional groups and individuals more susceptible to direct fire effects.

Keywords. Epigeic reptile, fire-associated faunal mortality, fossorial reptile, histopathology, pulmonary oedema

Faunal injury or mortality arising from the effects of fire occurs when animals encounter and are susceptible to hazardous products and conditions produced during vegetation combustion (Engstrom, 2010). This includes exposure to toxic or super-heated gasses, smoke, anoxic conditions, and elevated temperatures above lethal levels (Dickinson et al., 2010; Engstrom, 2010; Jordaan et al., 2019, 2020a). However, little attention has been devoted to assessing the susceptibility of different faunal traits to variations in fire behaviour (Jordaan et al., 2020b). Despite the low fire-associated mortalities reported in most available literature (e.g., Jordaan et al., 2020a; however, see Esque et al., 2003; Buchanan et al., 2021; and Tomas et al., 2021 for examples of high numbers of fire-associated vertebrate mortalities), such information may ultimately inform or contribute to conservation assessments or practical management aspects (Smith et al., 2012; Jordaan et al., 2020b).

Fire behaviour refers to the expression of heat during burning events with regard to the rate of combustion, its spread over the landscape, the direction and height of thermal release, as well as the amount, movement, and distribution of gases and smoke produced during this process (Trollope, 1984; Trollope et al., 2002; Dickenson et al., 2010). These elements are, in turn, influenced by a series of circumstantial environmental conditions such as the prevailing wind direction and strength relative to the fire front, ambient temperature, relative humidity, the terrain, as well as the nature, biomass, moisture content, and size profile of the available combustible fuels (Trollope, 1999; Trollope et al., 2002). Such environmental conditions are often monitored or selected when implementing burning regimes to meet conservation objectives and manage fire-adapted habitats (Booysen and Tainton, 1984; Van Wilgen, 2009). For instance, burns conducted against the wind, which slows the spread of the fire front (known as backburns) result in most of the thermal energy being vented towards the soil surface. These burns are generally implemented to create firebreaks or controlled burns around infrastructure. In contrast, headfires are used to decrease woody encroachment and remove moribund plant material and are burnt with the wind, resulting in the fire front moving faster and directing most of the produced heat upwards away from the soil surface (Trollope et al., 2008). A combination of these basic fire types may also be used in conjunction to facilitate practical fire management and fire safety strategies.

Fire behaviour has been suggested to directly affect the susceptibility of faunal species to vegetation combustion

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according to their adaptations, habitat selection, life history traits, and the physical condition of individuals (Jordaan et al., 2020b). Following a prescribed burn conducted on the Munywana Conservancy (hereafter Munywana) in KwaZulu-Natal province, South Africa, which incorporated backburns on two fronts and a headfire, the subsequent burn scars were surveyed for fire-induced reptile fatalities. These transects produced specific reptile mortality profiles corresponding to variations in fire behaviour. Based on these results, we describe the associated pathology of collected specimens to identify possible traits and physical conditions which may predispose functional ecological groups, specific species and individuals to the effect of variations in fire behaviour.

Methods

Munywana is situated in northern KwaZulu-Natal province, South Africa. The area falls within the Maputaland Centre of Endemism (Martindale and Naylor, 2018) in the eastern moist sub-tropical zone (Maud, 1980) of the Maputaland Coastal vegetation belt (Mucina and Rutherford, 2006). The edaphic character of the area is varied, with the Mozambican/Maputaland coastal plain dominating the northern section and more clay soils derived from siltstone, rhyolite, and basalt underlying the central and southern sections (Maud, 1980; Martindale and Naylor, 2018).

On 14 August 2018, a management burn (estimated size 250 ha; -27.7350°N, 32.4320°E) was conducted in the north-eastern corner of the conservancy in Maputaland Pallid Sandy Bushveld vegetation underlain by moderately deep aeolian sands (Martindale and Naylor, 2018). No rocks or other incombustible cover material were observed in the burn scar. The terrain is primarily flat, sloping slightly towards the south-eastern corner of the management block.

The burn was initiated to fulfil a combination of management objectives, including removing moribund herbaceous material and controlling the woody encroaching shrub *Helichrysum krausii*. Burning operations were initiated by the Munywana management team between 09:30 h and 09:50 h along the southern border of the management block, using drip torches to create a 20–40 m wide backburn along the border road. The firebreak continued north along the eastern border road starting at 10:10 h. After firebreaks were installed, a headfire burning from the north was ignited at 11:25 h. Wind speed, ambient temperature and humidity were monitored during the fire using a Kestrel 3500 weather meter.

To quantify the relative density of fire-induced reptile mortalities, separate walking transects were conducted in the areas burnt during the southern and eastern firebreaks and the headfire as soon as it was safe to do so. The survey was undertaken by a single observer (PRJ) by walking two parallel transects through selected sections of the burn scar, recording the locations of each observed fire fatality and its overall condition and position within 2 m on each side of the transect (Jordaan et al., 2019, 2020a, 2022). As no reptile fatalities were encountered during the first transect, specimens were subsequently sought using timed active searches. All encountered mortalities were photographed *in situ* before being collected and catalogued.

Following fieldwork, specimen identification was confirmed using Branch (1998). Representative photographic records were uploaded to the Biodiversity and Development Institute Virtual Museum at the Percy Fitzpatrick Institute of African Ornithology ReptileMAP (BDI VM RM, vmus.adu.org.za). Specimens were examined externally (Cooper, 2008) prior to collecting tissue samples that were fixed in 10% buffered formalin for later examination. Smaller specimens (body width <20mm) were cross-sectioned into 10–20 mm segments (Jordaan et al., 2019, 2020a, b; Jordaan and Steyl, 2021), whilst larger individuals were dissected, and their organs removed and trimmed into pieces 10–20 mm in diameter to aid in the formalin fixation process. Haematoxylin and eosin-stained sections were prepared from the fixed tissues (Bancroft and Gamble, 2002) to facilitate histopathological examination. This examination attempted to identify the facet of combustion responsible for the death of individuals by investigating the mechanism of mortality (Jordaan et al., 2019, 2020a, b).

Results

During the management burn, average wind speed ranged between 1.3 m/s and 5.1 m/s, and the ambient temperature increased from 26 °C at the onset of the burn to 33 °C at 13:00 h when the general area which was surveyed in the headfire was burnt. The prevailing wind direction remained predominantly North to South for the duration of the burn. Humidity decreased from 63% at the time of the first ignition to 40% at 13:00 h.

Due to the high moisture content from morning dew, the vegetation in the southern firebreak was only partially combusted, leaving some herbaceous stems and the tops of some *H. krausii* bushes intact. This incomplete combustion produced thick clouds of smoke which resulted in hazardous fieldwork conditions, and as a result the post-fire survey could only start at 11:00, almost an hour after the first firebreak was initiated. The burn scar was surveyed using two parallel transects spanning a distance of 1000 m in total (equal to a strip of 4000 m^2) which yielded no reptile mortalities. Unquantified active searches were then initiated throughout the burn scar for 20 minutes to locate any specimens. During the active searching, three Puff Adder *Bitis arietans arietans* (Merrem, 1820) fatalities were encountered (Fig. 1A; BDI VM RM 181981) all of which were associated with burnt *H. krausii* bushes (Table 1). All three specimens exhibited blue opaque eyes, indicating that they were in the process of preparing for ecdysis. The two smaller specimens were confirmed as males (total length [TL] 502 mm, mass 0.198 kg; and TL 454 mm, mass 0.13 kg) from their distended charred hemipenes. The largest specimen (TL: 728 mm, mass: 0.825 kg) was confirmed as a female during dissection. Two of the specimens had oral blood seepage. Histopathological examination was only conducted on tissues of one of the male *B. a. arietans* specimens. Extensive fat reserves were evident during dissection as well as histopathological examination. Significant pulmonary congestion and oedema were observed during the histopathological examination of lung tissue (Fig. 2A) and several other organs were also severely congested.

The eastern firebreak was surveyed using two parallel transects of 600 m each, covering a total area of 4800 m^2. In contrast to the southern firebreak, the eastern firebreak exhibited near-complete vegetation combustion, including detrital material. Seven deceased Lowveld Dwarf Burrowing Skinks *Scelotes bidigittatus* FitzSimons 1930 were collected during the transect (Fig. 1B), all of which were located underneath burnt *H. krausii* bushes. These fossorial skinks appeared to have vacated the soil layer in favour of the surface during the fire. Four specimens exhibited no external injuries (Fig. 1B; BDI VM RM 181980). The remaining three specimens showed varying degrees of desiccation or thermal damage, including one specimen which was found with its mouth partially cremated (BDI VM RM 181979), however this damage was likely sustained post-mortem as no pathological signs of hypereosinophilic tissue responses or blistering was observed. Microscopically, severe pulmonary congestion with varying levels of oedema was present in all examined *S. bidigittatus* (Fig. 2B). Two individuals also exhibited widespread alveolar

Figure 1. Fire-induced reptile mortalities encountered during post-fire surveys on Munywana Conservancy, KwaZulu-Natal province, South Africa, photographed *in situ*. (A) Puff Adder *Bitis a. arietans* (southern firebreak); (B) Lowveld Dwarf Burrowing Skink *Scelotes bidigittatus* (eastern firebreak); (C) Short-snouted Grass Snake *Psammophis brevirostris* (headfire); and (D) Common Wolf Snake *Lycophidion capense capense* (headfire). Photographs by PR Jordaan.

Table 1. Diversity of reptile mortalities encountered during surveys conducted on the Munywana Conservancy, Kwazulu-Natal province, South Africa, following a management burn.

Common name	Species	Southern backburn	Eastern backburn	Headburn
		20-minute active search	1200 m transect (4800 m²)	1000 m transect (4000 m²)
Puff Adder	*Bitis a. arietans*	3	0	0
Common Wolf Snake	*Lycophidion c. capense*	0	0	1
Short-snouted Grass Snake	*Psammophis brevirostris*	0	0	2
Lowveld Dwarf Burrowing Skink	*Scelotes bidigittatus*	0	7	0
Total per survey		**3**	**7**	**3**
Derived density (individuals per hectare)		**<2.50**	**14.58**	**7.50**

haemorrhage.

The headfire resulted in near to complete combustion of the herbaceous layer. A section of the area burnt during the headfire around 13:00 h was surveyed using two parallel transects of 500 m each, spanning 4000 m^2. Three reptile fatalities from two species, Short-snouted Grass Snake *Psammophis brevirostris* Peters 1881 ($n = 2$) (Fig. 1C) and Common Wolf Snake *Lycophidion capense capense* (Smith, 1831) ($n = 1$), were encountered within the surveyed strip (Fig. 1D). Unlike the specimens from the previous transect, all three snakes were found in the open, where grassy patches were burnt. Whilst both *P. brevirostris* fatalities (BDI VM RM 181987) had obvious thermal injuries on their bodies, tail, and especially the eyes - which were partially cremated - the *L. c. capense* specimen (BDI VM RM 181986) exhibited no visible thermal injuries during the initial external inspection. Microscopic examination, however, provided evidence of epidermal corneal vesiculation ("micro-blistering") and separation from underlying epidermal tissue in all three specimens (Fig. 2C). Hypereosinophilia of the peripheral subcutaneous musculature indicated terminal thermal injuries in all three specimens. During the histopathology examination, both *P. brevirostris* were found to have recently ingested large meals, whilst no prey items were evident in the gut of the *L. c. capense*.

Discussion

The functional ecological adaptations of species influence their spatial occupancy within a specific habitat, largely dictating to what extent and which aspects of vegetation combustion individuals might be exposed to (Jordaan et al., 2020b). The fire-induced reptile mortalities collected from the three sections of the same management burn during this study yielded unique diversity profiles with no species in common between transects, despite the homogenous terrain and vegetation. Subsequently, the mechanisms of mortality associated with different fire behaviours were investigated using histopathological analyses to identify the vulnerabilities of the represented functional groups.

Three of the four encountered species are predominantly surface-dwelling or epigeic, however their general behaviour and mobility potential vary, likely affecting their inherent responses and ability to evade fires. For instance, *Bitis a. arietans* is generally a sluggish ambush predator with a propensity to seek shelter under low vegetation rather than fleeing from active threats, whereas *P. brevirostris* is an active foraging snake, frequently moving over the terrain surface (Branch, 1998), thus making it more likely to try and evade the fire by fleeing. *Lycophidion c. capense* is also an active epigeic snake but does not possess the speed of *P. brevirostris* and it may therefore rely on methods other than mobility, such as entering earthen burrows or sheltering under non-combustible surface objects if available, to escape fires.

A full gut and high fat reserves could affect locomotion, hampering escape attempts enough to allow individuals to be overtaken by the fire front or other detrimental conditions derived from vegetation combustion (Jordaan et al., 2019). During dissection, all *B. a. arietans* exhibited high levels of body fat as did both *P. brevirostris*, while both *P. brevirostris* had also recently ingested large meals (a rodent and a rodent and unidentified skink (*Trachylepis*), respectively). Considering that both reptile species collected from the headfire lacked clear signs of pulmonary oedema but displayed extensive thermal damage during histopathological analyses, it suggests that these specimens were burnt to death when they were overtaken by and directly exposed to the fire front. It should, however, be noted that not all thermal

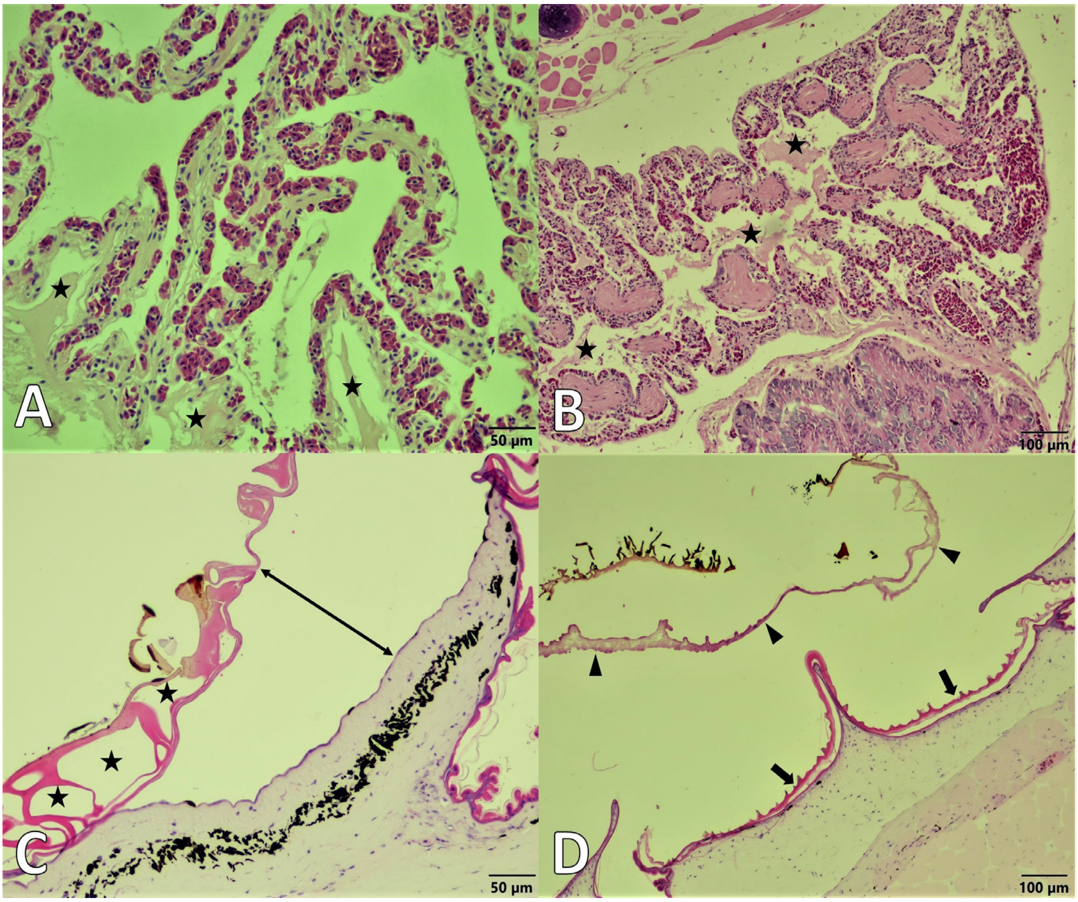

Figure 2. (A) Puff Adder *Bitis arietans arietans* (200x magnification) and (B) Lowveld Dwarf Burrowing Skink *Scelotes bidigittatus* (100x magnification) lung tissue exhibiting severe alveolar congestion and moderate to severe variable proteinaceous oedema (stars) suggestive of acute, terminal heart failure. (C) Short-snouted Grass Snake *Psammophis brevirostris* with severe stratum corneum vesiculation (stars) and corneal separation from the underlying epidermis (double arrow) resulting from thermal injury (200x magnification); compared to (D) Puff Adder *Bitis a. arietans* normal ecdysis exhibiting sloughing/separation of the old stratum corneum (triangles) from the newly synthetised stratum corneum (arrows) (100x magnification). Photomicrographs stained with haematoxylin and eosin.

injuries sustained by reptiles contribute to or result in mortality (e.g., Jordaan et al., 2022). In contrast to the other species, *S. bidigittatus* has a limited ability to move above ground, displaying a relatively shallow (Branch, 1998) but "strictly fossorial" lifestyle (Maritz and Alexander, 2008).

Based on previously published accounts, snakes preparing for ecdysis are more susceptible to the effects of fire (Beaupre and Douglas, 2012; Jordaan et al., 2019, 2020a, b). All three *B. a. arietans* collected during this study were preparing to shed their skin, and this was confirmed during histopathological analyses where the epidermal detachment between the examined *B. a. arietans* specimen preparing for ecdysis (Fig. 2D) and the thermal blistering observed in the *P. brevirostris* specimens from the headfire transect could clearly be discerned (Fig. 2C). If *B. a. arietans* relies on its natural behaviour of crypsis to avoid threats (in this case, the fire), a higher mortality density would be expected for this common viperid with both non-shedding and shedding individuals represented in samples. This suggests that these *B. a. arietans* mortalities were as a direct result of their preparing for ecdysis, rather than some other ecological reason.

Indications of smoke inhalation during light microscopic analyses manifest as soot and carbon deposits in airways and lung tissue (Stern et al., 2014; Peters et al., 2021) and evidence of smoke inhalation in reptiles has only very rarely been documented (Jordaan et al., 2020b). None of the examined pulmonary tissue collected during this study contained any carbon particles or residue, ruling out smoke inhalation as a cause of death for any of the analysed specimens. Neither was terminal bronchiolar epithelial ciliation affected (see Jordaan et al., 2019), suggesting that physical heat-induced pulmonary injury was unlikely for the analysed samples. As has been speculated previously (Jordaan et al., 2019, 2020b), death most likely ensued following inhalation of a mixture of noxious gases originating from combustion in association with anoxia. The rate at which heart failure occurs is indirectly proportional to the amount of pulmonary oedema, with samples exhibiting high levels of oedema indicative of a comparatively longer period of acute strain on the heart in contrast to lower levels of pulmonary oedema, which is indicative of rapid mortality. The observed variability in pulmonary oedema in the different specimens suggests slight differences in the rate at which acute heart failure occurred between species.

The possible subsurface transport of gasses from smouldering detrital material (Massmann et al., 2010) has been suggested to affect fossorial reptiles, including several species of soil-living skinks (Jordaan et al., 2019, 2020b) and the prevalence of cardiogenic pulmonary congestion and oedema in the examined *S. bidigittatus* would suggest fatal consequences from inhaling toxic levels of noxious gasses. Compared to the southern firebreak, the higher level of detrital combustion observed along the eastern firebreak likely relates to both the hotter and drier ambient conditions when burning took place, and the fire burning directly against the wind closer to the soil surface for an extended distance. The slow progression of the backburn against the wind likely increased the thermal energy vented towards the soil surface, promoting detrital ignition and combustion which produced subsurface gas transportation (Massman et al., 2010), subsequently affecting fossorial reptiles. Pulmonary samples from the analysed *B. a. arietans* specimen from the southern firebreak exhibited severe congestion and oedema, similar to the condition of the *S. bidigittatus* material. This indicates that the same mechanism of mortality from noxious gas inhalation leading to heart failure was at play.

More information is required regarding the direct impact of fire on fauna to contextualise observed mortalities, including seasonal considerations (Jordaan et al., 2020b; Buchanan et al., 2021), while regional population estimates are required to allow mortality rates to be calculated (see Jordaan et al., 2020a). The results from this study suggest that the biology and behaviour of functional species groups and the physical condition of individuals may predispose or shield reptiles to specific fire behaviours (Jordaan et al., 2020b; Jordaan and Steyl, 2021). In this case, it would appear as though slow-moving backburns have the potential to affect shallow-living fossorial reptiles and ambush/sit-and-wait snakes preparing for ecdysis, whilst faster-moving headfires can overtake and directly expose epigeic species to fatal temperatures. Additionally, the susceptibility of some reptiles to fire may be contingent or compounded by physical conditions either constraining mobility (high fat reserves, full gut, being gravid) or affecting an individual's ability to avoid fatal fire conditions (e.g., Jordaan et al., 2019). The effect of different ignition methods or burning strategies (e.g., the linear spread of fire for block burns versus point ignition for mosaic burns) may also affect fire-induced injury or mortality in reptiles but has not been compared or assessed.

The current study suggests that management objectives and environmental conditions affecting fire regimes could potentially disproportionately influence specific reptile functional groups, although larger sample sizes are required to confirm this. Reptiles living in fire-prone habitats have developed strategies to contend with natural fire frequencies and intensities, and as such direct mortalities associated with fire are considered inconsequential when compared to indirect effects of post-fire habitat modification (Engstrom, 2010). However, such considerations are likely to become more pertinent in future when taking anthropogenically modified fire regimes and climate change into consideration (Esque et al., 2003; Buchanan et al., 2021; Tomas et al., 2021).

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