African Journal of Range & Forage Science 2021: 1–15
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This is the final version of the article that is
published ahead of the print and online issue

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AFRICAN JOURNAL OF
RANGE & FORAGE SCIENCE
ISSN 1022-0119 EISSN 1727-9380
https://doi.org/10.2989/10220119.2021.1918765

A review of the responses of medium- to large-sized African mammals to fire

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An improved understanding of how fire affects African mammals is important for the management of both fire regimes and mammal populations. The response of mammals (>5 kg) to fire was reviewed to identify habitat preferences, and to inform fire management. Sixty-four studies reported on 51 species at 34 locations. Body size was strongly correlated with fire response, with smaller grazing species more likely to respond positively to fire (i.e. to occupy recently-burnt areas) than larger browsing species. Frequently-studied species (≥4 studies) were classified as either ambivalent in their responses to fire (four large browsers) or as responding positively to fire (fourteen grazers). An additional 30 less frequently studied species (<4 studies), including carnivores, were preliminarily assigned to fire response categories. Almost all studies were conducted in savanna and grassland vegetation, with the fire-prone dystrophic miombo, and more arid sites under-represented. Much of the research was aimed at establishing the preferences of a rare or declining species of concern, and fire management recommendations often called for increasing fire frequency to benefit such species. However, it is clear that co-occurring species have different requirements. We conclude therefore that managers should aim to promote spatial heterogeneity through fire application.

Keywords: browser, carnivore, fire management, grazer, herbivore, hind-gut fermenter, mixed-feeder, ruminant

Supplementary material: available at https://doi.org/10.2989/10220119.2021.1918765

Introduction

Fire is a natural phenomenon that has shaped the structure and evolution of the African environment, and a large proportion of the continent is prone to frequent fires (Bond and Keeley 2005). The elements of historical fire regimes, including the frequency and intensity of fires, have largely been altered through human-induced land-use change, attitudes and policies (Bowman et al. 2009), and continued alterations to fire regimes can be anticipated as a result of *inter alia* global climate change and rising human population numbers (Archibald et al. 2009; Moritz et al. 2012). Most of Africa has also, until relatively recently, been home to a diverse range of free-roaming large mammal species that evolved in these fire-prone landscapes, but that now require active management, because of unprecedented declines in population numbers in recent decades (Craigie et al. 2010; Visconti et al. 2011; Ripple et al. 2015; Archer et al. 2018). The effects of fire are most easily observed as changes to the structure and composition of vegetation (Higgins et al. 2007), and fire management is therefore usually focussed on vegetation (Nieman et al. 2021a). Fire also affects large mammals either directly (e.g. through fire-induced mortalities) or indirectly (e.g. through changes to food resources or habitat structure), and has the potential to accelerate large mammal extinction rates (Brook et al. 2008; Ward et al. 2020). Mammals may respond to fire either immediately, for example, by suffering mortalities or changing their movement patterns (Woolley et al. 2008) or over time by responding to the natural regrowth of herbaceous material following fire (Eby et al. 2014; Burkepile et al. 2016), and changes to the woody structure of the vegetation (Smit and Prins 2015).

In general, African mammals are well adapted to surviving in fire-prone environments, and may even depend on their habitat being periodically burned (Olindo 1971). It has long been known that the preference shown by herbivores for burnt areas is as a result of increases in the nutrient quality of post-fire regrowth (Rowe-Rowe 1982; Wilsey 1996; Van de Vijver et al. 1999; Sensenig et al. 2010; Eby et al. 2014), but recent research has suggested that herbivores may also select open (burnt) landscapes to improve predator detection (Hopcraft et al. 2005; Valeix et al. 2009). In both instances, differences in the behaviour of individual species in response to fire may depend on factors relating to body size. For example, smaller-bodied herbivores (5–200 kg) require more energy and nutrients relative to their body weight (Demment and van Soest 1985), and should therefore be more attracted to burnt areas to benefit from nutrient increases (Eby et al. 2014). In contrast, larger-bodied herbivores (>200 kg) have greater gut capacity and retention time, and can therefore extract nutrients from the lower-quality forage in unburnt landscapes (Hopcraft et al. 2012). Larger-bodied herbivores are also less vulnerable to predation (Sinclair et al. 2003; Radloff and du Toit 2004), whereas smaller-bodied species may avoid unburnt landscapes, because they provide better cover for predators. In addition, changes to the structure of vegetation brought about by changes in fire regimes could potentially negatively affect grazing herbivores if it reduces the available forage material or increases predation risk. Increased woody thickening, because of a reduction in fire frequency and intensity, is an example of such a change (Gandiwa and Kativu 2009). Although fire affects herbivore behaviour, herbivores also influence fire regimes by, for example, reducing fuel loads or altering vegetation structure and plant species assemblages (Smit and Coetsee 2019). Holistic biodiversity management will therefore have to account for the complex interactions and feedbacks between fire and herbivory (Hempson et al. 2015; Donaldson et al. 2018). Far less is known about the responses of predators to fire. Some studies indicate that predators will select areas with high densities of prey (typical of burnt landscapes) (Green et al. 2015), whereas others suggest that areas that provide good cover are preferred (typical of landscapes unaffected by fire) (Hopcraft et al. 2005; Balme et al. 2007; Eby et al. 2013; Davies et al. 2016).

An understanding of how fire influences large mammals could be important for the management of both mammal populations and fire regimes, increasingly so as a result of mounting pressures placed on protected areas for the conservation of Africa's last remaining wildlife (Barnes et al. 2016). However, the relationship between fire and large mammals in Africa is not fully understood. The scant information on the responses of large African mammals to fire has been summarised in book chapters (Bigalke and Willan 1984; Frost 1984; de Ronde et al. 2004), and was assessed by Parr and Chown (2003), but many new studies have since been published, and an updated review is needed. Quantitative systematic reviews offer the opportunity to assess information from the peer-reviewed literature (Pullin and Stewart 2006), to identify trends, consistency, and gaps in understanding, and to inform the revision of management policies where appropriate. In this paper, we provide a review of the response of large (>5 kg) African mammals to fire, and identify trends and gaps in existing research. Specifically, we identify (1) the species most often included in fire response research, and examine the relationship between body size, feeding guild and digestive strategy and large mammal species response to fire, (2) the regions, countries and vegetation types where studies have been conducted, (3) the scope of investigation, including *inter alia* the sampling procedure, length and design of the reviewed studies, and (4) the recommendations made to environmental managers in the reviewed literature.

Materials and methods

Search strategy

We performed a literature search in the SCOPUS and Web of Science databases, first using the following search terms: fire* OR wildfire OR burn* AND Africa* AND mammal* OR wildlife. Thereafter, subsequent searches were made using the following search query: fire* OR wildfire OR burn* AND Africa AND χ, where χ = individual genera of large African mammals e.g. '*Tragelaphus*' (total of 52 genera). All papers published on or before August 2020 were included. Searches included titles, abstracts and keywords. All identified papers were examined, and we excluded papers that were not relevant to our specific aims (e.g. papers that did not explicitly deal with responses of mammals to fire, papers that focussed on non-mammalian species, non-terrestrial mammals, mammals with body sizes <5 kg or domestic mammals). A total of 36 papers or book chapters were retained from these searches, and an additional 28 papers were added from the reference lists in retained papers, to include as many relevant studies as possible. The final dataset of papers and book chapters included in this review was therefore 64 (Supplementary material 1). Unpublished reports, policy statements and theses were not considered.

Database setup

The reviewed papers were used to compile a database with information on (1) study species, (2) study location, (3) scope of investigation, and (4) study focus and management recommendations (Supplementary material 2).

Study species

Subspecies of several Artiodactyla species were considered at species-level for the purposes of this study, except for *Syncerus caffer* (buffalo) where subspecies (the Cape buffalo *Syncerus caffer caffer* and African forest buffalo *S. c. nanus*) were considered separately, because of the large difference in body size between these two subspecies (Supplementary material 3). Species were classified into four body size categories, namely: medium-sized mammals (5–50 kg), medium- to large-sized mammals (51–200 kg), large mammals (201–500 kg), and very large mammals (>500 kg). Species were also classed as either grazing, browsing or mixed-feeding herbivores, carnivores or omnivores, and herbivores were further classed as either ruminants or hind-gut fermenters (Gagnon and Chew 2000; Kingdon et al. 2013). The current conservation status of all species and subspecies were noted based on the 2020 IUCN Red List of Threatened Species (http://www.iucnredlist.org/).

Study location

Studies were grouped according to country and study location therein. In addition, each study was categorised by vegetation type, based on the 50 sub-Saharan vegetation types described by Sayre et al. (2013). In some instances, single studies could be assigned to more than one vegetation type. The geographic scale of each study was categorised as either local (studies that were confined to a single vegetation type at a single location), regional (studies that included more than one vegetation type and/or that were undertaken at multiple locations) or national (studies conducted at the level of a country).

Scope of investigation

Each of the studies was categorised by its scope of investigation. Studies were first divided into those that included (a) both pre- and post-fire sampling; (b) post-fire sampling only; or (c) reported on the cumulative effects of multiple fires over multiple years. Secondly, papers were categorised as single-species studies or those that reported on more than one species. Thirdly, studies were categorised based on their duration, i.e. whether the study took place over less than a year or considered the effects of multiple fires over 1 to 5 years, or >5 years.

Study focus and management recommendations

Studies were divided into four categories based on their primary objectives and reported outcomes. These were: a) species-level responses to fire (i.e. studies that reported on the responses of an individual species to fire), b) community-level responses to fire (i.e. studies that reported on the responses of groupings, such as grazers or herbivores to fire), c) historic fire regime evaluation or reconstruction, and d) the impact of fire on habitat structure or forage availability. Any recommendations that were made for fire management or policy development were also noted. The recommendations were subsequently simplified and grouped into discrete categories for comparison.

Additionally, the responses of species to fire were classified into immediate responses (i.e. responses recorded during or within a few days after a fire), short-term responses (i.e. responses recorded at any time after a fire, but before the next fire), and long-term responses (i.e. responses associated with habitat changes brought about by multiple fires). Some studies were assigned to more than one category. Thereafter, the behavioural responses of species to fire was classified into one of three categories: positive responses to fire (e.g. selection of post-fire regrowth or a short-term preference for burnt areas or long-term preference for habitats subjected to frequent fires); negative responses to fire (e.g. active avoidance of burnt areas or a comparative short-term preference for unburnt areas or long-term preference for habitats subjected to infrequent or no fires); or neutral/ambivalent responses to fire (e.g. no clear preference for either burnt or unburnt patches or new post-fire regrowth or older vegetation). The number of studies in which respective species were reported to have either positive, negative or neutral responses to fire was noted, and this was used to compare responses among different body size, feeding guild and digestive strategy categories. Only species that were found in ≥5 individual studies were included in these analyses.

Almost two decades ago, Parr and Chown (2003) published a critique of faunal fire research in Southern Africa, in which they recommended that future studies should be based on a suite of large-scale and experimental approaches, with the latter firmly grounded in the principles of sound experimental design. They also noted that the key components of experimental design should include controls, replication, randomization, and interspersion. We therefore examined our selected papers to assess the degree to which papers published after this critique had met any of these criteria.

Results

We identified 64 studies that described the responses of large mammals to fire. The earliest paper was published in 1964 (Brynard 1964), after which publications slowly increased until the start of the 21st century, after which the rate of publication increased, with up to four (2005) or five (2015) new papers per year (Figure 1). Since the most recent synthesis by de Ronde et al. (2004), 37 additional studies have been published, and an additional 12 older studies included here were not cited by de Ronde et al. (2004).

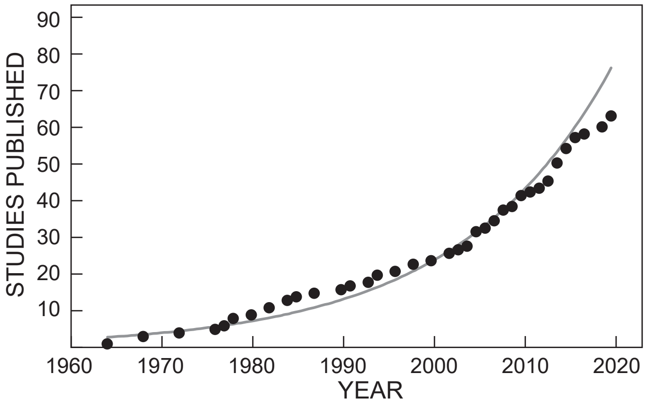

Figure 1: The cumulative number of studies on the response of large mammals to fire in Africa published between 1964 and 2020

Species covered in fire-related studies

A total of 51 large African mammal species belonging to 35 genera, 11 families and five orders were included in fire-related studies (Supplementary material 3). The majority of species belonged to the order Artiodactyla (37 species), and included the families *Bovidae* (35 species), Giraffidae (1 species), and Suidae (1 species). Species of the order Artiodactyla were included in 80.7% of all reviewed studies. The remaining 14 species belonged to the orders Perissodactyla (families Rhinocerotidae and Equidae), Carnivora (families Felidae, Mustelidae, Canidae and Hyaenidae), Primates (family Hominidae), and Proboscidea (family Elephantidae). The species most frequently (≥8 studies) included in the literature were: plains zebra (16 studies), impala (14 studies), blue wildebeest (13 studies), hartebeest (10 studies), common warthog (8 studies), roan antelope (8 studies), common tsessebe (8 studies), and African savanna elephant (8 studies).

Species ranged in body size from 6 kg (Kirk's dik-dik) to 6 000 kg (African savanna elephant). The smallest size class (5–50 kg) contained the highest number of studied species (22 species), and the number of studied species in each size class declined with increasing sizes, so that the largest size class (>500 kg) contained the fewest number of species (7 species). Nearly two thirds of the studies (61.4%) dealt with species of conservation concern. Twenty-three (39.0%) of the studied species or subspecies were listed as being of conservation concern by the IUCN, with seven species considered Endangered (EN) or Critically Endangered (CR). An additonal 16 species were listed as Vulnerable (VU) or Near-Threatened (NT).

Most ungulate species whose responses to fire were reported in the literature were grazers (19 species), and were included in 57.9% of all studies. Browsing or mixed-feeding mammals contained a similar number of species (12 and 11 species, respectively), but mixed-feeders were included in more studies than browsers (25.1 and 16.9% of all studies, respectively). The majority of ungulates (38 species) whose responses to fire were reported were ruminants (85.7%), whereas six species were hind-gut fermenters. A disproportionally large number of studies (21.9%) nonetheless focussed on hind-gut fermenters, particularly zebras. The remaining nine non-ungulate species were classified as either carnivores or omnivores (primates and side-striped jackal).

Study location

The literature included studies from 34 locations in 10 African countries. More than 80% of studies came from only three countries, namely South Africa (62.5%), Tanzania (14.1%) and Kenya (7.8%). Similarly, three locations accounted for more than 70% of all study locations, these being Kruger National Park, South Africa (11 studies), Serengeti National Park, Tanzania (9 studies) and Nylsvley Nature Reserve, South Africa (5 studies). Almost all studies were conducted either entirely (90.6%) or partially within a protected area (4.7%), whereas only three studies took place outside of protected areas.

Most studies (75.0%) reported results at a local scale (i.e. a single vegetation type and location), whereas the remaining literature was at regional (23.4%) or national (1 study) scale. The studies took place in 18 of the 50 African vegetation types identified by Sayre et al. (2013). Almost two thirds (60%) of all studies were in savanna woodlands, with a surprizing proportion (16%) in relatively fire-free forest or riparian vegetation (Supplementary material 4). Studies in scrub or thicket vegetation, and in grasslands, accounted for a further 16% and 10% of all studies, respectively.

Scope of investigation

Approximately two thirds of all studies (65.5%) reported on the responses of mammals to single fires, whereas the remaining third (30.1%) reported on the cumulative effects of multiple fires over multiple years. Only two studies (3.6%) included some form of pre-fire sampling. Notably, almost all the studies (88.2%) reporting on the cumulative effects of multiple fires over multiple years were published after 2005.

The reviewed literature was also relatively evenly divided between single-species studies (46.9%), and studies focussing on multiple species assemblages (53.1%). Single-species studies were most common for black rhinoceros (4 studies), sable antelope (4 studies), African savanna elephant (3 studies), and impala (3 studies). Most observations of responses were based on the reaction within a single fire season (49.1%), whereas 22.6% were based on all fires that took place over one to five years, and 26.4% of studies considered all fires over more than five years. One study did not state the period over which burning took place.

Study focus and management recommendations

Most studies (81.3%) reported on species-level responses to fire, whereas five studies (7.8%) reported on responses at the level of co-occurring mammal assemblages, and another five on the impact of fire on the habitat structure or forage availability for mammals. The remaining category (i.e. historic fire regime evaluations or reconstructions) included two studies (3.1%).

Recommendations for fire management or policies were made in less than half of the reviewed studies (39.4%). The most common recommendation was to increase fire frequencies (10 studies), for the purpose of improving forage quality and availability for grazers, and for preventing late dry season fires. A similar number of studies (8 studies) recommended an increase in the spatial or temporal heterogeneity of fire application, to adequately cater for all facets of biodiversity. Five studies recommended that fire frequencies be decreased or that fire be excluded entirely to retain forage throughout the dry season and to allow previously over-utilised vegetation to recover. Other recommendations included that fires be applied in the early dry season (4 studies) to promote nutritious forage for large mammals during the dry season or that fires be applied in the early wet season (2 studies) to improve forage quality for grazers. One study proposed that thresholds of potential concern (TPCs) be defined and monitored as a form of adaptive management.

Species-specific responses of herbivores to fire

Most studies reported on the short-term response of herbivores to fire (44 studies), whereas fewer reported on the immediate (7 studies) or long-term responses to fire (23 studies). The number of studies that dealt with a particular species ranged from 1 to 16 per species (mean = 4.2 studies per species, Table 1 and Supplementary material 5). More species (79.5%) were noted to respond positively to fire, than either negatively or neutrally (Figure 2). Of those herbivore species that were cited in ≥5 different studies (15 species), an inverse relationship was found between body size and response to fire ($r^2 = 0.76$), with larger species having more of a negative response to fire (i.e. moving away from recently-burnt areas), whereas smaller species were more likely to react positively to fire (i.e. attracted to recently-burnt areas, Figure 3). Among feeding guilds, grazing herbivores showed the strongest positive response to fire, whereas the number of studies reporting negative responses to fire were comparatively higher for mixed-feeders and browsing herbivores. Species from all three guilds were nonetheless more likely to show a positive response to fire (Figure 4a). Similarly, both hindgut fermenters and ruminants were more likely in general to respond positively to fire, but hindgut fermenters were more likely than ruminants to respond negatively to fire (Figure 4b).

There were 18 large herbivorous mammal species whose responses to fire were described in at least four publications, and we assigned fire response types to these species. Of these, the majority (14 species) displayed positive or predominantly positive, responses to fire. The remaining four species were classified as having neutral or ambivalent responses to fire, in that they frequented both burnt and unburnt areas with no evidence of a strong preference for either. The documented responses to fire of each of these 18 species is summarised in Table 1. The responses to fire of an additional 30 species identified in our review were described in three or less studies, and we have preliminarily placed these into fire response categories based on this limited information (Supplementary material 5). Species classified as being negatively affected by fire were either forest species (forest elephants, chimpanzees or gorillas), whereas one was a browser (greater kudu).

Table 1: African mammal species response to fire (positive, negative or ambivalent), with documented responses to fire summarised for species that were included in four or more published studies

Species	Number of studies	Conservation status	Fire response type	Responses to fire
African savanna elephant	8	Vulnerable	Ambivalent	Mortality of both young and adult elephants has been recorded in intense fires (Woolley et al. 2008). Studies have otherwise reported mixed responses to burnt areas by elephants. On the one hand, elephants showed preferences for annually burnt areas, have been noted to feed on recently burnt twigs, and the probability of finding bull elephants was reportedly higher in areas with high fire frequencies (Frost 1984; Burkepile et al. 2016; MacFadyen et al. 2019). On the other hand, several studies found that elephants avoided burnt areas (Bell and Jachmann 1984; Woolley et al. 2008; Sensenig et al. 2010). It seems therefore that elephants are not strongly influenced by fire, as is typical of mixed feeders with hindgut fermentation strategies.
Black rhinoceros	4	Critically Endangered	Ambivalent	Black rhinoceros have been found to feed on regenerating browse material after a fire, and to have higher overall feeding levels in burnt areas (Mukinya 1977; Emslie and Adcock 1994). On the other hand, other studies have found that black rhinoceros selected areas that burnt infrequently (sites with <0.6 fires y^{-1}, and maximum occupancy at sites with fire frequencies of <0.1 fires y^{-1}) (Anderson et al. 2020), and avoided areas that were recently burnt (Odendaal-Holmes, Marshal, and Parrini 2014).
Blesbok/Bontebok	6	Least Concern (Blesbok)/ Vulnerable (Bontebok)	Positive	All studies on this species noted that both subspecies are attracted to burnt areas, and show a preference for new post-fire regrowth (du Plessis 1972; Novellie 1978; Beukes 1987; Kraaij 2010; Kraaij and Novellie 2010; Rowe-Rowe 1982). These responses appear to be typical of grazing mammals and indicate that regular burning would be beneficial for these species.
Blue wildebeest	13	Least Concern	Predominantly positive	Most studies (Archibald et al. 2005; Burkepile et al. 2016; Donaldson et al. 2018; Green et al. 2015; Hassan and Rija 2011; Mariotti et al. 2020a; Moe et al. 1990; O'Kane et al. 2014; Tomor and Owen-Smith 2002; Wilsey 1996; Yoganand and Owen-Smith 2014) indicated that blue wildebeest showed preferences for recently burnt areas where post-fire regrowth was available or for areas that were burnt annually. There were two studies that indicated that wildebeest either selected unburnt patches more than burnt patches (Mariotti et al. 2020b) or that they showed no particular preference for burnt or unburnt patches (Eby et al. 2014). The bulk of evidence nonetheless indicates that wildebeest respond positively to regular burning, as is typical of grazing mammal species.
Cape buffalo	6	Least Concern	Ambivalent	Many studies have shown that Cape buffalo select for burnt areas immediately after a fire or show a preference for areas subject to annual burns (Archibald et al. 2005; Burkepile et al. 2013; Donaldson et al. 2018; Zavala and Holdo 2005). Others have found that the attraction of buffalo to burnt sites immediately after a fire is short-lived, and that buffalo don't select for burnt areas long after a fire (Donaldson et al. 2018). Field (1976) found no difference in the time buffalo spent in burnt and unburnt plots, and Hassan and Rjia (2011) found that buffalo persistently occurred in unburnt patches.

Table 1: (cont.)

Species	Number of studies	Conservation status	Fire response type	Responses to fire
Common tsessebe	8	Least Concern	Predominantly positive	For common tsessebe, only one study found no difference in their abundance between burnt and unburnt patches (Wilsey 1996). The remaining information indicates that tsessebe prefer burnt areas and green flushes, and that they occur in burnt landscapes after a fire (Eby et al. 2014; Green et al. 2015; Gureja and Owen-Smith 2002; Hassan and Rija 2011; Pacifici et al. 2015; Tomor and Owen-Smith 2002), as is typical for grazing mammals.
Common warthog	8	Least Concern	Predominantly positive	Most studies indicated a preference by warthogs for burnt areas, as well as areas subject to short fire return intervals (Archibald et al. 2005; Burkepile et al. 2013; Green et al. 2015; Klop and Van Goethem 2008; Moe et al. 1990; Sensenig et al. 2010). One study found that warthogs selected unburnt landscapes more frequently than burnt landscapes (Hassan and Rija 2011).
Giraffe	5	Vulnerable	Ambivalent	Mixed results in the responses of giraffes to fire have been reported. Giraffes have been seen to occur in equal densities in burnt and unburnt plots (Burkepile et al. 2016; Hassan and Rija 2011), but have also been found to show a preference for burnt areas, compared with unburnt areas (Moe et al. 1990; Zavala and Holdo 2005), and in another study, to select for unburnt plots over burnt areas (Burkepile et al. 2013).
Grant's gazelle	7	Least Concern	Predominantly positive	Most studies indicated that Grant's gazelles displayed a clear preference for burnt areas and post-fire regrowth (Eby et al. 2014; Green et al. 2015; Moe et al. 1990; Sensenig et al. 2010; Wilsey 1996; Zavala and Holdo 2005). One study (Hassan and Rija 2011) found that Grant's gazelles occurred equal densities in both burnt and unburnt areas.
Grey rhebok	4	Near Threatened	Positive	All studies have found grey rhebok to prefer feeding on post-fire regrowth, compared with vegetation that had not been burnt for some time, and to be attracted to areas subject to regular burns, likely in response to the increased nutritional value and ease of accessibility of new regrowth (Beukes 1987; Kraaij and Novellie 2010; Oliver et al. 1978; Rowe-Rowe 1982).
Impala	15	Least Concern	Predominantly positive	A large majority of studies have concluded that impalas prefer burnt areas, where they have been observed to congregate immediately after a fire, as well as in the longer term following a burn (Archibald et al. 2005; Donaldson et al. 2018; Eby et al. 2014; Gandar 1982; Green et al. 2015; Moe et al. 1990; O'Kane et al. 2014; Scholes and Walker 1993; Sensenig et al. 2010; Wilsey 1996; Wronski 2003; Zavala and Holdo 2005). Most likely, the increases in non-N nutrients caused by burning plays a major role in attracting impala to burnt landscapes (Eby et al. 2014). A few studies have noted impalas to be more abundant in unburnt, compared with burnt areas (Burkepile et al. 2013; Burkepile et al. 2016) or to show no clear preference for either (Hassan and Rija 2011).
Oribi	7	Least Concern	Positive	All studies on the responses of oribi to fire have concluded that they prefer burnt areas and small firebreaks, as well as post-fire regenerating regrowth (Klop and van Goethem 2008; Mduma and Sinclair 1994; Moe et al. 1990; Oliver et al. 1978; Rowe-Rowe 1982; Shackleton and Walker 1985).

Table 1: (cont.)

Species	Number of studies	Conservation status	Fire response type	Responses to fire
Plains zebra	16	Near Threatened	Predominantly positive	Studies have almost exclusively found that zebras show a preference for burnt landscapes, compared with unburnt landscapes. They occur in higher densities in recently burnt areas, opting to feed on post-fire regrowth and recently burnt twigs, and spend more time in burnt areas (Archibald et al. 2005; Burkepile et al. 2013; Burkepile et al. 2016; Donaldson et al. 2018; Eby et al. 2014; Frost 1984; Green et al. 2015; Gureja and Owen-Smith 2002; Hassan and Rija 2011; Mariotti et al. 2020a; Moe et al. 1990; Sensenig et al. 2010; Tomor and Owen-Smith 2002; Venter et al. 2014). In two studies, no difference in the abundance of plains zebras was found between burnt and unburnt patches (Mariotti et al. 2020b; Wilsey 1996).
Roan antelope	8	Least Concern	Predominantly positive	Roan antelopes prefer taller grasses characteristic of unburnt patches and can occur at higher densities in areas with less frequent fires (Pacifici et al. 2015). Despite this, roan antelopes have been shown to be attracted to newly burnt areas and to concentrate their grazing in burnt landscapes (Dörgeloh 1998; Gureja and Owen-Smith 2002; Heitkönig and Owen-Smith 1998; Klop and van Goethem 2008; Tomor and Owen-Smith 2002).
Sable antelope	7	Least Concern	Positive	All studies on sable antelopes have noted a preference for burnt patches, post-fire regrowth, and areas subject to high fire frequencies (Asner et al. 2015; Marshal et al. 2016; Pacifici et al. 2015; Parrini and Owen-Smith 2010). Because of this, it has been suggested that increasing the frequency of fire could promote population growth in areas where they have declined (Marshal et al. 2016).
Steenbok	5	Least Concern	Positive	All studies on the response of steenbok to fire have shown this species to be attracted to burnt areas, areas subject to annual burns or areas subject to triennial burns (as opposed to areas subject to longer fire return periods) (Burkepile et al. 2013; Burkepile et al. 2016; Hassan and Rija 2011; Moe et al. 1990; Zavala and Holdo 2005).
Thomson's gazelle	5	Least Concern	Positive	Thomson's gazelles showed a preference for burnt areas and green post-fire regrowth in all studies that have investigated their response to fire. Thomson's gazelles occurred in higher densities in burnt areas than in unburnt areas (Eby et al. 2014; Green et al. 2015; Hassan and Rija 2011; Moe et al. 1990; Wilsey 1996).

The use of experimental designs

We located a total of 36 papers that were published subsequent to Parr and Chown's critique in 2003. The overriding majority of these papers (32 out of 36) presented results based on structured observations rather than on formal experiments. Most of these studies were based on observations of mammals in burnt or unburnt areas along transects (9 papers, see for example Eby et al. 2014; Hassan and Rija 2011), whereas others used observations on plots (5 papers, see for example Burkepile et al. 2013; Wronski 2003) or data derived from remote sensing (3 papers, see for example Archibald et al. 2005). Papers in this category also included cases where observations of mammal responses were used together with environmental variables to construct predictive models of mammal responses to fire (8 papers, see for example Anderson et al. 2007; Farfan et al. 2018). Two papers reported anecdotal accounts without the observations being made in a formal comparative way (i.e. by differentiating between burnt and unburnt areas). Only two papers reported on findings based on experimental designs that included replication and controls. The first of these was Sensenig et al. (2010), who applied burn treatments on blocks of differing size, with unburnt blocks acting as controls. The second was reported by Donaldson et al. (2017), who applied replicated fire treatments on plots of differing sizes, and excluded herbivores from parts of the plots as controls.

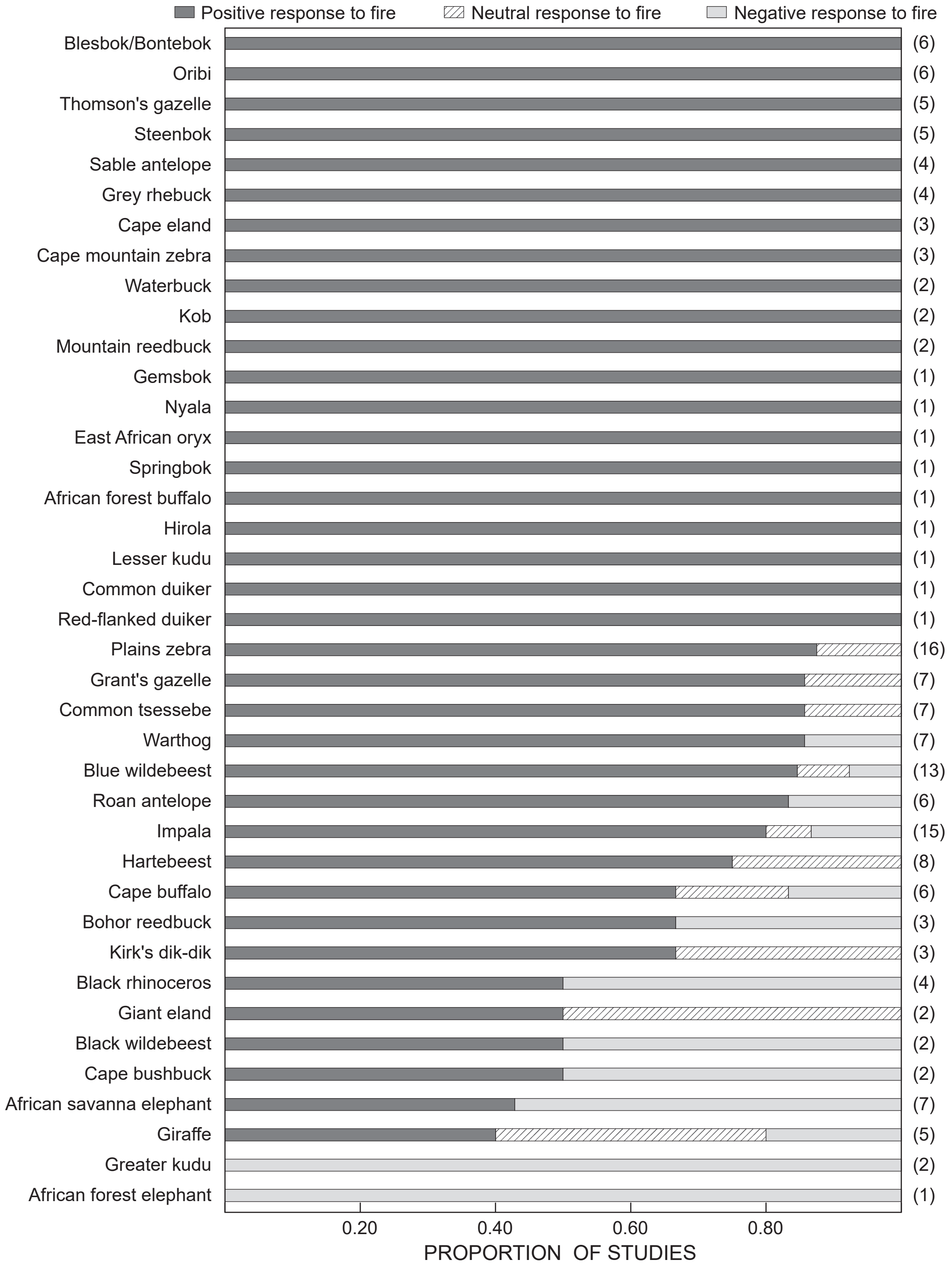

Figure 2: The proportion of studies reporting either positive, negative or neutral responses to fire for individual herbivore species. The number of studies reporting the response of a species to fire is shown in parentheses

Discussion

Determinants of fire response types

We placed large mammal species into three fire response categories based on the findings of studies reviewed here. Species showing a positive response to fire (i.e. species that showed preferences for burnt areas or post-fire regrowth) were most common, with grazers of the family *Bovidae* showing the most positive reaction, followed by mixed-feeders and browsers. Grazers accordingly appear to be more attracted to burnt areas than browsing species, likely as a response to the abundance of new nutrient-rich grass regrowth after fire (Archibald et al. 2005; Klop and van Goethem 2008). Hindgut fermenters, such as zebras, were also slightly less likely to show a positive response to fire than ruminant species, as also reported by Sensenig et al. (2010).

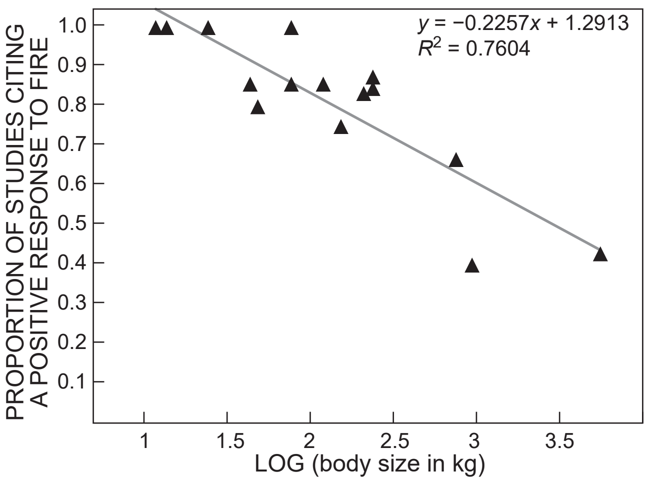

Figure 3: The relationship between herbivore species body size and the proportion of studies that noted a positive response to fire for that species included in five studies or more

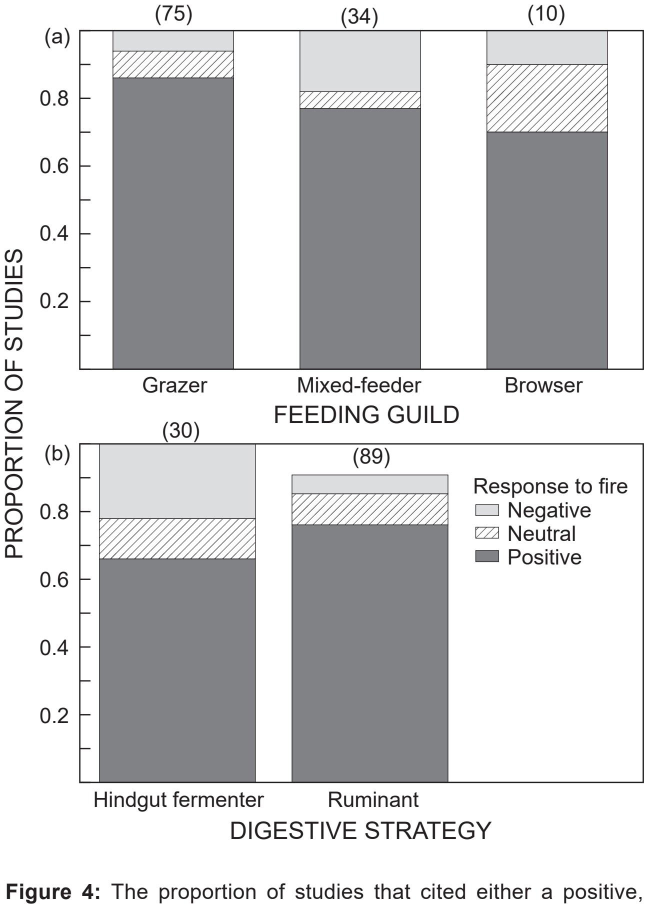

Figure 4: The proportion of studies that cited either a positive, negative or neutral response to fire for (a) browsing, grazing or mixed-feeding herbivores, and (b) hindgut fermenting and ruminant species, included in >5 studies. Numbers in parentheses above bars indicate sample sizes

Literature on the bulk-grazing Cape buffalo showed contradictory results with some suggesting a strong preference for burnt areas immediately after a fire (e.g. Donaldson et al. 2018), but others indicated selection for unburnt patches (e.g. Hassan and Rija 2011). Cape buffalo's response to fire can therefore be considered as ambivalent, similar to that of African savanna elephant, black rhinoceros, and giraffe. These species all noticeably belong to the largest size class considered in this review (>500 kg), and the predation risk for these species is presumably lower (Sinclair et al. 2003; Radloff and du Toit 2004). Eby et al. (2014) reported that a clear pattern for burnt area preference based on mammal body size had not been established, and that the relationship required additional investigation. Our review suggests that an allometric relationship exists, where smaller-bodied mammals are more likely to respond positively to the presence of burnt environments than larger-bodied species. It therefore seems that species below a mass of 500 kg, and especially those below 200 kg, would be more likely to be affected by changes in fire frequency brought about by management. Furthermore, an increase in herbivores <200 kg, as a result of increased fire frequencies, could benefit predators, such as leopards, wild dogs and cheetahs, which prey on smaller mammals, whereas an increase in larger herbivores in less frequently burnt environments could benefit lions. Future studies could consider investigating the relationship between body mass and fire responses at a finer scale. For example, antelope <20 kg will likely be negatively affected by more frequent fires, because of a loss of cover, whereas the positive responses shown by herbivores to burnt areas will likely become less pronounced for species closer to 500 kg, as access to sufficient forage quantity becomes more important.

Although elephants, giraffes, Cape buffaloes and black rhinoceroses could therefore at times be attracted to burnt areas, because of the highly nutritious regenerating vegetation (Eby et al. 2014), they are likely not faced with the same predation pressures as smaller-bodied herbivores. The larger species are therefore likely confronted with a trade-off between opting for high quality vegetation in burnt landscapes and the high quantities of forage in unburnt landscapes; resulting in the contradictory results reported in the literature. Presumably, encouraging a mosaic of burnt and unburnt areas would provide large-bodied herbivores with the opportunity to benefit from some nutrient-rich or otherwise attractive forage in recently-burnt areas (as reported by Emslie and Adcock 1994 and Ferwerda et al. 2006), whereas at the same time allowing them to obtain a sufficient quantity of forage from unburnt areas. This in turn suggests that fire managers of natural ecosystems that support a variety of grazing and browsing mammals of different sizes, should aim to maintain a landscape burnt at moderately frequent intervals, with a mosaic of different post-fire ages, to cater for the full spectrum of requirements.

Few species identified in the literature showed a clear negative response to fire, likely because research has taken place in regularly-burnt ecosystems, where the component species are adapted to fire. For example, it can be assumed that species living in environments less prone to fire, such as forest-dwelling species, would be more likely to respond negatively to the occurrence of fire, as shown by Farfan et al. (2019) for common chimpanzees, western lowland gorillas and African forest elephants, but few studies have been conducted in these environments. Land-use conversion (e.g. agricultural expansion and logging) and global climate change will continue to facilitate the spread of fire into areas where vegetation and climate historically precluded its spread (Cary et al. 2002; Bowman et al. 2011). It therefore seems important to investigate the effects of fire on fire-sensitive mammals, so that they can be better understood. Additionally, little is known about the extent of large mammal mortalities during fires that could be influencing mammal demographics (Woolley et al. 2008). Finally, little research has been done on the responses of carnivores to fire, despite their importance in Africa (Ripple et al. 2014). It is unlikely that fire regimes would have to be tailored to meet the needs of predators, because their conservation is more strongly linked to the maintenance of healthy populations of prey species. Nonetheless, it is interesting to note that predator species may differ in their preferences for burnt or unburnt areas. Green et al. (2015) noted an increase in smaller carnivores, such as jackals, for up to a year after a fire, whereas larger carnivores, such as lions, leopards, cheetahs and spotted hyenas only preferred burnt landscapes up to 120 days after the fire. A similar preference for burnt areas was shown by honey badgers (Frost 1984), which were able to locate food more easily in burnt landscapes, and it is possible that many smaller carnivores (e.g. jackals) would similarly prefer burnt landscapes, because of the increased vulnerability (i.e. decreased cover and food) of prey items (e.g. rodents) (Leahy et al. 2015). Predators respond to fire by, for example, moving into unburnt landscapes, but their ability to react to fire may become diminished in the future, as their available ranges become increasingly smaller, and predators become more confined to fenced protected areas (Packer et al. 2013; Cushman et al. 2016).

Study locations

A strong geographical bias was evident in the reviewed literature, with the majority of studies originating from three protected areas in South Africa (Kruger National Park and Nylsvley Nature Reserve), and Tanzania and Kenya (the Serengeti-Mara ecosystem). The attractiveness of these protected areas as research sites is likely related to factors such as the availability of research facilities and accommodation, field experiments and long-term datasets, proximity to universities, popularity as tourist destinations, as well as the age and size of the protected area, and whether or not there are in-house researchers with whom to collaborate (van Wilgen et al. 2016). Apart from South Africa, no other studies were found in neighbouring southern African countries, and the paucity of research in southern and west African countries is probably as a result of financial constraints, political instability (e.g. civil war rendered many countries, such as Angola, northern Namibia, Zimbabwe and Mozambique, inaccessible to researchers until the mid-1990s) and a general lack of accessibility and infrastructure to support research.

Almost all studies were conducted in savannas and grasslands, because most fires occur there (Archibald et al. 2010), whereas vegetation types less prone to fire, such as xeric sites and forests, were comparatively less prominent in the reviewed literature. The effect of relatively infrequent fires on available forage for herbivores may be more pronounced in arid environments (Trollope et al. 2014), and empirical studies in arid environments are therefore required to effectively improve management. According to Sayre et al. (2013), mopane savanna that was the most common vegetation type studied, is confined to southern Africa and receives low mean annual precipitation (MAP) <600 mm. In contrast, the second (eastern and southern African dry savanna and woodland) and third (eastern African moist woodland and savanna) most studied vegetation types extend into eastern Africa as well, and receive lower (200–450 mm) and higher (>650 mm) MAP, respectively. The dominant woody species occurring in each of these three vegetation types are similar, and include predominantly *Terminalia, Combretum, Vachellia, Senegalia, Colophospermum, Stereospermum, Grewia, Adansonia, Sclerocarya, Albizia, Diospyros, Kigelia, Balanites* and *Boscia* species. Notably, only one study (Frost 1996) has been carried out in the fire-prone, dystrophic miombo and associated broadleaved savanna vegetation type, despite its widespread occurrence spanning 2.7 million km^2 across seven countries (Kutsch et al. 2011). Conversely, despite its limited extent, somewhat longer fire return periods (van Wilgen et al. 1994) and low biomass of large mammals (Boshoff and Kerley 2001), Cape Mediterranean shrublands (fynbos) were included in a relatively large number of studies.

Design of research on large mammal responses to fire

In 2003, Parr and Chown (2003) stated that the understanding of how fire affects fauna in Southern Africa was fragmentary, and highlighted key aspects of faunal fire research that needed to be improved. These included, for example, more detailed descriptions of study methods in research articles (e.g. information on fire duration, season, ignition methods and time of day), the replication of fire experiments, and that future studies be based on a suite of large-scale and experimental approaches. From our review, it is clear that the bulk of research on large mammal responses to fire has remained firmly rooted in observational studies, with very few studies making use of a formal experimental design. In reality, the essential components of experimental design (controls, replication, randomization, and interspersion) are inherently difficult to accommodate in faunal-fire studies. Designing landscape-scale experiments to determine the responses of free-roaming large mammals to fire will remain challenging, because fire regimes cannot be adequately controlled, and replicating studies is notoriously difficult. For example, an ambitious landscape-scale experiment called LASHFIRE (Large Scale Herbivory-Fire Interaction Research Experiment) was proposed to be implemented in the Kruger National Park, South Africa, in April 2000 (Biggs and Potgieter 1999), but the project never came into fruition, because it was ultimately proven to be too difficult. Most experimental work in Africa has been conducted at the scale of small plots (1–10 ha). Almost all of this work was aimed at establishing the effects of fire on vegetation, and faunal responses, especially large mammals, were not considered in the original experimental design. For example, van Wilgen et al. (2007) were only able to report the results of a long-term plot-based fire experiment in terms of small mammals, birds and invertebrates, and not in terms of large mammal responses. The only study of which we are aware that explicitly considered herbivory in combination with fire was reported by Trollope (1980) and Hester et al. (2006). In this study, fire treatments on small (1 ha) plots were combined with browsing by goats in savanna vegetation. However, plot-based studies are usually too small to draw landscape-scale conclusions. Most studies considered in this review were conducted inside protected areas, and were designed to evaluate the responses of large mammals to fire through post-fire sampling. How we manage fires will remain important for sustainable mammal conservation initiatives, particularly in small, fenced reserves that may accentuate the effect of fire on large mammals by preventing movement in reaction to fire (Packer et al. 2013). Additionally, where appropriate, pre-fire sampling should be considered in future studies as an extension to simple post-fire sampling, to be able to better describe how and why mammal distributions change in the landscape when a fire occurs.

The rise of remote sensing in the 21st century provides a possible solution to overcome some of the limitations associated with landscape-scale fire experiments. Additionally, remote sensing offers a way to attain information on past fires over extended time periods in areas where no historical records are available (Nieman et al. 2021b), to be used in conjunction with ground-based studies. This may therefore help to identify landscapes most suited for the allocation of specific on-the-ground research projects by describing and comparing fire regimes in different areas; for example, landscapes that have been subject to variable fire treatments (e.g. a mixture of short, intermediate and extended fire return periods). Given the advances in remote sensing technologies for fire and related environmental research in recent years (Gitas et al. 2012), we expect that this form of data collection will become more important in the future, and could assist with the interpretation of mammal responses to fire.

Fire management

The importance of maintaining all facets of biodiversity became increasingly recognised and accepted in fire management in the 21st century, but the expected progression to community-level studies, as opposed to single-species studies, was not evident in the reviewed literature. In fact, there was no evidence that studies diversified thematically over time. Nearly two thirds of the studies identified in this review examined rare species of conservation concern (e.g. black rhinoceros and elephant) or locally declining species (e.g. sable and roan antelope), and these studies were typically designed with a narrow, single-species focus, often clearly stating the decline of a particular species as the main motivation for the research (e.g. Marshal et al. 2016). Consequently, fire management recommendations were focussed only on the particular species in question, and did not consider the possible different requirements of co-occurring species.

More than half of the studies reviewed did not make any explicit recommendations regarding fire management or policy development. This poses a potential barrier to the effective transfer of new understanding to the managers responsible for large mammal conservation. However, we acknowledge that many such recommendations may be available in grey literature, which was not included in this review, because of the difficulty in locating these documents (Parr and Chown 2003). From the reviewed literature, the most common recommendation was to increase fire frequencies to promote the formation of short-grass areas (Beukes 1987; Donaldson et al. 2018), provide fresh regrowth for grazers and remove unpalatable material (Lemon 1968; Rowe-Rowe 1982; Grant and van der Walt 2000; Magome et al. 2008; Kimitei et al. 2015) or to prevent late dry season fires (Lemon 1968), and maintain open areas for African forest buffalo (van der Hoek et al. 2013). Given the stated objectives of the reviewed literature, the recommendation to increase fire frequency is understandable, because it would benefit the large mammal species concerned. However, an increase in fire frequency may significantly reduce woody cover in the long-term (Anderson et al. 2020), potentially transforming landscapes to a grass-dominated state (Bond et al. 2005; Hoffmann et al. 2012). Therefore, although this recommendation may promote the population growth of some large mammal species in the short-term, it does not consider the long-term conservation of other facets of biodiversity. It is also simplistic, because fire frequency is influenced by a multitude of interacting factors, notably variable rainfall and grazing pressure, and is often not easily controlled by management (van Wilgen et al. 2004). Similarly, some studies advocated for a decrease or complete exclusion of fire, which could have undesired consequences in the form of woody encroachment, potentially leading to a reduction in species richness and diversity (Furley et al. 2008). The reasons for suggesting a reduction in fire frequency was to allow for previously over-utilised vegetation to recover (du Plessis 1972; Kraaij 2010), to increase access to preferred forage for black rhino (Anderson et al. 2020), to prevent the reduction of Na and P in migrating zones of zebra and blue wildebeest caused by too frequent fires (Anderson et al. 2007), and to retain food resources throughout the dry season for elephant (Bell and Jachmann 1984). The second most common recommendation found in the reviewed literature was to increase the spatial or temporal heterogeneity of fires, which would putatively cater for all facets of biodiversity. The goal of achieving spatial heterogeneity is more likely to be achievable, as has been demonstrated in a number of areas (Brockett et al 2001; van Wilgen et al. 2004). The specific reasons for recommending the heterogeneous application of fire were to optimise herbivore population growth (Yoganand and Owen-Smith 2014; Pacifici et al. 2015) to maintain refuge areas that would allow for re-colonization (de Ronde et al. 2004), to supply the requirements of all animals in terms of forage quantity and quality (Hassan and Rija 2011), to maintain constant availability of nutritious fodder (Moe et al. 1990), and to reduce competition for resources in small fenced reserves (Mariotti et al. 2020b; Sensenig et al. 2010). We therefore encourage managers of protected areas to promote spatial heterogeneity through the use of fire, so that the requirements of co-occurring species with differing requirements for vegetation of different post-fire ages can be met, especially in smaller protected areas. Patch mosaic burning (Brockett et al. 2001) provides a practical way to achieve this, provided that the outcomes in terms of fire patterns, and vegetation and faunal responses, are monitored to establish whether or not the desired results are being achieved.

Acknowledgements — This study was funded by the Earthwatch Institute, under the Majete Wildlife Research Programme, Malawi (grant to AJL), the DSI-NRF Centre for Invasion Biology, Stellenbosch University, and the National Research Foundation of South Africa (grant 109467 to BWvW). WAN acknowledges logistical support received from African Parks Ltd.

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Manuscript received: 7 November 2020, revised: 12 April 2021, accepted: 14 April 2021
Associate Editor: C Wigley-Coetsee