Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment

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Abstract   Every year large proportions of northern Australia's tropical savanna landscapes are burnt, resulting in high fire frequencies and short intervals between fires. The dominant fire management paradigm in these regions is the use of low-intensity prescribed fire early in the dry season, to reduce the incidence of higher-intensity, more extensive wildfire later in the year. This use of frequent prescribed fire to mitigate against high-intensity wildfire has parallels with fire management in temperate forests of southern Australia. However, unlike in southern Australia, the ecological implications of high fire frequency have received little attention in the north. CSIRO and collaborators recently completed a landscape-scale fire experiment at Kapalga in Kakadu National Park, Northern Territory, Australia, and here we provide a synthesis of the effects of experimental fire regimes on biodiversity, with particular consideration of fire frequency and, more specifically, time-since-fire. Two recurring themes emerged from Kapalga. First, much of the savanna biota is remarkably resilient to fire, even of high intensity. Over the 5-year experimental period, the abundance of most invertebrate groups remained unaffected by fire treatment, as did the abundance of most vertebrate species, and we were unable to detect any effect of fire on floristic composition of the grass-layer. Riparian vegetation and associated stream biota, as well as small mammals, were notable exceptions to this general resilience. Second, the occurrence of fire, independent of its intensity, was often the major factor influencing fire-sensitive species. This was especially the case for extinction-prone small mammals, which have suffered serious population declines across northern Australia in recent decades. Results from Kapalga indicate that key components of the savanna biota of northern Australia favour habitat that has remained unburnt for at least several years. This raises a serious conservation concern, given that very little relatively long unburnt habitat currently occurs in conservation reserves, with most sites being burnt at least once every 2 years. We propose a conservation objective of increasing the area that remains relatively long unburnt. This could be achieved either by reducing the proportion of the landscape burnt each year, or by setting prescribed fires more strategically. The provision of appropriately long unburnt habitat is a conservation challenge for Australia's tropical savanna landscapes, just as it is for its temperate forests.

Key words: biodiversity, conservation, fire frequency, fire management, tropical savannas.

INTRODUCTION

Australia is arguably the most flammable of all continents, and wildfire is indelibly etched into the Australian cultural and physical landscapes (Pyne

1991; Bradstock *et al.* 2002). Most Australians live in coastal southern Australia, and their fire imagery is driven by the spectacular conflagrations that periodically rage through the eucalypt woodlands and open forests of those regions. The management of forest fires in southern Australia has generated intense public controversy and scientific debate, generated by trade-offs between the protection of people's lives, property and timber assets on one hand, and the maintenance of biodiversity values on the other (Gallus 1994; Calver *et al.* 1996; Burrows & Abbott 2003). In

particular, there is considerable concern over impacts on biodiversity of the frequent fuel-reduction burning that is extensively used to reduce fire 'hazard' in these forests (Gill 1977; Williams *et al.* 1994; Gill & McCarthy 1998). <mark>The concern is especially acute for the wide variety of faunal groups that are sensitive to habitat simplification arising from frequent burning</mark> (Catling 1991; Woinarski & Recher 1997; York 2000).

The savanna woodlands and open forests of tropical northern Australia provide a striking contrast with temperate southern Australia in terms of fire behaviour and ecology. Fire is a routine part of the annual wet–dry cycle of tropical Australia, with up to half or more of some regions being burnt each year (Gill *et al.* 1990; Russell-Smith *et al.* 1997; Edwards *et al.* 2001). These fires are of low to moderate intensity, typically being restricted to the grass-layer, and rarely, if ever, entering the canopy (Williams *et al.* 1998). Such relatively low fire intensities in sparsely populated regions mean that protection of people and property is not a dominant issue. Nevertheless, fire management in northern Australia is highly controversial, generating extensive debate in both public (Andersen & McKaige 1998) and scientific arenas (Bowman *et al.* 1988; Lonsdale & Braithwaite 1992; Andersen 1996, 1999).

Much of the savanna woodlands and open forests of the higher rainfall zone of north-western Australia is managed for biodiversity conservation, explicitly so in National Parks and other reserves, and in a *de facto* way on Aboriginal lands. These savannas are extensively burnt by conservation managers early (May/June) in each dry season, in order to promote patchiness and reduce the incidence of higher-intensity wildfires that inevitably occur late (October/November) in the dry season (Press 1987; Russell-Smith 1995). Such late-season fires have only a fraction of the intensity of temperate forest fires (Williams *et al.* 1998), but are nevertheless widely perceived as being ecologically 'destructive', and their mitigation is a primary driver of contemporary fire management. <mark>This extensive use of frequent, prescribed burning to prevent higher-intensity wildfire therefore has many parallels with fire management in southern Australia. However, in contrast to southern Australia, the ecological effects of fire frequency, and the contribution of prescribed fires to them, has received little critical attention in the tropical north (Andersen 1996). This contrasts with the situation in neotropical savannas, where research has focused on fire frequency rather than intensity (Hoffmann & Moreira 2003).</mark>

A landscape-scale fire experiment was recently completed by CSIRO and collaborators at Kapalga research station in Kakadu National Park, Northern Territory, Australia, designed to inform conservation management by providing an improved understanding of the ecological effects of different fire regimes (Andersen *et al.* 1998). A comprehensive account of the results of the experiment is given in Andersen *et al.* (2003a). Here we provide a synthesis of the effects of experimental fire regimes on biodiversity at Kapalga, with particular consideration of fire frequency and, more specifically, time-since-fire. We then explore the implications of these results for conservation management. This follows a recent synthesis of results from a longer-term but hectare-scale fire experiment at Munmarlary, elsewhere in Kakadu (Russell-Smith *et al.* 2003).

THE KAPALAGA EXPERIMENT

The Kapalga experiment addressed conservation management of the regionally dominant savanna woodlands and open forests of northern Australia. These habitats are considered to be generally resilient to fire in the sense that vegetation rapidly recovers (Andersen 1996). A variety of other important habitats, such as sandstone plateaux, floodplains and monsoon rainforest, also occur in the savanna landscape, and often support relatively 'fire-sensitive' vegetation (Russell-Smith & Bowman 1992; Bowman & Panton 1993; Russell-Smith *et al.* 1998). These other habitats are obviously important in the context of regional fire management, but are not considered in this paper. It is also important to note that Kapalga's savannas are specifically representative of monsoonal tallgrass systems dominated by annual *Sorghum* species (Mott *et al.* 1985), which are especially fire-prone. These are the dominant systems throughout the western half of the Top End (including the major regional National Parks Kakadu, Litchfield and Nitmiluk), as well as the northern Kimberley region of Western Australia. Fire frequency tends to be lower in regions dominated by perennial grasses, such as eastern Arnhem Land (Bowman *et al.* 2004).

The Kapalga study is highly noteworthy for fire experiments (Parr & Chown 2003) in that it was conducted at the landscape-scale with replication (Andersen *et al.* 1998). Experimental units comprised 15–20 km^2 catchments, and each experimental fire regime was applied independently to at least three of these. The experiment involved a wide range of studies, covering fire behaviour, atmospheric chemistry, nutrient cycling, hydrology and stream dynamics, vegetation, and a wide range of fauna, including invertebrates. Experimental fires were lit for 5 years, from 1990 to 1994, with baseline data collected for up to 2 years before, and 1 year after, experimental burning.

The effects of three fire regimes tested at Kapalga are examined here:

- **Early** – annual fires lit early (May/June) in each dry season, as is commonly practised by conservation managers. The intensity of these fires averaged 2100 kWm^{-1}.

- **Late** – annual fires lit late (September) in the dry season, as commonly occurs as uncontrolled wildfires. The intensity of these fires averaged 7700 kWm^{-1}.
- **Unburnt** – no fire.

A fourth regime, 'Progressive', with annual fires lit progressively through the dry season as the country dried out, was also tested at Kapalga in an attempt to simulate traditional Aboriginal burning practices (Andersen *et al.* 1998). However, this treatment failed to reproduce the fine-scale spatial patterns characteristic of traditional burning, and instead resulted in very extensive fires similar to those of the other treatments. The 'Progressive' treatment produced few unique results (Andersen *et al.* 2003a), and so is not considered further here.

BIODIVERSITY RESPONSES TO FIRE AT KAPALGA

Tree dynamics

Mortality of dominant trees increased linearly with increasing fire intensity (Williams *et al.* 1999), with total basal area remaining relatively unchanged under Early fires, but declining by about 20% over the experiment under Late fires (Fig. 1). Mortality showed a bimodal pattern with respect to tree size, with small saplings and old, large trees being most sensitive. The two dominant eucalypts, *Eucalyptus miniata* and *Eucalyptus tetrodonta*, were less sensitive to relatively high-intensity fires than were the subdominant and understorey trees *Erythrophleum chlorostachys* and *Terminalia ferdinandiana*, respectively.

The Early fires scorched the canopies of the eucalypts and *Er. chlorostachys*, but all sprouted new leaves
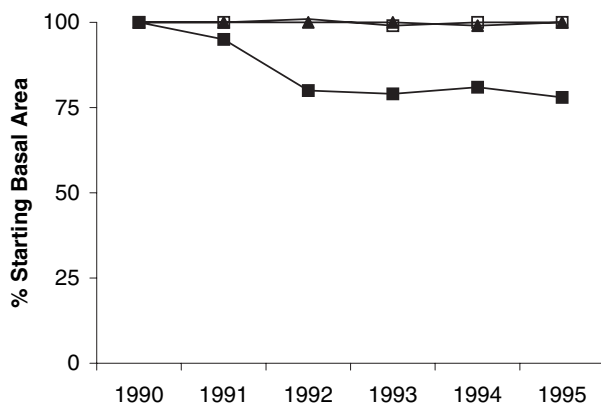
within a month, which was two or three months earlier than for seasonal leaf flushing under Unburnt conditions. Leaf fall was more extensive in these species following the Late fires, but resprouting was again rapid, and at about the same time as leaf flush in Unburnt trees. Leaf phenology in *T. ferdinandiana*, which is deciduous over the dry season, was unaffected by fire.

There were few differences in the density of fire-suppressed 'woody sprouts' (<2 m tall) of the dominant tree species between fire treatments, although sprout survival was lowest in Unburnt catchments. There was no evidence of invasion by rainforest taxa in Unburnt catchments over the course of the experiment. This is consistent with other studies showing that far longer periods of fire exclusion are required for rainforest invasion in Australian savannas (Bowman *et al.* 1988; Fensham 1990; Fensham *et al.* 2003; Woinarski *et al.* 2004), even near rainforest boundaries (Bowman & Fensham 1991).

Detailed studies were conducted on flowering and seed dynamics in *E. miniata* and the common savanna shrub *Acacia oncinocarpa*. For *E. miniata*, Late fires substantially reduced both the proportion of trees that initiated floral buds, and the density of floral buds in the canopy. Although Early fires did not significantly reduce tree fecundity, they substantially reduced the development of ovules from bud initiation through to seed-set. Successful seed production was ultimately at least five times higher in the Unburnt than in the Early and Late regimes (Setterfield 1997a). A similar pattern was found for *A. oncinocarpa* (Setterfield 1997b). Rates of seedling emergence were also reduced under both burning regimes, probably due to higher canopy cover and lower grass cover in Unburnt catchments, and the higher abundance of seed harvester ants in the two burnt regimes (Setterfield 2002). Frequent fire therefore reduced the chances of seedling establishment in these tree and shrub species (Table 1), as is the case in savannas elsewhere in the world (Hoffmann 1998).

The above results show that fire regimes have complex effects on savanna tree dynamics, influencing mortality and recruitment in different ways (cf. Hoffmann 1999). The computer simulation model *Flames* (Cook & Liedloff 2001) has been developed to explore the longer-term consequences of variation in fire frequency, fire timing and patterns of fire spread on tree populations. Preliminary simulations indicate that the initial marked declines in tree basal area observed under Late fires will not continue, but a stable population of mid-sized fire tolerant trees may persist for at least several decades even under annual late-season burning.

Seasonal streams are an important feature of Kapalga's savanna landscapes, and the riparian vegetation features many species that are characteristic of

Fig. 1. Proportional change in live basal area of trees between 1990 and 1995 under (□) Unburnt, (▲) Early and (■) Late fire regimes (modified from Williams *et al.* 1999).
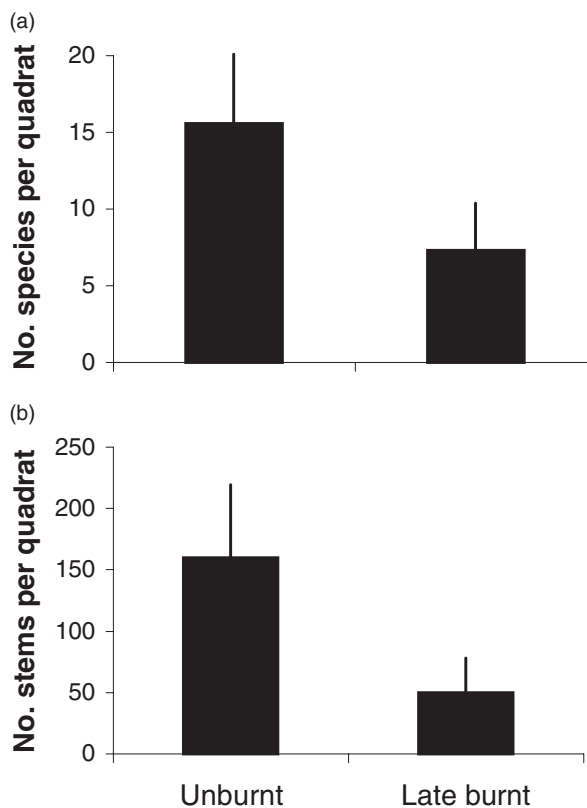
Table 1.   Annual seed budgets and seedling survival rates for *Eucalyptus miniata*, and *Acacia oncinocarpa* (the latter was not common enough in Late compartments for analysis). Reproduced with permission from Setterfield (2002)

	Unburnt	Early	Late
E. miniata			
Seedfall (seeds m^{-2})	18.1	1.5	1.8
Seedling establishment (% of available seed)	8	6.5	3.5
No. of established seedlings (seedlings m^{-2})	1.4	0.1	0.06
Seedling survival after 1 years (seedlings m^{-2})	0.2	0	0
A. oncinocarpa			
Seedfall (seeds m^{-2})	60	5	–
Seedling establishment (% of available seed)	6.5	2	–
No. of established seedlings (seedlings m^{-2})	3.9	0.1	–
Seedling survival after 1 years (seedlings m^{-2})	1.2	0.03	–

Fig. 2.   Mean (+ SE) (a) tree richness and (b) density in riparian zones of Unburnt and Late burnt catchments (data from Douglas *et al.* 2003).

rainforest rather than savanna habitats (Douglas *et al.* 2003). Studies of riparian vegetation at Kapalga commenced after experimental treatments were initiated, so the robustness of results is limited by a lack of baseline data. However, it seems clear that, in contrast to savanna trees, those of riparian zones were highly sensitive to fire. Unburnt riparian zones had twice as many tree species and about three times the density of woody plants as those in Late catchments (Fig. 2). Burning Early in the dry season resulted in intermediate riparian tree density and canopy cover.

Grass-layer vegetation

Grass-layer vegetation was remarkably resilient to experimental treatments at Kapalga, with fires having no detectable effect on either diversity or floristic composition (R. J. Williams *et al.* 2003). Floristic composition was related to variation in annual rainfall and pre-existing sorghum cover, but not to fire intensity. Some key species, however, were significantly affected by fire treatment. For example, the cover of *Alloteropsis semialata*, a key food resource for granivorous birds (Woinarski 1993), increased in Unburnt relative to Early and Late compartments. Interestingly, fires had a very muted effect on the cover of annual sorghum, which is widely believed to be promoted by frequent fire (Russell-Smith *et al.* 2003; Bowman *et al.* 2004). There were some local reductions in sorghum cover in the absence of fire (Andersen & Müller 2000), but there was no evidence of widespread increases in density following frequent fire, even in areas where it was of low abundance (R. J. Williams *et al.* 2003).

The general resilience of grass-layer plants in relation to fire at Kapalga seems to be typical of monsoonal tallgrass systems (Bowman *et al.* 1988), although not necessarily of other savanna habitats in northern Australia (P. R. Williams *et al.* 2003). It contrasts sharply with the marked indirect effects of longer-term (>10 years) fire exclusion, where the grass-layer is suppressed by competition from an enhanced mid-storey (Fensham 1990; Russell-Smith *et al.* 2003; Woinarski *et al.* 2004).

Stream biota

As for riparian vegetation, studies of stream biota at Kapalga commenced after experimental treatments were initiated, so baseline conditions are unknown. However, it seems clear that experimental fire treatments had a very marked effect on aquatic biota of the pools that form at the end of the wet season in Kapalga's streams. Compared with Unburnt catchments, streams in Late catchments contained six times as many species of aquatic macrophytes, and over 10 times the biomass (Douglas *et al.* 2003). Catchments

burnt early in the dry season had similarly low richness of aquatic plants to that found in Unburnt catchments. These results can be linked to fire-induced changes to the riparian zone, with denser vegetation in Unburnt catchments reducing inputs of both solar radiation and sediment. The increased productivity of aquatic macrophytes in Late catchments was reflected by aquatic macroinvertebrate richness, which was up to double that occurring in Unburnt catchments (Fig. 3). Fish were not sampled during the experiment, but presumably were affected by fire-induced changes in water conditions and the productivity of aquatic macrophytes and macroinvertebrates.
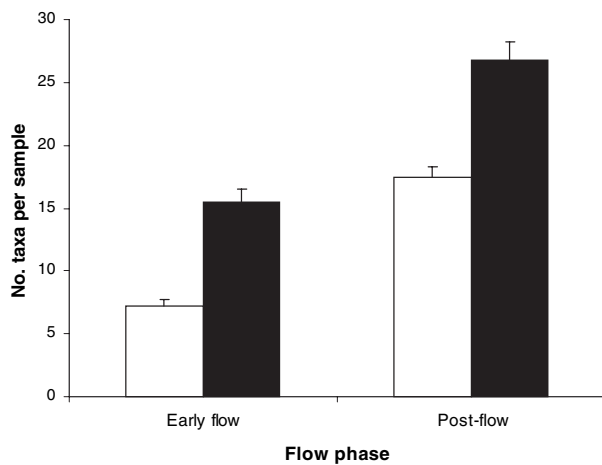
Fig. 3. Mean (+ SE) taxon richness of aquatic macroinvertebrates in streams of (□) Unburnt and (■) Late burnt catchments at Kapalga (data from Douglas *et al.* 2003).

Terrestrial arthropods

Pitfall traps and sweep-nets were used to sample ground-active and grass-layer arthropods, respectively. Of the 11 ordinal-level taxa considered from pitfall catches, only five showed any change in total abundance in relation to fire (Table 2). Ants dominated pitfall catches (representing 80% of all individuals caught) and were the most responsive group, declining markedly in abundance in the absence of fire while increasing in burnt catchments (see also Andersen 1991). In contrast, the abundances of Homoptera, silverfish, spiders and beetles all declined under Late fires. As for the ground-active fauna, fewer than half of the ordinal-level taxa from sweep catches showed significant change in abundance in relation to fire. The major trend within the responsive groups was for abundance to decline in the absence of fire, whether Early or Late (Table 2).

Changes in total abundance do not necessarily indicate the extent of impact on species diversity and composition. Species-level responses have been assessed for grasshoppers and beetles. As in overall abundance, fire treatment had no significant effect on the abundance of the most common grasshopper species, and no marked effect on the number of species (Andersen *et al.* 2003c). However, fires did have a significant effect on overall species composition of grasshoppers, with Unburnt assemblages differing from those experiencing either Early or Late fires. Interestingly, the seasonal timing (and therefore intensity) of fire made no significant difference. These results were mirrored by grass-layer beetles, where assemblages from Unburnt catchments also diverged from those of burnt catchments, whether Early or Late (Orgeas & Andersen 2001). In contrast, ground-active beetles remained unaffected by Early fires, but Late

Table 2. 'Ordinal'-level invertebrate taxa whose abundances were significantly influenced by fire treatment at Kapalga (data from Andersen & Müller 2000). Taxa remaining unaffected by fire treatment were springtails, flies, mites, crickets, wasps and heteroptera on the ground, and spiders, flies, heteroptera, ants, grasshoppers and wasps in the grass-layer

Taxon	*P*-value from ANOVA	Response
Ground		
Ants	<0.001	Decrease in absence of fire, and increase under both Early and Late regimes
Spiders	0.024	Decrease under Late regime
Homoptera	0.004	Decrease under Late regime
Silverfish	0.015	Decrease under Late regime
Beetles	0.046	Decrease under Late regime
Grass-layer		
Crickets	0.001	Increase under both Early and Late regimes
Beetles	0.043	Increase under both Early and Late regimes
Homoptera	0.019	Increase under both Early and Late regimes
Caterpillars	0.030	Decrease under Late regime

fires prevented the build-up in species that otherwise occurs following the first rains of the wet season (Blanche *et al.* 2001).

These results suggest two key conclusions regarding savanna invertebrates and fire. First, most invertebrate groups are highly resilient to fire, particularly in the context of the high levels of spatial and temporal variation shown by invertebrate populations in relation to other factors such as rainfall (Andersen & Müller 2000). Second, for those groups affected, there was a trend for ground-active groups to be sensitive to Late fires, whereas grass-layer groups were influenced more by fire occurrence rather than its intensity.

Terrestrial vertebrates

General assessments of vertebrate responses to fire were made using pit-traps, and by calls, sightings, tracks, faeces and other signs during diurnal and nocturnal sampling, with almost 20 000 individuals comprising 139 species being recorded (Corbett *et al.* 2003). Species were categorized into one of 13 functional groups based on systematics, trophic position and habitat use in order to identify broad vertebrate responses (Table 3). Fire had a significant effect on vertebrate abundance in only three of these groups (Table 3). The abundance of arboreal frogs increased in burnt (both Early and Late) compared with Unburnt catchments, but this response was driven by a single species, *Litoria bicolor* (Corbett *et al.* 2003). The abundance of terrestrial lizards decreased under Late fires compared with Early and Unburnt treatments, but again this was driven by a single species,

the skink *Carlia amax*. The abundance of litter lizards and snakes also decreased under Late fires. This was despite no statistically significant responses of individual species, and appears to be the only case of a genuine functional group (rather than dominant individual species) response to fire treatment. Clearly, the general attributes used to establish vertebrate functional groups were not appropriate for identifying fire-response functional groups (and were not intended to be so).

Fire treatment had a greater effect on individual species than was indicated by functional group responses, but the overwhelming result was that the abundances of most species recorded commonly enough for statistical analysis remained unaffected by fire treatment. Fire had a significant effect on just one out of 11 frog species, five out of 16 lizards, and five out of 25 birds (Corbett *et al.* 2003). The fire-affected species showed a wide range of responses, including declines under Late fires (e.g. spotted tree monitor *Varanus timorensis*, bauxite rainbow skink *Carlia amax*, lemon-bellied flycatcher *Microeca flavigaster*, Australian owlet nightjar *Aegotheles cristatus*), increases under Late fires (brown goshawk *Accipiter fasciatus*, red-backed kingfisher *Todiramphus pyrrhopygia*), and increases in Unburnt relative to any burning (swamplands lashtail *Lophognathus temporalis*, robust ctenotus *Ctenotus robustus*, barking owl *Ninox connivens*).

One of the Top End's iconic vertebrate species, the frilled lizard *Chlamydosaurus kingii*, was the subject of a mark-recapture and radio-telemetry study (Griffiths & Christian 1996). The lizards effectively sheltered from Early fires by climbing to the tops of trees or by taking refuge in hollowed termite mounds. All 17 lizards monitored during Early fires survived, but seven (30%) of 24 lizards perished during Late fires. Despite such mortality, lizard densities were ultimately highest in Late compartments (0.78 ha^{-1}, compared with 0.65 ha^{-1} in Early and 0.13 ha^{-1} in Unburnt), due to increased prey accessibility and migration from unburnt areas (Griffiths & Christian 1996).

Small (<2 kg) mammals were inadequately covered by general vertebrate assessments, and so were investigated in a dedicated study. A total of 96 160 trap-nights over 6 years resulted in over 5000 captures of 12 small mammal species. Total abundance and species richness, and the abundances of six of the seven most common species, were all significantly affected by fire treatment, making small mammals by far the most sensitive faunal group assessed at Kapalga (Corbett *et al.* 2003). Of the seven species that were sufficiently abundant for statistical analysis, three (northern quoll, *Dasyurus hallucatus*; fawn antechinus, *Antechinus bellus*; and northern brown bandicoot, *Isoodon macrourus*) were clearly most abundant in Unburnt catchments, two (northern brushtail possum, *Trichosurus vulpecula*; and grassland melomys,

Table 3. Summary responses of vertebrate functional groups to experimental fire regimes at Kapalga. *P*-values indicate effects of experimental fires on abundance, with significant values in bold. Data from Corbett *et al.* (2003)

Functional group	No. species	No. records	*P*
Forest passerines	9	5172	0.391
Diurnal raptors (15)	15	426	0.213
Other diurnal predatory birds (7)	7	2419	0.357
Nocturnal predatory birds (9)	9	725	0.363
Ground birds (4)	4	425	0.093
Arboreal frogs (4)	4	735	**0.016**
Terrestrial frogs (15)	15	2547	0.143
Arboreal lizards	12	1253	0.379
Terrestrial lizards	22	4669	**<0.001**
Litter lizards and snakes	8	265	**0.029**
Other snakes	16	45	0.152
Arboreal mammals	6	579	0.153
Terrestrial mammals	12	645	0.573

Melomys burtoni) were more variable but tended to be most abundant in Unburnt catchments, and one (pale field rat, *Rattus tunneyi*) declined under all treatments but especially Late. The dusky rat, *Rattus colletti*, was the only common species remaining unaffected by experimental fires. Overall, Early compartments supported higher populations of small mammals than occurred in Late compartments, but the overwhelming result was the importance of unburnt habitat for maintaining large populations (Fig. 4).

Survival and reproduction are key variables influencing population growth, and these were calculated for the four most common small mammal species. Annual survival was highest in Unburnt habitat for three of these species (northern brown bandicoot, northern quoll and grassland melomys), and reproduction rates were highest in Unburnt habitat for two (northern brown bandicoot and grassland melomys) (Pardon *et al*. 2003; A. D. Griffiths & R. W. Braithwaite unpubl. data, 1996).

The association of high small mammal densities with unburnt habitat at Kapalga is consistent with some previous studies in the Top End. For example, the black-footed tree rat, *Mesembriomys gouldii*, strongly favours habitat with a well developed mid-story, which is characteristic of relatively low fire frequency (Friend & Taylor 1985; Friend 1987). Similarly, Kerle (1998) concluded that high fire frequency is detrimental to northern brushtail possums. Both these species are arboreal. Ground-active small mammals, on the other hand, have generally been thought to benefit by the small-scale habitat patchiness created by low-intensity fire (Braithwaite 1995, 1996). This might in fact be true for extremely low-intensity fires occurring very early (April/early May) in the dry season, which were not examined at Kapalga, but is evidently not the case for the bulk of early season management fires.
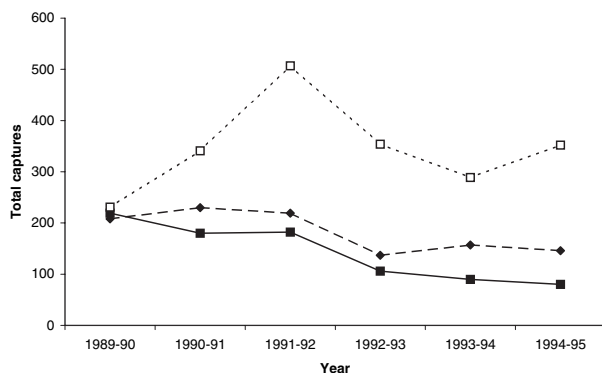
The effects of fire on small mammal populations at Kapalga are superimposed on very marked spatial and interannual variation that occurs independently of fire (Andersen & Braithwaite 1996; Braithwaite & Griffiths 1996; Braithwaite & Müller 1997). Small mammal populations have declined markedly at Kapalga and elsewhere in the Kakadu region since the mid-1980s for reasons that are not clear (Woinarski *et al*. 2001). The declines began before experimental treatments were imposed, and under the same fire regime as that occurring during the development of very high population densities through the 1970s.

Synthesis

The Kapalga experiment has yielded a wide range of information on ecological responses to different fire regimes in savanna woodlands and open forests. However, two recurring themes emerge. First, overall effects were unexpectedly low given that experimental treatments encompassed the most extreme fire regimes possible, from annual fires of maximum intensity on one hand to no fire at all on the other. For most species examined, populations remained unaffected by fires over the 5-year experimental period. Annual high-intensity fire had a clear impact on tree mortality, but the overall effect on biodiversity was surprisingly low, especially compared with the high variation that can occur from year to year independently of fire. The abundance of most invertebrate groups remained unaffected by fires, as did the abundance and species richness of most vertebrate functional groups, and we were unable to detect any effect of fire on floristic composition of the grass-layer. It is very likely that we would have found stronger effects if experimental fires were applied over a longer period, but our results clearly demonstrate that much of the savanna biota is highly resilient to fire, even of relatively high intensity. Riparian vegetation, stream biota and small mammals were notable exceptions to this general resilience.

The second theme to emerge from Kapalga is that when fires did have a significant effect, the contrast was often between burning on one hand, whether Early or Late, and unburnt habitat on the other. This was especially true for faunal biodiversity, and particularly for grass-layer arthropods and small mammals. The reductions in small mammal populations under all burning treatments is particularly noteworthy, given the serious concerns over their conservation status. However, it must be noted that the effects of extremely low-intensity fires occurring very early (April/early May) in the dry season were not examined at Kapalga, and small mammals might in fact benefit by the small-scale habitat patchiness created by such fires (Braithwaite 1995, 1996).

Fig. 4. Total captures of small mammals under different burning treatments at Kapalga: (◆) Early, (■) Late, (□) Unburnt. The 1989–1990 data were collected prior to imposition of burning treatments. Modified from Corbett *et al*. (2003)

MANAGEMENT IMPLICATIONS

The overall resilience of much of the savanna biota to even high-intensity fire is good news for conservation managers, as it buffers against widespread ecological change following isolated management 'mistakes'. However, fire, and more particularly variation in fire regimes (Gill 1977), remains an important challenge for conservation management in northern Australia.

Species vary in their responses to fires, and so fire management inevitably involves trade-offs for biodiversity. This is clearly illustrated by the effects of fire on streams at Kapalga, with Late fires having a severe impact on riparian vegetation on one hand, but strongly promoting aquatic biodiversity on the other. However, such trade-offs can be effectively managed by assessing the outcomes of fire management at a regional rather than local scale (Keith *et al.* 2002). Within a region it is possible to have both healthy riparian vegetation and a diverse aquatic biota, but just not in the same place. A regional approach enables managers to avoid compromise solutions that might maximize biodiversity locally, but compromise broader conservation goals.

A regional perspective therefore allows conservation managers to shift their focus from managing for a biodiversity 'common denominator' to ensuring that those taxa most at risk under prevailing regimes are effectively catered for (Samson & Knopf 1999). In northern Australia this approach has been adopted at the broader regional scale by focusing attention on the more fire-sensitive vegetation types such as rainforest and sandstone heathland, which are threatened by prevailing fire regimes (Russell-Smith & Bowman 1992; Russell-Smith *et al.* 1998). Results from Kapalga indicate that a similar approach needs to be taken for the more fire-sensitive taxa occurring within generally fire-resilient savanna habitats. In particular, several key elements of the savanna fauna strongly favour less frequently burnt habitat, or, more particularly, longer times-since-fire (Gill & McCarthy 1998; Woinarski *et al.* 2004). They include a range of extinction-prone small mammals whose abundances have declined markedly across northern Australia over recent decades (Woinarski *et al.* 2001; Woinarski 2004). The importance of unburnt habitat might be particularly acute at such times of generally low abundance. A range of ground-feeding granivorous birds such as the masked finch (*Poephila personata*) and partridge pigeon (*Geophaps smithii*) also favour relatively infrequently burnt habitat (Woinarski *et al.* 1999), and these have likewise suffered serious population declines across northern Australia in recent times (Franklin 1999). There is considerable potential for using such fire-sensitive species as indicators of effective fire management at a regional scale (Andersen *et al.* 2003b).

The occurrence of relatively long fire-free intervals would also appear to be important for the long-term
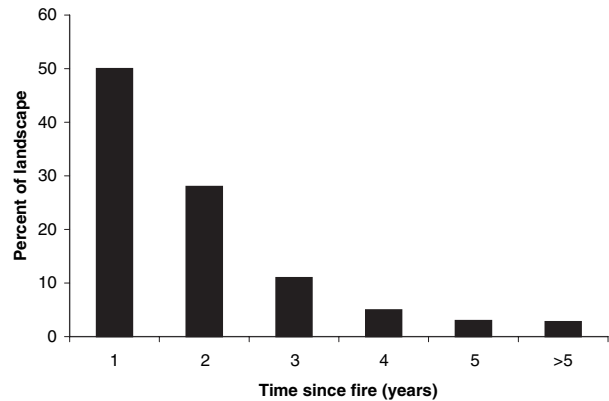
Fig. 5. Time-since-fire profile of lowland savanna in Kakadu National Park obtained from satellite imagery (data recalculated from Gill *et al.* 2000). Similar profiles occur in the other major Top End National Parks, Litchfield and Nitmiluk (Edwards *et al.* 2001).

sustainability of savanna tree populations (Setterfield 2002). Fire substantially reduced seed production and seedling establishment (Table 1), and it has been well documented that high fire frequencies prevent seedlings and woody sprouts from entering the canopy and reaching reproductive maturity (Higgins *et al.* 2000; Peterson & Reich 2001). It is estimated that fire-free intervals of at least 4 years are required for woody sprouts to escape the 'fire trap' in mesic savannas of northern Australia (Hoare *et al.* 1980; Russell-Smith *et al.* 2003; Williams *et al.* 2003a).

An examination of time-since-fire profiles of Kakadu and other Top End National Parks indicates a serious lack of long unburnt habitat catering for relatively fire-sensitive savanna species. For example, about 70% of all lowland savanna sites in Kakadu are burnt at least once every 2 years (see also Braithwaite & Estbergs 1985), with less than 3% of the landscape remaining unburnt for more than 5 years (Fig. 5; see also Woinarski 2004). Similarly, nearly 90% of Bradshaw Station, a 9100-km^2 property in the northern Victoria River District, has a minimum fire return interval of less than 3 years (Yates & Russell-Smith 2003). Such high fire frequencies also occur in the northern Kimberley region of Western Australia (Fisher *et al.* 2003). Results from Kapalga suggest that increasing the area of relatively long unburnt habitat would have significant conservation benefits in higher rainfall areas throughout the western monsoonal region of northern Australia.

MANAGING FIRE FREQUENCY

How might a reduction in fire frequency, or, more particularly, an increase in area of relatively long unburnt habitat, be achieved? If it is assumed that fire occurs at random, the variation in area of land with

different post-fire ages can be modelled in relation to the total area of land that is burnt annually (Fig. 6a). If 50% of the country is burnt each year, as is typical for lowland savanna in the Top End, then only about 10% of the land would remain unburnt for longer than 3 years, and greater than 3% longer than 5 years. This closely matches the time-since-fire profiles of the Top End's major National Parks (Fig. 5).

Still assuming random fires, managers have two basic options for increasing the proportion of the land-scape remaining relatively long unburnt. The first is to reduce the amount of land burnt each year. If 40% of the country were burnt annually, then the proportion of land remaining unburnt for longer than 3 years would double to approximately 20%, and nearly 8% would remain unburnt for longer than 5 years. The area remaining unburnt for longer than 5 years increases exponentially as the total area burnt declines from 40% (Fig. 6a). In contrast, if the total area burnt each year increases to 70% then less than 2% would
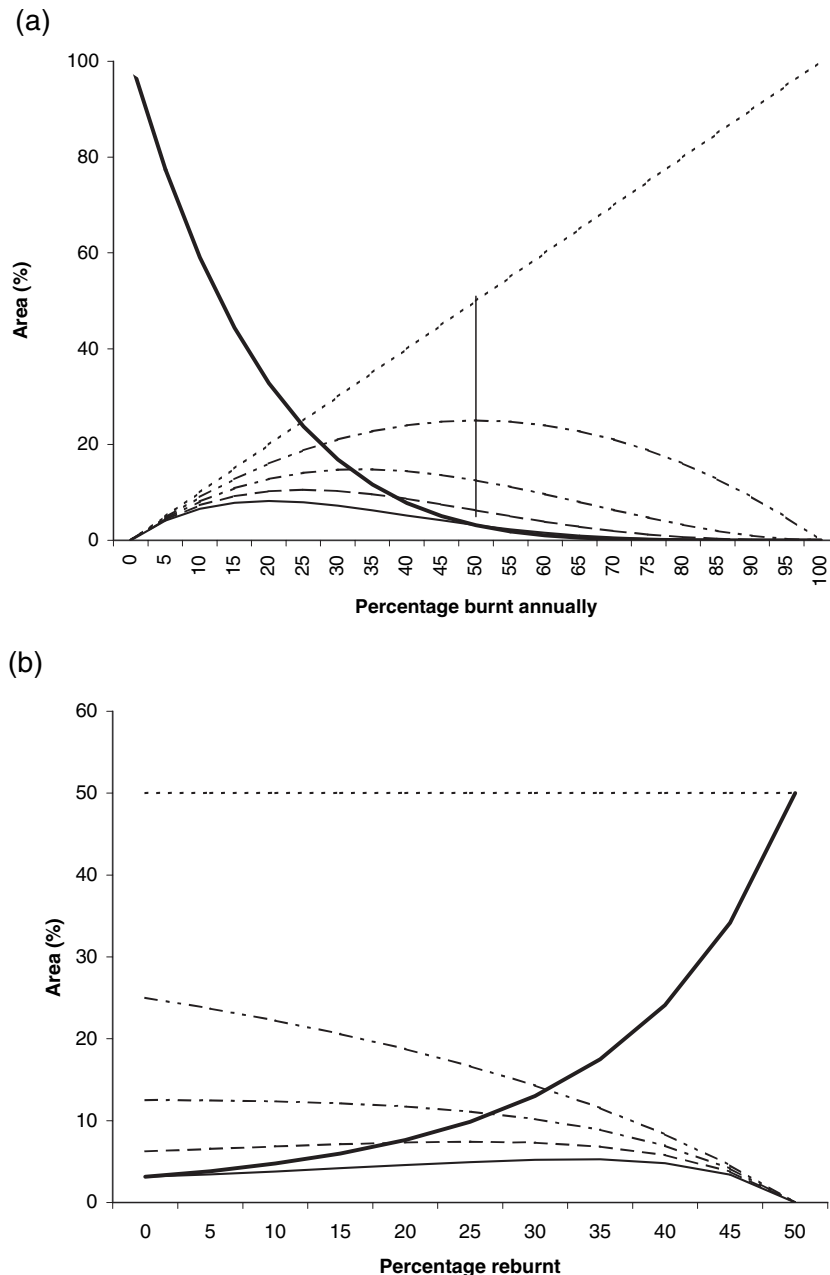
Fig. 6. Time-since-fire profiles according to different fire management scenarios, showing proportions of the landscape of varying post-fire age. In (a), fires are assumed to occur randomly in space, and the total area burnt is varied. The vertical line indicates areas of different post-fire ages if 50% of the landscape is burnt each year. In (b), the total area burnt each year is held constant at 50%, and the proportion of the total landscape that is reburnt annually is varied. - - - 1 year, – - - – 2 years, – – – 3 years, – – – 4 years, —— 5 years, ▬▬ >5 years. Modified from Andersen *et al.* (2003c).

remain unburnt for longer than 3 years, and there would be negligible habitat remaining unburnt for longer than 5 years.

In some regions conservation managers appear to have little control over the area burnt each year, due to a high incidence of unauthorized burning. For example, in Kakadu National Park a remarkably constant 50–60% of lowland savanna is burnt each year, regardless of the extent of prescribed burning early in the dry season (Gill *et al*. 2000; cf. the situation for Litchfield and Nitmiluk, Edwards *et al*. 2001). In this situation, a reduction in prescribed burning will not necessarily achieve a more desirable time-since-fire profile.

An increase in the area of relatively long unburnt habitat can also be achieved by locating fires more strategically in terms of deliberately avoiding previously unburnt habitat. In the most extreme case, if exactly the same places were left unburnt every year, then the landscape would consist of equal parts never burnt and burnt annually, assuming that the total area burnt is fixed at 50%. If 25% of the landscape is reburnt annually (with another 25% burnt at random), then about 22% of the land (nearly twice that given random burning) would have remained unburnt for more than 3 years, and about 10% (>3 times) for more than 5 (Fig. 6b). The concept of using strategically placed fires to maintain long unburnt habitat has been successfully implemented elsewhere in Australia (Richards *et al*. 1999).

CONCLUSION

As in conservation management more generally (Hansen *et al*. 1993), fire management on conservation lands is most effective when guided by specific objectives that go beyond vague motherhood statements such as 'conservation of biodiversity' or 'creation of habitat heterogeneity' (Andersen 1999; Richards *et al*. 1999). A clear vision for nature conservation can be difficult to achieve because of people's differing value systems, and this challenge is particularly acute on Aboriginal lands (Langton 1998; Pearce *et al*. 1996; Andersen & McKaige 1998). However, this does not preclude the setting of specific objectives that would produce widely supported conservation outcomes. There is widespread support for the notion that a diversity of fire regimes is necessary for the maintenance of biodiversity at the landscape scale (Martin & Sapsis 1992), but clear targets are necessary for such a notion to be operationally effective. Results from Kapalga highlight the importance of unburnt habitat to savanna biodiversity. Given current burning patterns in Top End National Parks, we propose the conservation goal of substantially increasing the extent of relatively long unburnt habitat.

We realize that our proposal is unquantified, and that this needs to be addressed. It is unclear what might be an ideal target for the area remaining relatively long unburnt, or even how such a figure should be arrived at. However, we feel that such ambiguity ought not prevent the current area being substantially increased. Similarly, it is unclear exactly what period of time constitutes 'relatively long unburnt'. There is a pressing need for further research focusing on the ecological significance of different fire-free periods, particularly around what appears to be the critical time of 3–5 years (Andersen *et al*. 2003b). There is also a priority need for disentangling the significance of time-since-fire from that of fire frequency over a longer period. A new experiment focusing on fire frequency and time-since-fire has been established at the Territory Wildlife Park near Darwin, as part of the Bushfire Cooperative Research Centre.

Prescribed burning early in the dry season will always remain a key tactical tool for effective fire management in northern Australia. However, its application needs to be mindful of the deleterious impacts of high fire frequency on key components of savanna biodiversity, even if fire intensity is relatively low. The savanna woodlands and open forests of tropical northern Australia might provide a striking contrast with temperate southern Australia in terms of fire behaviour and ecology, but the ecological importance of managing fire frequency, and in particular the provision of appropriately long unburnt habitat, is one thing they have in common.

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