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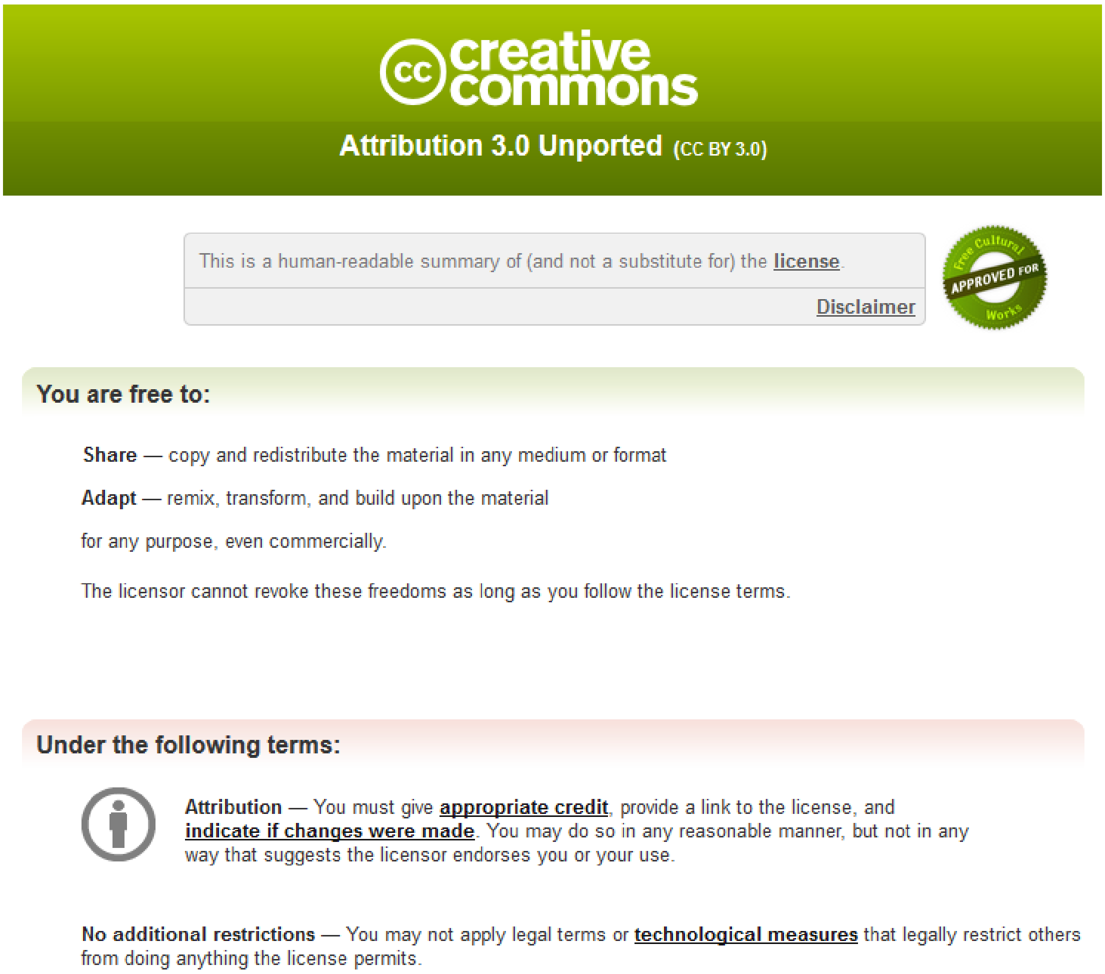
Ecosphere, 2015; 6(6):99-1-99-22

Originally published at:
http://doi.org/10.1890/ES14-00519.1



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Fire impacts recruitment more than survival of small-mammals in a tropical savanna

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Citation: Griffiths, A. D., and B. W. Brook. 2015. Fire impacts recruitment more than survival of small-mammals in a tropical savanna. Ecosphere 6(6):99. http://dx.doi.org/10.1890/ES14-00519.1

Abstract. The frequency and spatial patterning of fire for optimal biodiversity conservation is often poorly understood by managers, in part due to a lack of understanding of the mechanisms responsible for altering population dynamics of individual species. We investigated changes in the vital rates (survival and recruitment) of four small mammal species (three marsupials and one rodent) in a tropical savanna under four different experimental fire treatments applied at a landscape scale. Apparent survival declined in all fire treatments for only one of four small mammal species (northern brown bandicoot *Isoodon macrourus*). Recruitment was reduced in three of four species in multiple fire treatments. The suppression of recruitment in the northern brown bandicoot and the brushtail possum *Trichosurus vulpecula* populations was greatest immediately after the initial fire treatment was applied, compared to remaining treatment applications in successive years, possibly due to an elevated fire intensity as a result of higher initial fuel loads. The results suggest that higher intensity fire impacted recruitment more than survival for small mammals at this site. To assist fire managers to conserve small mammal populations in tropical savannas, we recommend fire regimes that optimise habitat resources for recruitment. This may be achieved by a reduction in fire frequency and managing fuel loads to prevent an increase in fire intensity.

Key words: Australia; *Antechinus bellus*; apparent survival; capture-mark-recapture; *Dasyurus hallucatus*; fire experiment; frequency; intensity; *Isoodon macrourus*; *Melomys burtoni*; recruitment; *Trichosurus vulpecula*.

Received 18 December 2014; accepted 29 December 2014; final version received 10 February 2015; **published** 23 June 2015. Corresponding Editor: R. R. Parmenter.

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INTRODUCTION

Fire is a common agent of disturbance in many ecosystems, and is widely used for fuel reduction (clearance of living and dead vegetation) and habitat management in many continents (Whelan 1995, Bradstock et al. 2002, Bond and Keeley 2005). However, the frequency and spatial patterning of fire required to conserve biodiversity is often poorly understood by managers, in part due to a lack of understanding of the relationship between fire events and population dynamics of species and community composition, and the logistical constraints on fire managers in implementing operational guidelines at the appropriate scale in the field (Bond and Archibald 2003, Parr and Andersen 2006). As a consequence of this limited understanding, many taxa may be at risk from altered burning practices, especially where long-standing practices like indigenous burning patterns have been disrupted by more recent settlement or changing land use (Swengel 2001, Bradstock et al. 2002, Clarke 2008).

Fire has been shown to alter the abundance of animal populations in many ecosystems (Whelan 1995). Evidence suggests that processes responsible for fire-related changes in abundance commonly act indirectly on animal populations (i.e., not through direct mortality) and the responses reflect the individual life history of species. Specifically, changes to vegetation structure can change resource availability, alter competitive pressures, increase predation and reduce individual fitness (Fox 1982, Fox et al. 2003, Converse et al. 2006). However, there is inadequate empirical evidence to support unified ecological theories that might be used to predict outcomes for particular fauna to a given fire regime (Lindenmayer et al. 2008). As a more tractable alternative, attention has shifted towards the use of functional traits to understand and predict biotic responses to fire regimes. However, this approach is more generalised, and relies on detailed information on species life history (Langlands et al. 2011, Keith 2012).

Variation in population size is a consequence of changes in demographic and movement parameters such as survival, recruitment, dispersal and immigration (Stearns 1992); changes in abundance following fire could be the result of any combination of these parameters. There are limited data on the demographic processes that are responsible for observed changes in abundance under different fire regimes, and the majority of research on the effects of fire on animal populations has focussed on change in relative abundance (Friend 1993, Whelan 1995, Sutherland and Dickman 1999, Whelan et al. 2002, Griffiths and Brook 2014). A reliance on changes in abundance to draw generalisations, or for making predictions about fire effects, is problematic because of idiosyncratic differences in fire history, fire and habitat characteristics, biotic interactions, climatic influences, and site-to-site variation in an organism's life history (Whelan 1995, Whelan et al. 2002, Driscoll and Henderson 2008, Lindenmayer et al. 2008).

Here we analyse a comprehensive long-term dataset to examine the effect of fire on the population dynamics of five small mammal species in the wet-dry tropical savannas of the iconic but fire-prone Kakadu National Park (Russell-Smith et al. 1997). Past work has revealed that small mammals appear to be the least resilient to fire of any major faunal group in Australia savannas (Andersen et al. 2003), and there is evidence to suggest a widespread decline has occurred during the last few decades across northern Australia and many historical extinctions in central and southern Australia (Woinarski and Braithwaite 1990, Woinarski et al. 2011). Specifically, we evaluate the effects of experimental fire regimes on demographic parameters (i.e., survival and recruitment). Based on a previous analysis of this dataset using only indices of abundance, Corbett et al. (2003) documented a significant increase in trapping rates in the unburnt treatment for six out of seven small mammal species and a significant decline in the high intensity treatment for three small mammal species. Later, Pardon et al. (2003) used more sophisticated modelling on one species that accounted for probability of recapture to demonstrate strong support for the hypothesis that survival of northern brown bandicoot was reduced in higher-intensity fire treatments.

In this study we aim to quantify and compare the impact of different fire treatments applied at a landscape-scale on survival and recruitment on multiple small mammal species with contrasting life histories. Specifically, we hypothesise that small-mammal survival and recruitment will decrease after fire events, either due to reduced availability of food and shelter or an increase in the number of animals lost to predators and altered competitive interactions (Newsome and Catling 1983, Sutherland and Dickman 1999). We apply capture-mark-recapture models to test competing hypotheses and use the results to assess the implications for fire-management practices.

METHODS

The data used in the analysis come from a detailed six-year, multi-site capture-mark-recapture study of small mammal populations at the Kapalga Research Station, Kakadu National Park (12°43′ S, 132°26′ E) (Fig. 1). The region has a wet-dry tropical climate, with a dry season from May to November, a wet season from December to April, and a mean annual rainfall of 1485 mm (Jabiru airport: Bureau of Meteorology 2005).

The capture-mark-recapture study was undertaken as part of an innovative landscape-scale

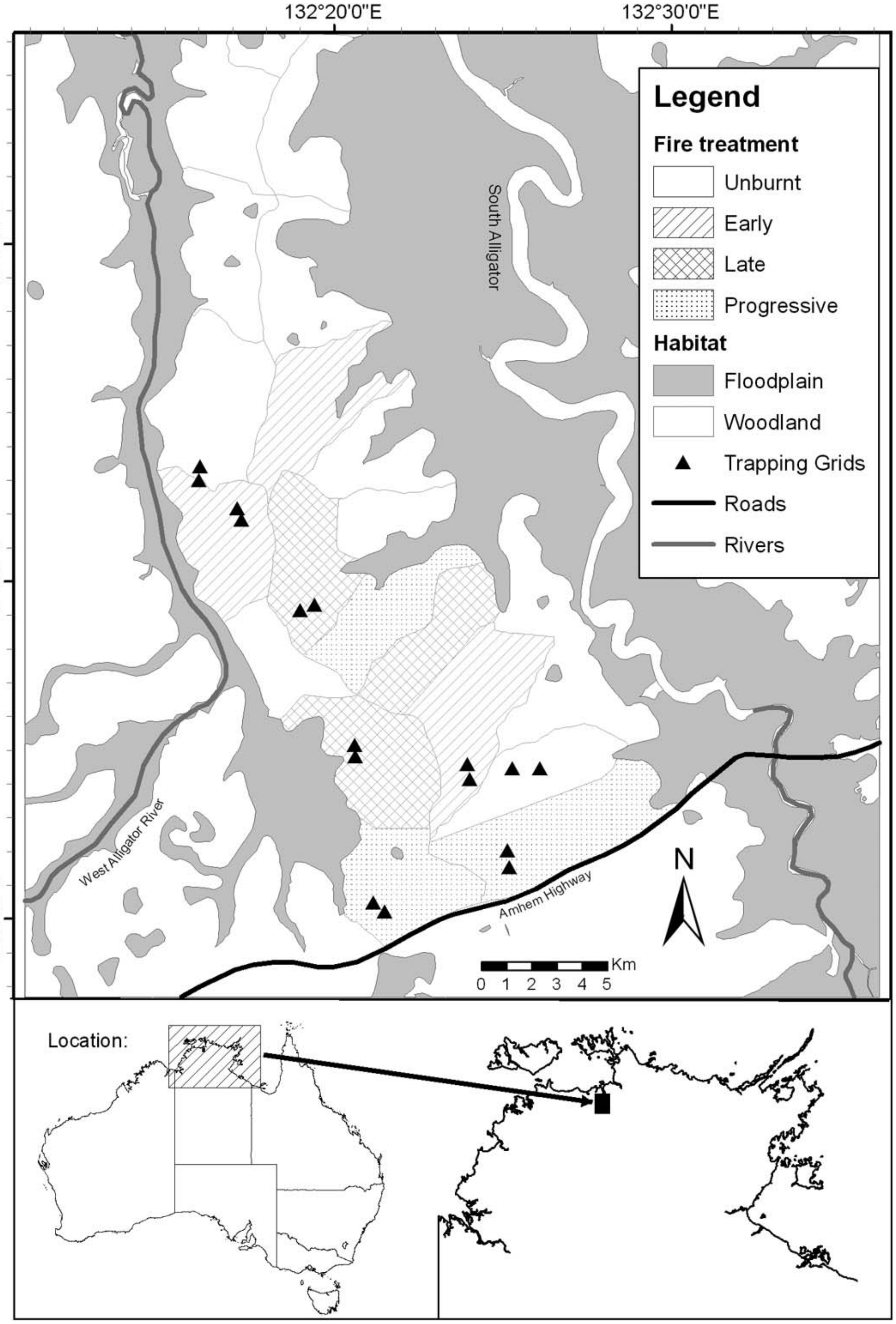

Fig. 1. Map of Kapalga Research Station showing the arrangement of experimental fire treatments and trapping grids. Fire treatments were applied annually from June 1990 to 1994.

fire experiment (Andersen et al. 1998). Four different fire treatments were applied to two replicate blocks (15–20 km^2 sub-catchments): (1) *Unburnt*—blocks protected from fire; (2) *Early*—blocks burnt in early dry season (June) with mean fire intensity = 2.1 MW m^{-1} (Williams et al. 2003) (see Appendix A: Fig. A1); (3) *Late*—blocks burnt in the late dry season (September) with mean fire intensity = 7.7 MW m^{-1} (Williams et al. 2003) (see Appendix A: Fig. A2); and (4) *Progressive*—blocks burnt repeatedly, in the early, mid- and late dry season (May, July and September) and fire intensity was not measured. After the first 12 months (July 1989 to May 1990) of the study, each of the four replicated fire treatments was applied and re-applied thereafter for the next five years (July 1990 to May 1995). The intention of the experimental treatments was to simulate the timing of different types of landscape fires which occurred within the region; the scale of the field-based experimental habitat manipulation was ground breaking (Andersen et al. 1998).

Each replicate block contained a pair of 8 ha trapping grids, with one of each pair oriented in riparian/woodland vegetation and the other located >500 m upslope in open forest (Braithwaite and Griffiths 1994) (Fig. 1). Each of the 16 grids was arranged as four rows at 50 m spacing with 20 trap sites at 20 m spacing. They were trapped with 1:4 trap type ratio (wire cage:solid-walled Elliott) for two nights every two months. The capture-mark-recapture study commenced in July 1989 and ended in May 1995 for a total of 92,160 trap-nights. Nine small mammal species were captured over the entire study. Of these, five small mammal species were trapped in sufficient numbers over the 36 trapping occasions to permit a rigorous capture-mark-recapture analysis: one rodent (grassland melomys *Melomys burtoni* Ramsay 1887) and four marsupials (northern quoll *Dasyurus hallucatus* Gould 1842, brushtail possum *Trichosurus vulpecula* Kerr 1792, northern brown bandicoot *Isoodon macrourus* Gould 1942 and fawn antechinus *Antechinus bellus* Thomas 1904).

At initial capture, all individuals were marked with uniquely numbered brass ear tags, sexed, and released immediately at the site of capture (see Appendix A: Fig. A3). Upon all subsequent recapture(s), individuals were re-weighed and then released at point of capture.

To estimate apparent survival and recapture rates we used the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) in Program MARK (White and Burnham 1999), implemented using the RMark 2.1.3 package (Laake 2013) for Program R 2.15.2 (R Development Core Team 2012). Apparent survival (Φ) is defined as the probability that a marked animal in the study population at occasion i survives until occasion $i + 1$ (i.e., between trapping occasions), while acknowledging that unobserved emigration from the trapping grid is possible (Pollock et al. 1990). Recapture (p) is defined as the probability that a marked animal in the study population at occasion i is captured during occasion i. Model assumptions include: (1) all animals having independent fates, (2) every marked animal have an equal probability of recapture and survival, (3) that no tags are lost, and (4) that if temporary emigration is present, it is random (Pollock et al. 1990). The link function was logit for the recapture and survival analyzes.

To estimate recruitment we used temporal symmetry models (Pradel 1996), also using Program MARK v6.2 and implemented in RMark. By analysing the encounter history of all marked individuals in the population going backwards in time, it is possible to estimate the probability of an individual entering the population. Recruitment (f) is defined as a per capita recruitment probability (i.e., net new animals per animal alive at occasion i enter the marked population between occasions i and $i + 1$). Assumptions for the temporal symmetry model follow the CJS model in addition to the area sampled does not change during the study, and the link function was logit for recapture and survival (because these are represented as proportions) and log for recruitment.

We analyzed the effect of different fire treatments, environmental conditions, sex-specific differences, and body size on recapture, survival and recruitment (Appendix B), based on the method of linear modelling of explanatory covariates originally proposed by Lebreton et al. (1992).

The effects of fire were characterized by three covariates: time since fire (tsf), fire treatment (fire) and pre/post fire treatment (pre.post). Time since fire was modeled as a linear trend, set to zero when a fire occurred immediately before a trapping occasion and accruing one unit thereafter until the next fire (Pardon et al. 2003). Fire treatment was modeled as a group (categorical factor) for each of the four fire treatments. Pre/post fire treatment was modeled as a time-specific covariate representing the situation that no fire treatment was applied to any of the eight compartments in the first twelve months of the study (i.e., no difference between unburnt and three fire treatments until the seventh trapping occasion).

Climate conditions influence the population dynamics of small mammals in the wet-dry tropics of northern Australia (e.g., Friend 1990, Braithwaite and Griffiths 1994, 1996). We modeled rainfall (mm; rain) as a time-specific covariate over the interval between two trapping occasions; this was assumed to relate to food availability. Temporal variations were represented by year, calendar month and linear trend, and were expressed as time-specific covariates. *Sex* (sex) was represented as a group (categorical factor). Body mass (mass) was modeled as an individual covariate. We constructed a priori candidate sets of models from these variables (not all subsets) based on known biology and the published ecological literature for each species, comprising additive and, for some models, interactive combinations. Each temporal covariate was scaled to range between zero and one. If the 95% confidence interval for the slope of the logit- or log-explanatory covariate (β) did not include zero, the relationship was considered statistically significant (Williams et al. 2002).

To make this complex analysis tractable, the capture-mark-recapture analysis proceeded in stages for both CJS and Pradel modelling (Lebreton et al. 1992). Initially, the most parsimonious models for the recapture component of the variation were determined, by setting a fixed survival model structure (i.e., 'global' model containing all covariates in additive combination). Following this sub-analysis, the best-supported recapture model was then used in all candidate survival models. When modelling recruitment probability, the best-supported model of recapture and survival was used to develop a candidate set. To avoid over-parameterising models, attention was given to keeping the ratio of effective sample size (n) to model parameter (K) high ($n/K > 40$). In most cases, this restricted the use of the fully time-parameterised models, whereby individual parameters were estimated for each of the 36 trapping occasions. When no individuals were captured in a trapping occasion we logically fixed recapture and survival parameters to zero. This occurred in the male northern quolls dataset due to their semelparous life history (i.e., annual die-off of all males in September and November each year) (Oakwood et al. 2001).

The CJS and Pradel models make two key assumptions: (1) parameter rate is constant within groups (i.e., sex and fire treatments) and (2) individuals are equally catchable (Williams et al. 2002). Violation of these assumptions can result in over-dispersion, leading to an underestimation of associated variances (Anderson et al. 1994). To assess whether the data met these assumptions, we did goodness-of-fit tests on a partially saturated model for each individual species, using the parametric bootstrapping procedure available in Program MARK v6.2 to estimate deviance in 1000 idealized simulations based on the structure of the fully saturated model (Cooch and White 2007). We calculated a variance inflation factor $\hat{c}$ (deviance of the fitted partially saturated model/mean deviance of 1000 simulated models) for each species separately. Tests were conducted using global CJS models because goodness-of-fit tests are not available for models containing individual covariates or temporal symmetry.

Model selection was based on Akaike's Information Criterion, corrected for small sample size: AIC_c (Burnham and Anderson 2002). The likelihood of each model, relative to others in the candidate set, was estimated with AIC_c weights (w) (Burnham and Anderson 2002) and models were ranked according to this measure. When overdispersion was evident we used the small-sample corrected quasi-Akaike Information Criteria (QAIC_c) for model selection and calculating model averaged estimates. In order to account for model-selection uncertainty (i.e., the decision of which model to use for inference when a number of models in the candidate set have similar support) and to guard against spurious results, the parameters and their standard error of each sampling occasion were estimated by model averaging (Burnham and Anderson 2002, Lukacs et al. 2010). Model averaging uses Akaike weights to estimate parameters and variances that are weighted by the relative strength of support for each model in the candidate set. Models with high Akaike weights contribute most to the final estimate of the parameter.

RESULTS

There was a total of 3055 captures representing 1926 individuals over the study period from July 1989 to May 1995. Goodness-of-fit tests on global capture-mark-recapture CJS models revealed there was strong evidence of lack of fit for the fawn antechinus dataset (Appendix C) and was not included in the capture-mark-recapture analyses. There was some evidence of over-dispersion for the northern quoll dataset ($\hat{c}$ = 1.11), and therefore we used QAIC$_c$. For the remaining three species there was little evidence of lack of fit with estimates of $\hat{c}$ close to 1.0, thereby satisfying the assumptions of independence between individuals and equal survival and catchability within the trappable population for each species (Appendix C).

There was evidence of fire treatments influencing survival of only one of the four small mammal species at Kapalga. The best-supported apparent-survival model for the northern brown bandicoot contained the interaction of fire treatment with a linear trend (Appendix D: Table D1); this is consistent with the results of Pardon et al. (2003). Model-averaged bimonthly survival estimates show a decrease in Late and Progressive treatments and less-pronounced decline in Early and Unburnt treatments (Fig. 2).

The three remaining species exhibited no clear effect of fire on apparent survival. For brushtail possums at Kapalga, there was no support for any models containing fire-related covariates and the model representing constant survival was ranked high in the candidate set (ΔAIC$_c$ = 1.58) (Appendix D: Table D2). Bi-monthly model-averaged survival estimates varied between 0.73 (SE = 0.03) and 0.89 (SE = 0.07) during the study period. For the northern quoll all top-ranked models contained seasonal and sex effects (Appendix D: Table D3). Survival was highest for males and females during the wet season and steadily decreased throughout the dry season until the mass male die off occurred. Similarly, there was limited evidence of fire effects on apparent survival for grassland melomys at Kapalga, with the best-supported model representing differential response to fire treatments with body mass (AIC$_c$ weight = 0.72) (Appendix D: Table D4). However, the 95% confidence intervals for the model coefficient for body mass overlapped with zero, indicating a non-significant effect (i.e., any signal that may have been present was overwhelmed by the variation in the data). Model-averaged survival estimates showed higher survival of grassland melomys in the Late and Progressive and very low survival in the Early fire treatments, however there was considerable uncertainty associated with all estimates, most likely a consequence of sparse data.

There was clear evidence that fire affected recruitment in three of the four species of small mammals at Kapalga. The best-supported recruitment model for the northern brown bandicoot contained the interaction of fire treatment and time since fire, plus an additive effect of rainfall (Appendix D: Table D1). Model-averaged bimonthly recruitment probability showed a sharp decline from initial values that corresponded to the first application of fire in all three fire treatments (Fig. 3). Increase in recruitment was apparent in early-dry-season months (March and May), indicating that new individuals born during the wet season had entered the trappable populations (Fig. 3). For the brushtail possum, there was strong support for fire effects on recruitment (Appendix D: Table D2). The best supported model (AIC$_c$ weight = 0.60) contained the parameter Pre/Post, which represented no fire treatment among each treatment in the first twelve months of the study then the application of fire to three treatments for the next five years (i.e., uniform difference in three fire treatments compared to *Unburnt*). Recruitment was significantly lower in the three burnt fire treatments following the initial fire in 1990 ($\beta = -0.26$, 95% CI: -0.37 to -0.14) compared to the *Unburnt* treatment. Model-averaged recruitment estimates were approximately 20% lower in the burnt fire treatments compared to the Unburnt treatment, and remained relatively constant thereafter throughout the study, with a small increase during dry season months (Fig. 4). Similarly, the top-ranked models for the northern

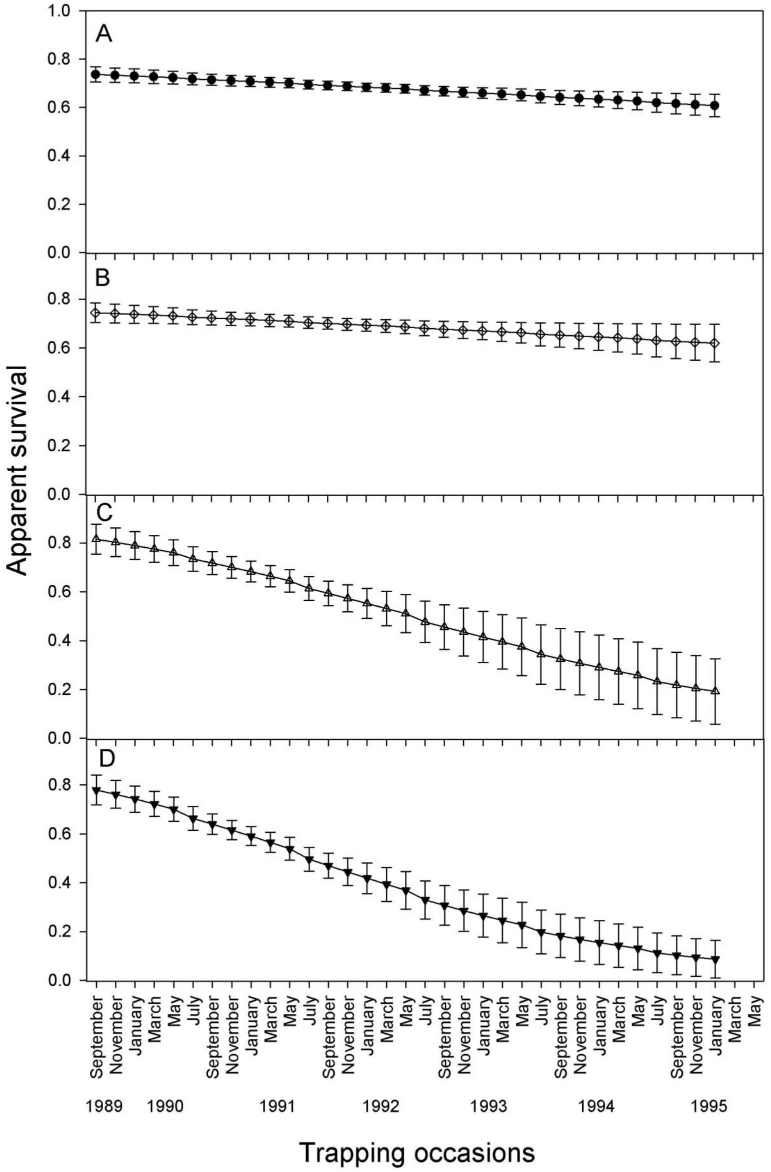

Fig. 2. Model-averaged estimates (± SE) of apparent survival probability in four fire treatments at Kapalga for the northern brown bandicoot. Each panel relates to a fire treatment: (A) *Unburnt*; (B) *Early* (fires lit in June); (C) *Late* (fires lit in September), (D) *Progressive* (June and September). Experimental fires were applied from June 1990 onwards.

quoll contained the fire-treatment factor (Appendix D: Table D3). Based on the best-supported model containing fire treatment, recruitment of northern quolls was significantly lower in the Late fire treatment ($\beta = -1.87$, 95% CI: -1.38 to -0.99) compared to all other treatments (Fig. 5). This translates to an approximately 20% decrease in recruitment over the study period, which was similar to that of the brushtail possum.

The grassland melomys was the only species that didn't exhibit a response to fire treatments. Recruitment of grassland melomys was highly seasonal, with models containing the covariate *Month* ranked in the top two models (Appendix D: Table D4). There was some evidence to suggest fire-affected recruitment, with the top-

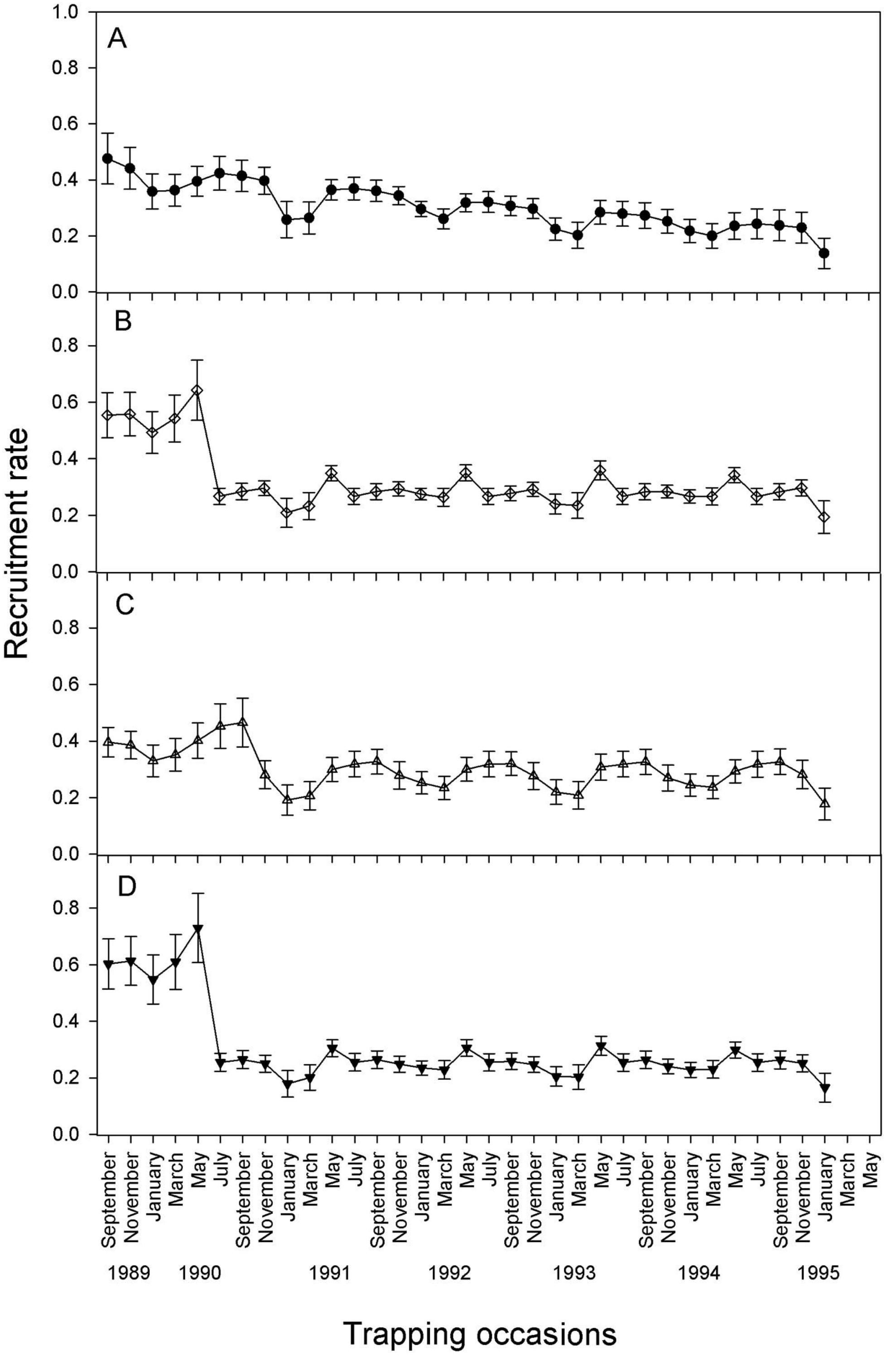

Fig. 3. Model-averaged estimates (± SE) of recruitment rate in four fire treatments at Kapalga for the northern brown bandicoot. Each panel relates to a fire treatment: (A) *Unburnt*; (B) *Early* (fires lit in June); (C) *Late* (fires lit in September), (D) *Progressive* (June and September). Experimental fires were applied from June 1990 onwards.

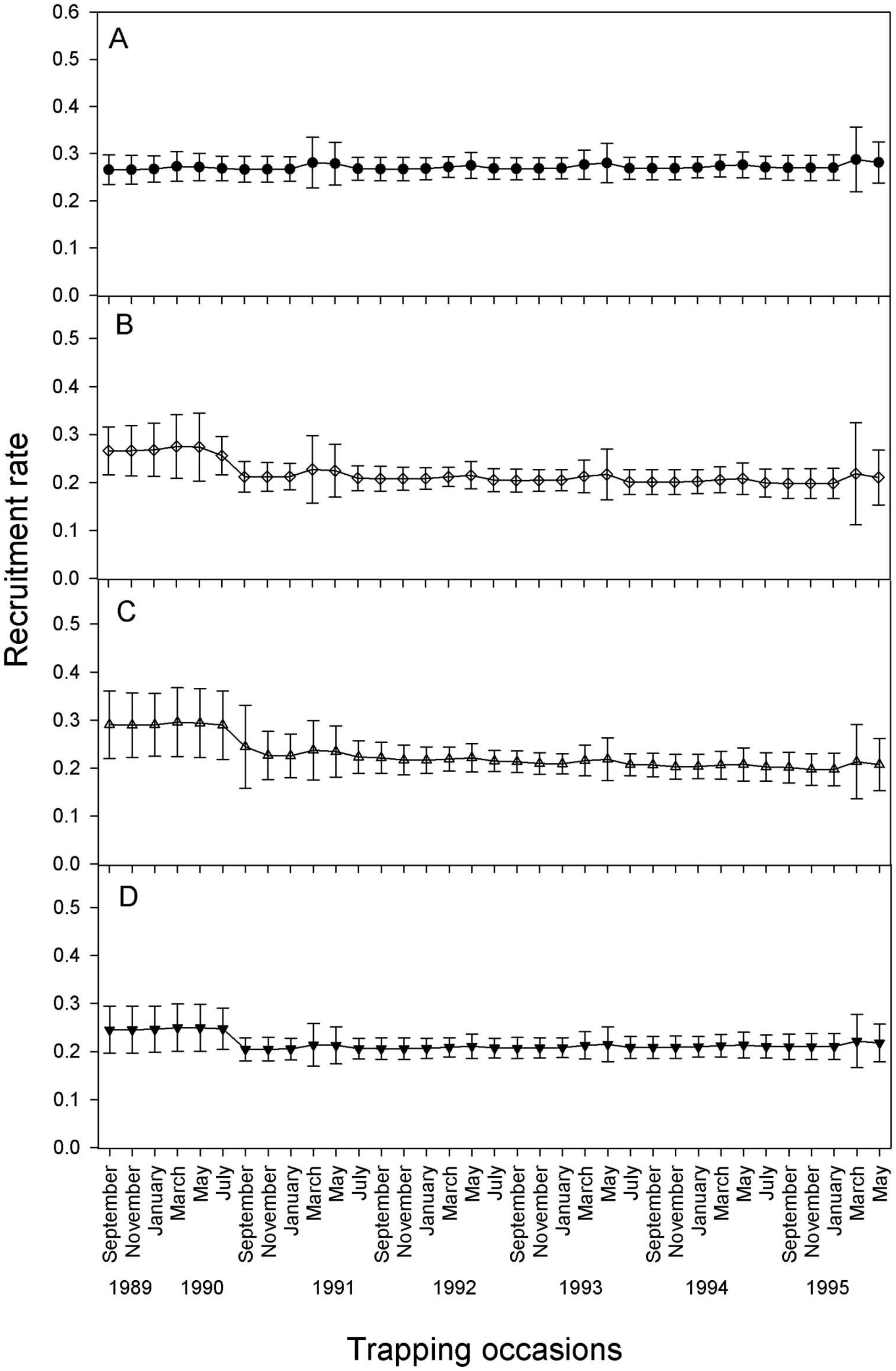

Fig. 4. Model-averaged estimates (± SE) of recruitment rate in four fire treatments at Kapalga for the brushtail possum. Each panel relates to a fire treatment: (A) *Unburnt*; (B) *Early* (fires lit in June); (C) *Late* (fires lit in September), (D) *Progressive* (June and September). Experimental fires were applied from June 1990 onwards.

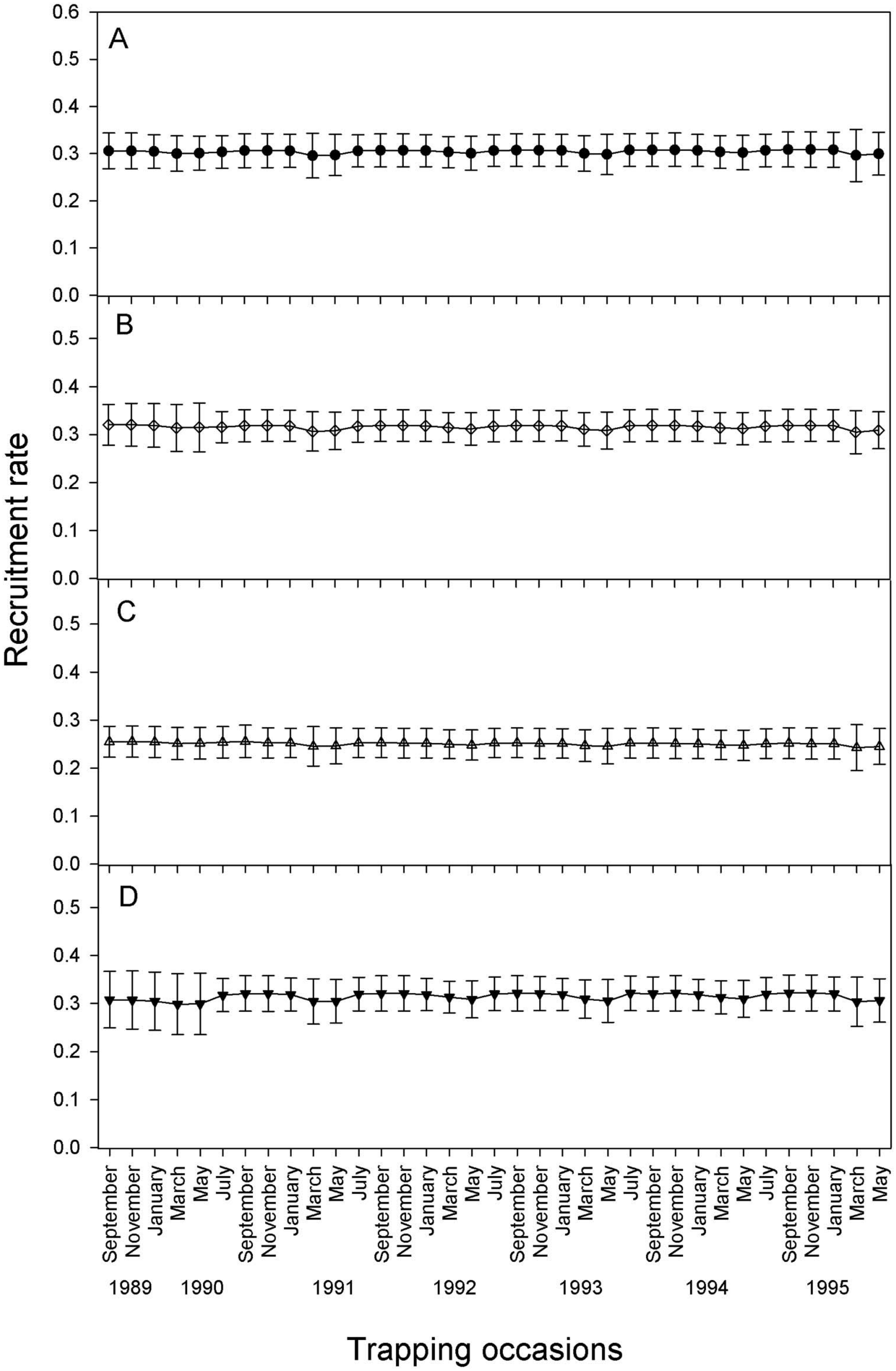

Fig. 5. Model-averaged estimates (± SE) of recruitment rate in four fire treatments at Kapalga for the northern quoll. Each panel relates to a fire treatment: (A) *Unburnt*; (B) *Early* (fires lit in June); (C) *Late* (fires lit in September), (D) *Progressive* (June and September). Experimental fires were applied from June 1990 onwards.

Table 1. Summary of key results of the effects fire treatments on vital rates for four small mammal species at Kapalga, Kakadu National Park, as inferred from the capture-mark-recapture models. Symbols indicate: ↓ decrease and ↑ increase.

Species	Survival (Φ)	Recruitment (*f*)
Northern brown bandicoot	↓ *Early, Late*	↓ *Early, Late, Progressive* (after first fire)
Brushtail possum	No response	↓ *Early, Late, Progressive* (after first fire)
Northern quoll	No response	↓ *Late*
Grassland melomys	No response	No response

ranked model containing the interaction of fire treatment and month (AIC_c weight = 0.86) (Appendix D: Table D4). Model-averaged recruitment estimates illustrated the strong seasonal pattern, and higher recruitment may have occurred in the Late and Early fire treatments during wet-season trapping occasions. However, model coefficients indicate no significant effect due to the overlap of 95% confidence intervals with zero.

DISCUSSION

The major finding of this capture-mark-recapture analysis is that fire can markedly affect the population dynamics of small mammal species by influencing vital rates such as survival and recruitment, but it does not exert a simple or universal effect across species. We hypothesised that the vital rates of species would be lower in fire treatments compared to unburnt 'controls', and that both measures would decrease as fire intensity increased. The modelling showed that apparent survival was significantly lower in one of four species, and recruitment was significantly lower in three species in higher intensity fire treatments (Table 1). Nonetheless, although the results are a product of a replicated landscape-scale fire experiment over six years, these data are not able to relate observed changes in demographic parameters directly to specific mechanisms such as fire-induced mortality or predation. They also represent somewhat extreme conditions, because fire was not permitted to occur under more realistic random spatio-temporal conditions that might lead to habitat mosaics of burnt and unburnt patches of varying ages in relative proximity.

Fire has been shown to reduce the survival of small mammals via indirect processes rather than direct mortality. Studies of survival of small mammal before and after fires have generally reported no direct mortality (Johnson 1995, Vernes 2000, Monimeau et al. 2002, Banks et al. 2011), although an intense wildfire caused significant mortality (35%) in the critically endangered Mount Graham Squirrel *Tamiasciurus hudsonicus* ssp. *grahamensis* (Koprowski et al. 2006). Recent experimental work has shown that increased predation was responsible for a reduction in survival of cotton mice *Peromyscus gossypinus* due to the removal of ground cover by fire (Morris et al. 2010, Morris et al. 2011). The results of the current analysis from Australia's tropical savannas indicate that northern brown bandicoot survival decreased in higher intensity fires, and this decline was gradual rather than sudden after the application of the experimental fires. Using the same data as this study, Pardon et al. (2003) suggested that a reduction in ground cover may have been responsible for the decrease in survival. However, we have shown here that the observed decline in bandicoot survival and abundance in the Unburnt treatment indicates additional unknown factors seem to have contributed to the observed decline.

The findings from this detailed study suggest that fire may affect recruitment more than survival for small mammals in the tropical savannas. Three species showed a significant reduction in recruitment compared to one species recording a decline in survival. Recruitment was lower in all three burnt treatments for both the northern brown bandicoot and brushtail possum, but only in the Late treatment for the northern quoll. Differences in reproductive strategies may explain the different response. The northern quoll has a synchronous annual breeding cycle whereby mating occurs between late May and early June, young are born in mid to late June, then left in dens located in tree hollows until they become independent by November (Braithwaite and

Griffiths 1994, Oakwood 2000). The timing and intensity of early-dry-season fire is unlikely to disrupt this cycle, whereas the timing and intensity of late-dry-season fire may cause significant mortality of young while in the pouch or den, thereby reducing recruitment. Begg et al. (1981) recorded a decrease of 65% of pouch young in northern quolls after a dry-season fire within Kakadu National Park.

There a number of potential causes for the post-fire reduction in recruitment at Kapalga. Northern brown bandicoots build nests of ground litter in shallow depressions and brushtail possum nest in tree hollows (Friend 1990, Kerle 1998). Both species breed continuously if conditions are favourable, but most reproduction occurs during the wet-season months after which young become independent in the subsequent dry season (Friend 1990, Kemper et al. 1990, Kerle and Howe 1992, Kerle 1998). There are a number of potential mechanisms to explain the decrease in recruitment associated with fire in these two species, including a lack of suitable nesting habitat or food resources, or high mortality of juveniles prior to entering the trappable population. In other studies of small mammal demography and fire, the proportion of female mountain brushtail possums carrying pouch young decreased following an intense wildfire caused by a reduction in shelter resources and migration out of burnt into unburnt habitat (Banks et al. 2011), whereas recruitment of brushtail possums was higher in burnt habitat after prescribed fuel-reduction burns (Isaac et al. 2008). Population collapse in northern Idaho ground squirrel *Spermophilus brunneus brunneus* was driven by mortality of older females after intense wildfire (Sherman and Runge 2002). Further research is needed to test the potential mechanisms responsible for the change in recruitment associated with fire.

An unexpected result was the impact of the initial fire treatment in 1990. The experimental fires in 1990 were substantially more intense than all other years due to elevated fuel loads in all compartments (Williams et al. 2003): mean fire intensity in 1990 was approximately double the average for the other four years. One Late compartment in 1990 recorded a fire intensity of 18 MWm^{-1} (compared to the five-year average = 7.7 MWm^{-1}). Recruitment in the northern brown bandicoot and brushtail possum populations decreased significantly after this first fire and remained low for the duration of the study. The extreme intensity of the initial fire treatment may have had a "catastrophic" impact (sensu Reed et al. 2003) on both the species with insufficient time for recovery due to successive applications of fire.

Sparse data and the inability to distinguish between temporary migration and survival place limits on the inference possible from these types of study. A factor potentially contributing to the sparse data for the small mammals of Kapalga was the relatively small number of trap nights (two) in each bi-monthly trapping occasion. Pollock et al. (1990) recommend a minimum of five nights per trapping occasion for capture-mark-recapture studies, and a larger trapping effort in this study may have resulted in improved precision for estimating parameters and testing competing hypotheses. Yet despite the limitations of the Kapalga capture-mark-recapture study, the results represent a dataset almost unprecedented in the literature on multi-species small-mammal population dynamics, and have allowed for robust inference about their demographic responses to fire. The analytical approach is based on replicated landscape-scale fire treatments, applied and monitored at a fine scale over a number of years, combined with modelling that accounts for variable detection of animals and the use of multi-model inference to strengthen the robustness of the estimated treatment effects.

The decline in small mammal fauna in Australia has attracted considerable attention due to Australia's disproportionately high number of recent vertebrate extinctions and threatened species (Smith and Quin 1996, Johnson 2006, McKenzie et al. 2007). Woinarski et al. (2001) hypothesise that inappropriate fire regimes are partly responsible for the widespread decline of small mammals in northern Australian tropical savannas. They re-trapped the same grids as this study, four years after the landscape-scale fire experiment had ceased, and recorded an increase in indices of relative abundance for four small mammal species and a decrease in seven. They suggested that fire may have been responsible for this decrease. The results presented here offer some support to this hypothesis. Species that showed a decrease in survival or recruitment (northern brown bandicoot, brushtail possum and northern quoll) were all species that declined in the re-trapping study of Woinarski et al. (2001) and the one species that did not respond to fire in this study (grassland melomys) had increased in abundance. Clearly, the link between regional-scale mammal decline and fire regimes is still weak, but the evidence presented in the current analysis can contribute to developing fire-management strategies that seek to optimize conditions and reduce risk for small mammal species in northern Australia (Parr and Andersen 2006, Clarke 2008). To accomplish this requires the development of spatially explicit population models based on the demographic parameters and treatment effects in this study to compare a range of fire management scenarios (e.g., Brook and Griffiths 2004).

The effect of fire on the vital rates of small mammal species was evident at Kapalga, especially via its impact on recruitment. Sherman and Runge (2002) have classified anthropogenically driven population declines into three types: (1) 'blatant disturbances' that result in a direct negative impact on life-history parameters (e.g., habitat loss, overhunting); (2) 'inappropriate variance' disturbances, creating increased fluctuations in life-history parameters (e.g., more frequent stochastic events); and (3) 'evolutionary traps' (e.g., facultative response to climate change). The results from this study suggest that fires may act principally as 'inappropriate variation' for some species of small mammals in the tropical savannas of northern Australia, where the timing and frequency of fire events interact with natural stochastic environmental conditions that drive the population dynamics on various time scales. A reduction in the frequency and intensity of fire in the tropical savannas of northern Australia may contribute to conservation of this at-risk faunal group.

ACKNOWLEDGMENTS

This study was built upon the shared foresight and commitment of CSIRO and Kakadu National Park in running the Kapalga Fire Experiment. We acknowledge that our work would not have been possible without their substantial investment. The study was conducted with approval from CSIRO's Animal Ethics Committee. We thank Graeme Gillespie, Stephen Garnett and two anonymous reviewers for their constructive comments on the manuscript. The study was partly funded by the World Wildlife Fund.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Fig. A1. Early-dry season fire at Kapalga Research Station, Kakadu National Park (image taken by B. McKaige CSIRO).

Fig. A2. Late-dry season fire at Kapalga Research Station, Kakadu National Park (image taken by B. McKaige CSIRO).

Fig. A3. Transferring a northern brown bandicoot from a cage trap to a holding bag for processing (image taken by B. McKaige CSIRO).

APPENDIX B

Table B1. Parameters used and their biological significance to construct capture-mark-recapture models of apparent survival (Φ), recapture probability (*p*), and recruitment rate (*f*), derived from binomial likelihood-based models for small mammals at Kapalga, Kakadu National Park. Category relates to how each parameter is used in the design matrix.

Name	Category	Used in	Apparent survival, recapture or recruitment is . . .	Notes
Null		*p*, Φ, *f*	constant	
Mass	Individual covariate	*p*, Φ	related to size of individual	Body mass at first capture and quadratic term used for non-linear effect to reflect an optimum value
Sex	Category	*p*, Φ,	sex-specific	
Fire treatment	Category	*p*, Φ, *f*	different among the four fire treatments	*Unburnt*, *Early*, *Late* and *Progressive*
Time since fire	Time-specific covariate	*p*, Φ, *f*	influenced by time since fire	Trapping occasions in which fires were lit immediately before numbered (0) and each interval thereafter accrued one unit
Fire Pre.post	Time-specific covariate	*p*, Φ, *f*	different between the first year and remaining five years when fire treatments were applied	All trapping grids were left unburnt in the first year and fire treatments first applied in the 1990 for the next five years
Rainfall	Time -specific covariate	*p*, Φ, *f*	influenced by total rainfall in the previous 2 months	Previous two monthly total rainfall (mm) in each trapping occasion
Month	Time -specific covariate	*p*, Φ, *f*	different among the months of the year	Six months corresponding to each trapping occasion
Year	Time -specific covariate	*p*, Φ, *f*	different among each year of sampling	Six years 1989–1995 (July to May)
Linear trend	Time -specific covariate	*p*, Φ, *f*	constrained by either a positive or negative linear, trend over the study	Capture intervals numbered from 1 to 35

APPENDIX C

Table C1. Summary of bootstrapped goodness-of-fit results for capture-mark-recapture datasets of five small mammal species at Kapalga, Kakadu National Park

Species	No. tagged individuals	Effective sample size	Observed model deviance	Mean bootstrap model deviance	$\hat{c}$	Ranking in bootstrap
Northern brown bandicoot	660	1369	1743.25	1743.53	1.03	531
Northern quoll	350	444	596.23	535.72	1.11	869
Brushtail possum	259	424	860.48	832.11	1.03	648
Fawn antechinus	417	530	591.12	485.91	1.21	971
Grassland melomys	240	288	257.34	253.76	1.01	550
Total	**1926**	**3055**				

Notes: Effective sample size is the total number of captures (and recaptures) of individuals. Observed model deviance is the deviance of the partially saturated CJS model used in bootstrapping procedure: model *p* (global) Φ (global). Mean bootstrap model deviance is the average deviance from 1000 bootstrap samples of the partially saturated model. $\hat{c}$ is the model deviance divided by mean bootstrap model deviance. The ranking in bootstrap is the rank of model deviance in sorted deviance of 1000 bootstrap samples.

APPENDIX D

Table D1. Summary of model-selection results for the northern brown bandicoot in Kakadu National Park, tropical northern Australia. K is the number of parameters. AIC$_c$ is Akaike's Information Criterion, corrected for small sample size. ΔAIC$_c$ shows the difference between the model AIC$_c$ and the lowest AIC$_c$ out of the set of models. AIC$_c$ weights (w_i) are the relative likelihood of model i (normalized to sum to 1). The bigger the delta the smaller the weight and the less plausible model i.

Number	Model	K	AIC$_c$	ΔAIC$_c$	w_i
Recapture					
1	p (∼fire × rain)	21	3070.4	0.0	0.251
2	p (∼fire × tsf)	21	3070.5	0.1	0.233
3	p (∼fire + rain)	18	3071.1	0.6	0.179
4	p (∼fire + sex + linear trend + rain + mass + mass^2)	22	3071.1	0.7	0.174
5	p (∼fire × tsf + sex + linear trend + rain + mass + mass^2)	26	3071.3	0.9	0.157
6	p (∼sex × fire)	21	3078.4	8.0	0.004
7	p (∼linear trend)	15	3081.0	10.6	0.001
8	p (∼rain)	15	3086.0	15.6	0.000
9	p (∼1)	14	3087.4	16.9	0.000
10	p (∼sex)	15	3088.9	18.5	0.000
11	p (∼mass + mass^2)	16	3089.4	18.9	0.000
12	p (∼sex × rain)	17	3089.5	19.1	0.000
Survival					
1	Φ (∼fire × linear trend)	16	3059.9	0.0	0.865
2	Φ (∼fire × year)	16	3064.1	4.2	0.110
3	Φ (∼fire + linear trend + sex + rain + mass + mass^2)	17	3067.2	7.3	0.023
4	Φ (∼fire × tsf + linear trend + sex + rain + mass + mass^2 + month + year)	23	3073.3	13.4	0.001
5	Φ (∼fire × tsf)	16	3076.2	16.3	0.000
6	Φ (∼linear trend)	10	3076.6	16.7	0.000
7	Φ (∼fire × month)	16	3076.7	16.9	0.000
8	Φ (∼year)	10	3077.2	17.3	0.000
9	Φ (∼rain + linear trend)	11	3078.5	18.6	0.000
10	Φ (∼fire)	12	3080.0	20.1	0.000
11	Φ (∼(mass + mass^2) × fire)	20	3081.3	21.4	0.000
12	Φ (∼fire + sex)	13	3081.7	21.8	0.000
13	Φ (∼mass + mass^2)	11	3081.7	21.8	0.000
14	Φ (∼fire + rain)	13	3081.8	21.9	0.000
15	Φ (∼pre.post)	10	3082.3	22.5	0.000
16	Φ (∼1)	9	3083.3	23.4	0.000
17	Φ (∼rain + mass + mass^2)	12	3083.5	23.6	0.000
18	Φ (∼month)	10	3084.5	24.6	0.000
19	Φ (∼rain)	10	3085.0	25.2	0.000
20	Φ (∼sex)	10	3085.1	25.2	0.000
21	Φ (∼fire × sex)	16	3087.5	27.6	0.000
Recruitment					
1	f (∼rain + (fire × tsf))	25	7469.8	0.0	0.835
2	f (∼fire × tsf)	24	7473.1	3.3	0.161
3	f (∼linear trend)	18	7481.0	11.2	0.003
4	f (∼year)	18	7483.2	13.4	0.001
5	f (∼fire × linear trend)	24	7487.9	18.0	0.000
6	f (∼year × fire)	24	7488.7	18.8	0.000
7	f (∼rain)	18	7506.7	36.9	0.000
8	f (∼month)	18	7507.0	37.2	0.000
9	f (∼1)	17	7507.0	37.2	0.000
10	f (∼fire)	20	7512.9	43.1	0.000

Notes: explanatory covariates used in candidate model sets include: fire, fire treatments; tsf, time since fire; pre.post, different between the first year and remaining five years when fire treatments were applied; sex, male and female; mass and mass^2, body mass and quadratic function; month, calendar month; year, July to May; rain, total rainfall between sampling occasions; linear trend, linear trend; 1, null model (constant). Symbols relate to structure of linear models: +, additive; ×, interaction.

Table D2. Summary of model-selection results for the brushtail possum in Kakadu National Park, tropical northern Australia. K is the number of parameters. AIC_c is Akaike's Information Criterion, corrected for small sample size. ΔAIC_c shows the difference between the model AIC_c and the lowest AIC_c out of the set of models. AIC_c weights (w_i) are the relative likelihood of model i (normalized to sum to 1). The bigger the delta the smaller the weight and the less plausible model i.

Number	Model	K	AIC_c	ΔAIC_c	w_i
Recapture					
1	p (~sex × fire)	22	1125.7	0.0	0.721
2	p (~rain + (fire × tsf))	23	1129.3	3.6	0.122
3	p (~fire + rain)	19	1129.7	4.0	0.101
4	p (~fire × rain)	22	1131.0	5.3	0.053
5	p (~fire × linear trend)	22	1136.9	11.2	0.003
6	p (~fire)	18	1138.9	13.2	0.001
7	p (~fire × tsf)	22	1140.3	14.6	0.001
8	p (~linear trend)	16	1150.6	24.9	0.000
9	p (~sex × (mass + mass^2))	20	1154.3	28.6	0.000
10	p (~rain)	16	1154.8	29.1	0.000
11	p (~sex × rain)	18	1156.7	31.0	0.000
12	p (~mass + mass^2)	17	1157.5	31.8	0.000
13	p (~1)	15	1162.1	36.4	0.000
14	p (~sex)	16	1163.4	37.7	0.000
Survival					
1	Φ (~rain)	10	1117.7	0.0	0.207
2	Φ (~fire + rain)	13	1118.7	1.0	0.124
3	Φ (~rain + mass + mass^2)	12	1118.9	1.2	0.112
4	Φ (~1)	9	1119.2	1.5	0.094
5	Φ (~rain × fire)	16	1119.3	1.6	0.089
6	Φ (~fire)	12	1119.4	1.7	0.088
7	Φ (~sex + rain)	11	1119.8	2.1	0.072
8	Φ (~mass + mass^2)	11	1120.8	3.1	0.043
9	Φ (~linear trend)	10	1121.3	3.6	0.034
10	Φ (~sex)	10	1121.3	3.6	0.033
11	Φ (~fire + sex)	13	1121.3	3.6	0.033
12	Φ (~(mass + mass^2) × fire)	20	1122.6	4.9	0.017
13	Φ (~sex + linear trend)	11	1123.4	5.7	0.012
14	Φ (~fire × pre.post)	15	1123.4	5.7	0.011
15	Φ (~fire × sex)	16	1123.9	6.2	0.009
16	Φ (~rain + (fire × tsf))	17	1124.2	6.5	0.008
17	Φ (~fire × tsf)	16	1124.3	6.6	0.007
18	Φ (~fire × linear trend)	16	1125.2	7.5	0.005
Recruitment					
1	f (~pre.post)	12	2959.2	0.0	0.484
2	f (~year × fire)	18	2960.6	1.4	0.237
3	f (~fire × linear trend)	18	2961.9	2.7	0.123
4	f (~fire × pre.post)	17	2962.9	3.7	0.076
5	f (~fire)	14	2964.3	5.1	0.037
6	f (~fire × tsf)	18	2965.6	6.4	0.019
7	f (~rain + (fire × tsf))	19	2965.9	6.7	0.016
8	f (~rain × fire)	18	2967.5	8.3	0.008
9	f (~rain × year)	14	2973.4	14.2	0.000
10	f (~month)	12	2975.4	16.1	0.000
11	f (~1)	11	2978.4	19.2	0.000
12	f (~year)	12	2979.6	20.4	0.000
13	f (~linear trend)	12	2979.8	20.6	0.000

Notes: See Table D1 for explanation of model terms.

Table D3. Summary of model-selection results for the northern quoll in Kakadu National Park, tropical northern Australia. K is the number of parameters. AIC$_c$ is Akaike's Information Criterion, corrected for small sample size. ΔAIC$_c$ shows the difference between the model AIC$_c$ and the lowest AIC$_c$ out of the set of models. AIC$_c$ weights (w_i) are the relative likelihood of model i (normalized to sum to 1). The bigger the delta the smaller the weight and the less plausible model i

Number	Model	K	QAIC$_c$	ΔQAICc	w_i
Recapture					
1	p (∼month)	18	4574.2	0.0	0.180
2	p (∼sex × fire)	24	4574.2	0.0	0.180
3	p (∼fire × (mass + mass^2))	28	4574.7	0.5	0.138
4	p (∼fire + rain)	21	4574.8	0.6	0.133
5	p (∼fire)	20	4575.4	1.2	0.098
6	p (∼fire × rain)	24	4575.4	1.2	0.098
7	p (∼month × sex)	20	4576.0	1.7	0.075
8	p (∼rain)	18	4578.7	4.5	0.019
9	p (∼year × fire)	24	4579.1	4.9	0.016
10	p (∼sex × rain)	20	4579.4	5.2	0.013
11	p (∼rain + (fire × tsf))	25	4579.5	5.3	0.013
12	p (∼fire × tsf)	24	4580.2	5.9	0.009
13	p (∼fire × linear trend)	24	4580.5	6.2	0.008
14	p (∼1)	17	4580.6	6.4	0.007
15	p (∼year)	18	4582.1	7.8	0.004
16	p (∼sex)	18	4582.3	8.0	0.003
17	p (∼linear trend)	18	4582.7	8.5	0.003
18	p (∼sex × (mass + mass^2))	22	4583.0	8.7	0.002
19	p (∼mass + mass^2)	19	4584.8	10.6	0.001
Survival					
1	Φ (∼sex × month)	6	4559.3	0.0	0.637
2	Φ (∼(sex × month) + linear trend)	7	4561.2	1.9	0.253
3	Φ (∼(sex × month) + fire)	9	4564.6	5.3	0.046
4	Φ (∼sex)	4	4565.7	6.4	0.026
5	Φ (∼sex + rain)	5	4567.3	8.0	0.012
6	Φ (∼sex + linear trend)	5	4567.3	8.0	0.012
7	Φ (∼fire × sex)	10	4569.5	10.3	0.004
8	Φ (∼sex + (tsf × fire))	11	4570.3	11.0	0.003
9	Φ (∼fire + sex)	7	4570.8	11.5	0.002
10	Φ (∼month)	4	4572.5	13.2	0.001
11	Φ (∼mass + mass^2)	5	4572.7	13.4	0.001
12	Φ (∼1)	3	4572.8	13.5	0.001
13	Φ (∼fire × pre.post)	8	4573.3	14.1	0.001
14	Φ (∼(mass + mass^2) × fire)	14	4573.9	14.6	0.000
15	Φ (∼fire × tsf + pre.post + linear trend + rain + sex + mass + mass^2 + year + month)	18	4574.2	14.9	0.000
16	Φ (∼year)	4	4574.3	15.0	0.000
17	Φ (∼linear trend)	4	4574.5	15.2	0.000
18	Φ (∼rain + mass + mass^2)	6	4574.7	15.4	0.000
19	Φ (∼rain)	4	4574.8	15.5	0.000
20	Φ (∼fire)	6	4577.4	18.1	0.000
21	Φ (∼fire × tsf)	10	4578.3	19.0	0.000
22	Φ (∼fire × linear trend)	10	4578.3	19.1	0.000
23	Φ (∼fire × year)	10	4578.4	19.1	0.000
24	Φ (∼fire + rain)	7	4579.4	20.1	0.000
25	Φ (∼rain + (fire × tsf))	11	4580.3	21.0	0.000
26	Φ (∼rain × fire)	10	4580.3	21.0	0.000
Recruitment					
1	f (∼fire)	8	171723.6	0.0	0.651
2	f (∼fire + rain)	9	171725.6	2.0	0.240
3	f (∼fire × tsf)	12	171728.6	5.0	0.053
4	f (∼fire × year)	12	171730.3	6.7	0.024
5	f (∼rain × fire)	12	171731.5	7.9	0.013
6	f (∼month × fire)	13	171732.3	8.7	0.009
7	f (∼rain + (fire × tsf))	14	171732.8	9.2	0.007
8	f (∼fire × linear trend)	14	171734.6	11.0	0.003
9	f (∼month)	6	171738.4	14.8	0.000
10	f (∼linear trend)	6	171739.4	15.8	0.000
11	f (∼pre.post)	6	171739.6	16.1	0.000
12	f (∼rain)	6	171740.0	16.4	0.000
13	f (∼1)	6	171740.1	16.5	0.000

Table D3. Continued.

Number	Model	K	QAIC$_c$	ΔQAICc	w_i
14	f (~year + rain)	8	171743.7	20.1	0.000
15	f (~year)	8	171743.8	20.2	0.000

Notes: See Table D1 for an explanation of model terms.

Table D4. Summary of model-selection results for grassland melomys in Kakadu National Park, tropical northern Australia. K is the number of parameters. AIC$_c$ is Akaike's Information Criterion, corrected for small sample size. ΔAIC$_c$ shows the difference between the model AIC$_c$ and the lowest AIC$_c$ out of the set of models. AIC$_c$ weights (w_i) are the relative likelihood of model i (normalized to sum to 1). The bigger the delta the smaller the weight and the less plausible model i.

Number	Model	K	AIC$_c$	ΔAIC$_c$	w_i
Recapture					
1	p (~1)	13	397.0	0.0	0.243
2	p (~pre.post)	14	397.5	0.5	0.184
3	p (~mass + mass^2)	15	398.7	1.7	0.103
4	p (~rain)	14	399.0	2.0	0.088
5	p (~linear trend)	14	399.1	2.1	0.084
6	p (~sex)	14	399.1	2.1	0.084
7	p (~sex × fire)	19	399.6	2.5	0.067
8	p (~fire)	16	399.9	2.8	0.058
9	p (~fire × (mass + mass^2)	23	400.5	3.5	0.042
10	p (~fire + rain)	17	401.4	4.3	0.027
11	p (~sex × rain)	16	403.3	6.3	0.010
12	p (~sex × (mass + mass^2)	18	405.2	8.2	0.004
13	p (~month × fire)	20	406.7	9.7	0.002
14	p (~fire × linear trend)	20	406.8	9.8	0.002
15	p (~fire × rain)	20	407.6	10.6	0.001
Survival					
1	Φ (~(mass + mass^2) × fire)	13	382.8	0.0	0.722
2	Φ (~mass + mass^2)	4	387.4	4.6	0.074
3	Φ (~rain + (mass + mass^2))	5	388.1	5.3	0.052
4	Φ (~fire × sex)	8	388.7	5.9	0.038
5	Φ (~(mass + mass^2) + fire)	7	389.0	6.2	0.033
6	Φ (~fire)	5	391.0	8.2	0.012
7	Φ (~1)	2	391.3	8.5	0.011
8	Φ (~fire + sex)	6	391.5	8.7	0.010
9	Φ (~fire + rain)	6	391.5	8.7	0.009
10	Φ (~rain)	3	391.8	9.0	0.008
11	Φ (~sex)	3	392.1	9.3	0.007
12	Φ (~pre.post)	3	392.7	9.9	0.005
13	Φ (~sex + rain)	4	392.7	9.9	0.005
14	Φ (~linear trend)	3	393.0	10.2	0.005
15	Φ (~fire × pre.post)	7	393.5	10.7	0.004
16	Φ (~sex + linear trend)	4	393.7	11.0	0.003
17	Φ (~rain × fire)	9	396.5	13.7	0.001
18	Φ (~fire + pre.post + linear trend + rain + sex + mass + mass^2 + year + month)	13	397.0	14.2	0.001
19	Φ (~fire × linear trend)	9	397.9	15.1	0.000
Recruitment					
1	f (~fire × month)	17	2084.4	0.0	0.862
2	f (~month)	11	2088.1	3.7	0.137
3	f (~year + rain)	12	2100.0	15.6	0.000
4	f (~rain × fire)	17	2111.7	27.4	0.000
5	f (~fire + rain)	14	2112.3	27.9	0.000
6	f (~linear trend)	11	2114.3	29.9	0.000
7	f (~rain)	11	2114.5	30.1	0.000
8	f (~fire × linear trend)	17	2114.6	30.2	0.000
9	f (~fire × year)	17	2115.3	30.9	0.000
10	f (~year)	11	2115.3	30.9	0.000
11	f (~sex + rain)	12	2115.8	31.4	0.000
12	f (~1)	10	2125.8	41.4	0.000
13	f (~fire)	13	2126.0	41.6	0.000
14	f (~fire × pre.post)	16	2128.8	44.4	0.000

Notes: See Table D1 for an explanation of model terms.