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How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model

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ABSTRACT

Species with strong preferences for early or late successional stages after fire may be extinction prone under current fire regimes. However, the extent of specialisation to time since fire is poorly understood, and, for reptiles, succession models for predicting responses are in the development phase. In this study we tested predictions of a reptile succession model, and identified species that may be fire specialists. Reptiles were sampled in five burnt and unburnt mallee *Eucalyptus* woodlands, Australia. Two, 400 m transects within each burn treatment were sampled using 11 pairs of pitfall-traps that were opened for five weeks over two summers. A habitat accommodation model of succession that was previously developed for mallee reptiles correctly predicted the observed responses of three of 16 common reptile species. A further four species showed non-significant trends in the predicted direction. However, eight other species showed unexpected responses. One species showed a strong interaction between burn age and location, requiring a two-dimensional successional model in contrast with the usual linear models explaining reptile responses to fire. One third of common species were not affected by fire and so may not have increased risks of extinction due to the fire suppression/incineration cycle. However, approximately half to two-thirds of common reptiles did have a fire response, so the risk of deterministic extinction in small fragments may be substantial. Further model development is needed to better predict fire responses and to assist the design of fire mosaics that can accommodate early and late successional fire specialists.

1. Introduction

Species that have specialist habitat requirements may be particularly vulnerable to extinction in fragmented landscapes (Fischer and Stocklin, 1997; Kolb and Diekmann, 2005). Specialising on a particular post-fire successional stage is one mechanism that may lead to a heightened risk of extinction. A single fire could burn the entire remnant, removing any long-unburnt habitat and placing late-successional specialists at risk of local extinction (Gandhi et al., 2001; Woinarski et al., 2004). However, fire suppression is common in many human-dominated landscapes, and it may be the early successional species that are most vulnerable to extinction in small remnants (Gibb and Hochuli, 2002; Hobbs, 2003). Cycles

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of fire exclusion for decades followed by complete incineration of a patch have the potential to eliminate early and late-successional species. To understand the magnitude of the threat to wildlife of the fire exclusion/incineration cycle, the number of fire specialists, species dependent on a particular post-fire period, needs to be established.

General patterns of how fauna respond during post-fire succession have been explored (Andersen, 1991; Fox et al., 2003; Friend and Wayne, 2003). For reptiles, most authors report patterns consistent with Fox's (1982) habitat accommodation model of succession, where the reptile community follows a predictable sequence based on the recovery of vegetation structure after fire (Mushinsky, 1985, 1992; Greenberg et al., 1994; Taylor and Fox, 2001a, b; Letnic et al., 2004). A detailed habitat accommodation model for reptiles was described by Caughley (1985) using a fire chronosequence in mallee *Eucalyptus* woodlands, Australia. Caughley (1985) identified three distinct fire responses (Fig. 1), showing that burrowing species are most common in recently burned sites, species that shelter in *Triodia*, a prickly clumping grass (Rice and Westoby, 1999), are most abundant after six years when *Triodia* recovers, but the litter dwelling species do not peak until 25 years after fire, when the leaf litter layer is well established. The responses reported by Caughley and others (Cogger, 1984; Woinarski, 1989; Schlesinger et al., 1997) imply that many reptile species may be fire specialists in Australian mallee communities.

Although there is ample evidence that fire can have a large effect on reptile community composition (Bradstock and Cohn 2002), there is growing evidence that fire has only a secondary influence compared with other processes (Cavitt, 2000; Bamford and Roberts, 2003). For example, in tropical woodlands of northern Australia, Trainor and Woinarski (1994) found that a moisture gradient had the dominant effect on reptile community composition, not fire. For reptiles in Australia's arid and semi-arid areas, there is a strong distinction between communities on sandy soils with *Triodia* species compared with communities on clay soils without *Triodia* (Cogger, 1984; Pianka, 1996; Driscoll, 2004). Furthermore, arid-zone reptiles can show strong responses to the amount of rainfall (James, 1991) or grazing (James, 2003; Driscoll, 2004). It is therefore uncertain whether a majority of reptile species should show strong responses to fire, or whether fire effects will be over-ridden by other local ecological processes.

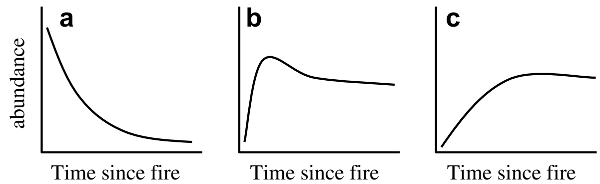

Fig. 1 – Three reptile succession trajectories after fire, based on Caughley's (1985) observed responses. (a) burrowing species that forage in open areas are most abundant after a fire then decline; (b) *Triodia* spp. specialist species decline after the fire but recover over approximately six years as *Triodia* re-grows and (c) leaf-litter specialists recover over approximately 25 years because leaf litter is slow to accumulate after fire.

In this study, we use a large-scale replicated natural experiment to test predictions about the abundance of species in early and late successional habitat that arise from Caughley's (1985) succession model. Replicated studies of animal responses to fire regimes are a major research gap (Whelan et al., 2002) and remain a research priority in fire-prone communities (Greenberg, 2000; Bradstock and Cohn, 2002; Parr and Chown, 2003; Bury, 2004). We also aim to ascertain the proportion of reptile species that are fire specialists with a preference for early or late successional habitat. These species may be vulnerable to decline in the absence of appropriate fire regimes.

2. Methods

2.1. Study area

Mallee communities are open woodlands with low, multi-stemmed *Eucalyptus* species (Specht, 1971). Mallee vegetation covered 383,000 square kilometers of Australia but 35% of that has been cleared (Australian Native Vegetation Assessment, 2001). On the Eyre Peninsula, South Australia, 56% of the landscape has been cleared, mostly before 1939, leaving a small number of very large mallee reserves, and many small remnants (Australian Native Vegetation Assessment, 2001; State of the Environment Report, 2003) (Fig. 2).

Mallee on the Eyre Peninsula is dominated by *Eucalyptus incrassata*, *E. brachycalyx*, *E. socialis* and other *Eucalyptus* species, with a shrubby understorey including *Melaleuca uncinata*, *Baeckea crassifolia*, *Phebalium bullatum*, *Callitris verrucosa* and spinifex (*Triodia irritans*), a sharply spined clumping grass (Specht, 1971; Robinson and Heard, 1985). The mallee regions of the Eyre Peninsula include extensive regions of parabolic and longitudinal dunes overlying solid limestone calcrete (Twidale and Campbell, 1985). There is a mediterranean climate with annual rainfall ranging from approximately 300 mm near Pinkawillinie to 400 mm near Hincks Conservation Parks (Schwerdtfeger, 1985). Although mallee is extremely flammable, it is regarded as frequently burnt if there is more than one fire in fifteen years (Bradstock and Cohn, 2002).

2.2. Survey design

At each of five locations, two sites were placed in a recently burnt area and two sites in an adjacent long-unburnt area. All burnt areas were the result of hot wildfires ignited by lightning or farm machinery. The long unburnt sites were all greater than 18 years old at the beginning of the study, and the recently burnt sites were between three and seven years old (Table 1). Caughley's (1985) model makes predictions about the relative abundance of species with particular ecological traits in early and late successional habitat. Using replicate fires in two age categories it is therefore possible to statistically test the model predictions.

Each of the four sites was sampled using 11 pitfall trap stations spaced at 40 m intervals along a 400 m transect. Sites were positioned so that they were at least 200 m from a fire