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Longer-term responses of a floodplain-dwelling marsupial to experimental manipulation of fallen timber loads

Ralph Mac Nally*, Gregory Horrocks

Australian Centre for Biodiversity: Analysis, Policy and Management, School of Biological Sciences, Monash University, Melbourne 3800, Australia

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Summary

Fallen timber is an important component of many aquatic and terrestrial ecosystems around much of the world. Its distribution and abundance has been extensively altered, especially over the past 200 years. While correlative evidence suggests that many species require fallen timber for them to occupy locations, there are few precisely controlled field experiments that show conclusively how species respond to variation in loads. We manipulated wood loads (ranging from 0 to 80 Mg ha^{-1}) and monitored the response over 6 years of a species of marsupial, the yellow-footed antechinus *Antechinus flavipes*. The antechinus appeared to prefer locations having fallen-timber loads $\geqslant$20 Mg ha^{-1}. Antechinuses avoided bare areas (i.e. 0 Mg ha^{-1}) and areas having finer forms of woody material. Changes in densities of the antechinus in excess of those occurring in the control plots were clear after 2 years following manipulation of loads, and were even more pronounced after almost 6 years. Therefore, we are confident that higher loads are favoured by the antechinuses. There was no evidence of breeding success by females in sites with $\leqslant$20 Mg ha^{-1}, and that the highest, consistent breeding activity was achieved at sites with the greatest fallen-timber loads (80 Mg ha^{-1}). Our results, which experimentally were designed to address responses to fallen-timber loads, were complicated by perturbations caused by managed flooding episodes of the experimental area. Flooding appears to lead to population booms of the antechinus, most probably related to irruptions of prey species such as carabid beetles and wolf spiders, which are large-bodied and are prey for the antechinus. Nevertheless, we show that there are differences in densities in different wood-load treatments even against a background of boom-and-bust dynamics associated with flooding.

Zusammenfassung

Stammtotholz ist eine wichtige Komponente in vielen aquatischen und terrestrischen Ökosystemen. Seine Verteilung und Menge sind, insbesondere während der letzten 200 Jahre, beträchtlich verändert worden. Während korrelative Ansätze nahelegen, daß viele Arten Totholz benötigen, um bestimmte Örtlichkeiten zu besiedeln, gibt es nur wenige kontrollierte Experimente, die belegen, wie einzelne Arten auf variable Totholzmengen reagieren. Wir manupulierten die Stammtotholzmengen (0 bis 80 t/ha) und beobachteten sechs Jahre lang die Reaktion einer Beuteltierart, der Gelbfuß-Beutelmaus *Antechinus flavipes*. Die Beutelmaus schien Flächen mit mehr als 20 t Totholz/ha zu bevorzugen und mied Flächen ohne Stammtotholz und solche mit feinerem Totholzmaterial. Die Erhöhung der Beutelmausdichten gegenüber Kontrollflächen war zwei Jahre nach der Totholzmanipulation klar erkennbar und noch deutlicher nach fast sechs Jahren. Wir sind deshalb sicher, daß höhere Totholzmengen von den Beutelmäusen bevorzugt werden.

*Corresponding author. Tel.: +61 3 9905 5642; fax: +61 3 9905 5613.
E-mail address: Ralph.MacNally@sci.monash.edu.au (R. Mac Nally).

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Es gab keine Anzeichen für erfolgreiche Reproduktion der Weibchen in den Gebieten mit weniger als 20 t/ha, aber dafür, daß die höchste Reproduktionsaktivität auf Flächen mit der größten Totholzmenge (80 t/ha) erreicht wurde. Unsere Ergebnisse, die die Reaktion auf Totholzmengen erfassen sollten, wurden durch Störungen verkompliziert, die auf geplante Flutungsereignisse zurückzuführen waren. Überflutung scheint zu Populationszunahmen zu führen, die höchstwahrscheinlich auf das Eindringen von großen Beutetieren der Beutelmaus, Laufkäfern und Wolfspinnen, zurückzuführen sind. Nichtsdestotrotz zeigen wir, daß es Dichteunterschiede zwischen den Totholzvarianten gibt, selbst vor dem Hintergrund einer stark flukturierenden Populationsdynamik.

Keywords: *Antechinus flavipes*; Environmental water allocations; *Eucalyptus camaldulensis*; Habitat manipulations; Logs; River red gum; Woody debris; Yellow-footed antechinus

Introduction

While habitat loss has been identified as the major ongoing threat to biodiversity sustainability around the world (Sala et al., 2000), reduction in habitat quality often is an insidious ally that affects the capacity of species to persist in whatever remnant habitats exist (Saunders, Hobbs, & Margules, 1991; Tomialojć & Wesolowski, 2004). Extent of remnant habitat is relatively straightforward to characterize, but habitat quality is much more difficult to assess because many attributes contribute to the utility of a given place for different species (Smyth, Mac Nally, & Lamb, 2002). That is, any one location has many attributes and different species respond in disparate ways to the state or nature of those attributes. Habitat suitability assessment, often done through statistical modelling, of which there is an immense literature (see for e.g. Scott et al., 2002), largely is correlative (e.g. Luck, 2002). There are relatively few experimental demonstrations of the actual dependence of individual species on habitat structure in a general sense (i.e. many concurrent habitat features) or in relation to specific habitat attributes, such as availability of tree hollows (Gibbons, Lindenmayer, Barry, & Tanton, 2002). There also are few demonstrations, to our knowledge, of differential reproductive performance associated with experimental manipulations of habitat characteristics. A major problem with the experimental analysis of the significance of habitat attributes is the difficulty in constructing and maintaining different configurations of habitat elements in different treatments.

One of the most precisely manipulable habitat elements is fallen timber. There has been an extensive amount of work on its manipulation in freshwater systems (e.g. Brooks, Gehrke, Jansen, & Abbe, 2004; Everett & Ruiz, 1993; Giannico, 2000) and in forests (e.g. Loeb, 1999; Lohr, Gauthreaux, & Kilgo, 2002). Knowledge of species' dependence on fallen timber is of great conservation significance because extensive harvesting (Mac Nally, Parkinson, Horrocks, & Young, 2002; Woldendorp & Kennan, 2005) and maintenance of many forests in a relatively immature state (Mac Nally, Bennett, & Horrocks, 2000) mean that there has been a widespread diminution of fallen-timber loads in many areas of the world (Clark, Clark, Brown, Oberbauer, & Veldkamp, 2002; Gower, 2003). While there have been experiments with fallen timber, there has been little exploration of the amounts needed for persistence (i.e. a graded series of loads rather than just "high" vs "low") or of the longer-term patterns of responses.

Here we report on the dynamics and responses of a small (males $\leqslant$80 g, females $\leqslant$60 g), invertebrate-eating marsupial, the yellow-footed antechinus, *Antechinus flavipes*, to experimental manipulations of fallen-timber loads in a floodplain forest in central Victoria, Australia. The yellow-footed antechinus generally is the only native small mammal in the extensive floodplain systems of the Murray River and its main tributaries (Mac Nally, Parkinson, Horrocks, Conole, & Tzaros, 2001). There are a few exotic small mammals (e.g. *Mus musculus*, *Rattus rattus*). While not restricted to floodplains, *A. flavipes* generally is more abundant in floodplain forests than in drier woodlands (H. Lada, R. Mac Nally and A. C. Taylor, unpublished data).

We have provided a preliminary report on the effects of wood-load variation on densities of the antechinus (Mac Nally & Horrocks, 2002), but the current study is important for two main reasons. First, we extend the post-experimental monitoring period from 2 to 6 years. There has been concern about the generally brief timespan of many ecological studies (e.g. Franklin, 1989) and the current work allows us to assess whether these initial responses were transient. Second, we describe differences in reproductive output associated with wood-load variation. Species of the genus are characterized by the phenomenon of male "die-off" following breeding (Mills & Bencini, 2000; Watt, 1997; Woolley, 1966), so populations consist of impregnated or lactating females for part of the year. Females also produce very underdeveloped young, which are suckled while in the marsupium (pouch). This allows one to register levels of reproductive activity of females as well as differences in density among fallen-timber loads. Given that persistence is tightly coupled to reproductive