Habitat change and restoration: responses of a forest–floor mammal species to manipulations of fallen timber in floodplain forests

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Mac Nally, R. & Horrocks, G., 2002. Habitat change and restoration: responses of a forest–floor mammal species to manipulations of fallen timber in floodplain forests. *Animal Biodiversity and Conservation*, 25.1: 41–52.

Abstract
Habitat change and restoration: responses of a forest–floor mammal species to manipulations of fallen timber in floodplain forests.— In forests and woodlands, fallen timber (logs and large branches) is an important habitat element for many species of animals. Fallen timber has been systematically stripped in many forests, eliminating an important structural element. This study describes results of a "meso–scale" experiment in which fallen timber was manipulated in a floodplain forest of the Murray River in south–eastern Australia. A thousand tons of wood were redistributed after one–year's pre–manipulation monitoring, while a further two–year's post–manipulation monitoring was conducted. The response of the main forest–floor small–mammal species, the Yellow–footed Antechinus *Antechinus flavipes*, to alterations of fallen–wood loads is documented. Results of the experiment will help to frame guidelines for fallen–timber management in these extensive floodplain forests.

Key words: Australia, Bayesian analyses, *Eucalyptus camaldulensis*, River Red Gum, Yellow–footed Antechinus.

Resumen
Cambio y restauración del hábitat: respuestas de una especie de mamíferos del suelo forestal a las manipulaciones de los árboles caídos en bosques inundados.— En los bosques y montes los árboles caídos (troncos y ramas gruesas) constituyen un importante elemento del hábitat para muchas especies de animales. Los árboles caídos han sido sistemáticamente descortezados en muchos bosques, eliminándose así un importante elemento estructural. Este estudio describe resultados de un experimento a escala mediana en el que los árboles caídos fueron manipulados en un bosque inundado del río Murray, en el sureste de Australia. Se redistribuyeron 1.000 toneladas de madera después de efectuar un control previo a la manipulación durante un año, realizándose otro control durante dos años después de la manipulación. Se documenta la respuesta de la especie de mamífero del suelo del bosque, el ratón marsupial de pies amarillos *Antechinus flavipes*, a las alteraciones de la madera caída. Los resultados de este trabajo pueden servir de ayuda para elaborar unas directrices marco para la gestión de los árboles caídos en bosques inundados.

Palabras clave: Australia, Análisis bayesiano, *Eucalyptus camaldulensis,* Eucalipto rojo, Ratón marsupial de pies amarillos.

(Received: 2 IV 02; Final acceptance: 7 V 02)

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ISSN: 1578–665X

Introduction

Ecologists and wildlife managers for many years have developed models linking occurrence of individual taxa to habitat characteristics (WIENS, 1989; MORRISON et al., 1998; KNIGHT & FOX, 2000; SCOTT et al., 2002). There is a general consensus that complex habitats with much "structure" offer opportunities for more species to persist locally through greater numbers of resource-exploitation opportunities (HUSTON, 1994; ROSENZWEIG, 1995; ORROCK et al., 2000) and the amelioration of the intensity of interspecific interactions, such as predation (SODERSTROM et al., 1998; CROOK & ROBERTSON, 1999; SONG & HANNON, 1999; LABBE & FAUSCH, 2000).

Human activities, especially over the past 500–700 years, have restructured habitats, and thus, perturbed related ecological processes. Anthropogenic habitat change very often has led to the simplification of habitats, such as reduced seral diversity, modified vegetation layering (often eliminating certain layers such as shrubs), changes in water flows and flooding in rivers, and so on (FORMAN, 1995). Recently, there have been developments in some countries to begin rehabilitation and restoration of habitats to address sharp drops in local biodiversity and deleterious changes in ecological functioning. In terrestrial systems, it is often difficult to quickly restore habitat structure because natural vegetation needs time to regrow, and some important elements, such as tree–hollows, may take decades to become established (BENNETT et al., 1994). Thus, not only is it challenging to accurately quantify the "amount" of restoration being done, but the long timeframes involved make it hard to assess whether the restoration actions have been successful (HOBBS & NORTON, 1996; LAKE, 2001).

One element of many terrestrial habitats that is comparatively easy to restore quantitatively is fallen wood (or large/coarse woody debris). Stripping fallen timber from forests, woodlands and rivers has been a major human activity and cause of ecological change in much of the world (MASER & SEDELL, 1994). Restoration of fallen timber in rivers, often called "snags", has been an important management issue for some time in many western countries because both the ecological and hydrological benefits of wood in rivers and streams have begun to be appreciated (GURNELL & GREGORY, 1995; WARD & STANFORD, 1995; CROOK & ROBERTSON, 1999; RHEINHARDT et al., 1999; GERHARD & REICH, 2000). However, restoration of fallen timber has rarely been undertaken in forests and woodlands, yet the ecological impacts of fallen–timber loss may be just as important (HARMON et al., 1986; MAC NALLY et al., 2001). There has been some recognition recently of the importance of fallen timber for biodiversity management in terrestrial systems, with specific guidelines having been written for some species (e.g. GARNETT & CROWLEY, 2000).

In south–eastern Australia, the extensive Murray–Darling Basin (1.06 x 10^6 km^2) has been greatly altered since Europeans colonized the continent in 1788 (CRABB, 1997). Apart from major changes in flow levels and flow regimes in the rivers (LAKE, 1995), a staggering number of trees (ca 10^{10} trees, WALKER et al., 1993) has been lost to facilitate wheat and sheep farming. Loss of the evapo-transpirational action of so many trees has allowed the ground–water table to rise, and, combined with the high salt loads in the lower soil strata, has led to dryland salinity emerging as the pre–eminent environmental problem facing southern Australia (CRABB, 1997). Massive tree loss also means a reduction in the potential source of fallen timber for forests and woodlands.

The River Red Gum *Eucalyptus camaldulensis* Dehnhardt, 1832 is one of the most characteristic Australian trees, dominating most watercourse margins and floodplains across the inland of the continent (BOLAND et al., 1984). It is thought that the forests typically used to consist of very large (4 m DBH trunks), spreading adult trees, widely separated from one–another. Germination is inundation–dependent, with characteristic "lines" of seedlings and saplings forming along margins of flooded areas at which waters remained for some months (CHESTERFIELD, 1986; BREN, 1988). The durability of its timber has rendered the River Red Gum an important tree for many purposes, such as its use for fencing posts and house stumps, while it has also been used extensively for domestic firewood and to fuel the paddle–steamer traffic along the Murray and Darling rivers, especially in the nineteenth century. There is a tremendous attrition of River Red Gum timber. In public–land forests of the Murray–Darling Basin alone, ca 1.15 x 10^5 t of firewood and ca 1.22 x 10^5 t of timber (including wood chips) are legally removed annually (CRABB, 1997). The forests also have been much diminished in total area owing to the fertility and moisture of the floodplains, which attracted agricultural exploitation (PARKINSON & MAC NALLY, 2000). These are the main reasons for the great changes in habitats of the floodplains of the Murray–Darling Basin since European settlement. The average current fallen–timber load is just 20 t/ha in lowland floodplains of the Murray River and its major tributaries, perhaps just 10–15% of pre–settlement loads (MAC NALLY et al., in press a).

This paper describes results of a "meso–scale" manipulation of fallen timber in River Red Gum floodplain forests at a site in northern Victoria, Australia. An outline of the experimental design is provided by MAC NALLY (2001). In short, the experiment involved the setting up of 34 one–hectare experimental plots, the conduct of pre–manipulation biodiversity surveys, the movement of ca 1000 t of fallen timber to construct eight treatments of differing fallen–timber loads, and subsequent monitoring of the effects of the experiment over two further years.

The numerical responses of the only native small mammal of the forest floors of River Red Gum floodplain forests, the Yellow–footed Antechinus *Antechinus flavipes* (Waterhouse, 1838) are described. Antechinuses are small, predominantly terrestrial, carnivorous marsupials (Phascogalinae, family Dasyuridae; ARMSTRONG et al., 1998) that consume invertebrates and occasionally small reptiles such as skinks (STATHAM, 1982; MENKHORST, 1995; LUNNEY et al., 2001). Yellow–footed Antechinuses can grow to over 100 mm and weigh over 70 g (STRAHAN, 1983; SMITH, 1984) although animals from this study were generally smaller (ca 35 g females, 42 g males). Almost all male antechinuses die following a short breeding season, leaving the habitats to the females and young (LEE & COCKBURN, 1985; WATT, 1997; LEUNG, 1999). Female antechinuses are seasonally monoestrus, producing a single litter annually. The timing of this yearly breeding season is highly synchronous in all antechinuses with the gestation and weaning period lasting 5–7 wk (COCKBURN, 1992; WOOLLEY, 1996). In Victoria, Australia, the species occurs from the south–west coast to Wodonga in the north–east extending into the Murray River floodplains. While the Yellow–footed Antechinus is generally uncommon (MENKHORST, 1995) it is not threatened and, indeed, is the most widespread of all antechinuses (STRAHAN, 1983). Nevertheless, the Yellow–footed Antechinus is the only, or predominant, native small–mammal in the floodplain forests of south–eastern Australia (MAC NALLY et al., 2001). Thus, it is a highly significant animal within these habitats ecologically and is likely to have a profound impact on the invertebrates occupying the River Red Gum floodplain forests (BALLINGER & YEN, in press) given the high metabolic rates and activity levels of species in this genus (KORTNER & GEISER, 1995; WESTMAN et al., 2002).

The objectives of this experiment are (1) to test whether these small mammals respond to a manipulation of a potentially important habitat–structural element in a way that is expected given our survey results (MAC NALLY et al., 2001), and (2), to discriminate experimentally among different wood–loads if responses do differ among treatments. In other words, how much fallen timber is desirable to support the on–going presence and reproductive success of this (and other) native species? Results of such experiments add weight to ecological and biodiversity considerations when guidelines for natural–resource management are framed, with much greater inferential support being attached to replicated field experiments than to observational programs "per se" (SIT & TAYLOR, 1998, Chapter 3).

Methods

Study area

The experiment was conducted on Gunbower Island (35°42'23"S 144°12'13"E), a 20,000 ha, Ramsar–listed wetland, which lies between the Murray River and Gunbower Creek near Cohuna, in north–central Victoria, Australia. The island formerly flooded almost every year, but with more extreme water extractions and flow regulation, flooding is much rarer now (CRABB, 1997). Gunbower Island is intensively exploited for firewood and post and railway–sleeper production, so silviculture and wood management are critical issues for preserving biodiversity in these forests.

Experimental design

A total of 341 ha plots were marked out. Wood–load measurements (average 27 t/ha) and habitat–structural ordinations were conducted prior to manipulation. The plots were located along three tracks in Gunbower State Forest, Peter Creek Track, Wee Wee Rup Track, Garner Break Track, to facilitate access for monitoring and for machinery used in manipulation of wood loads.

The 34 plots were randomly allocated to eight treatments during the wood–moving operations. Five treatments corresponded to loads of 0 t/ha, 20 t/ha, 40 t/ha, 60 t/ha and 80 t/ha (designated 0L, 20L, 40L, 60L, 80L) of aged, fallen wood (≥ 10 cm diameter). On all of these plots, fallen timber already on the plots was disturbed so that all woody debris was dislodged from previous footings. For logistic reasons, wood was transferred to plots requiring supplementation from nearby plots needing clearance or reduction. Wood from non–experimental locations nearby also was used to build up loads on some high–density (viz. 60L and 80L) treatment plots. Two treatments were controls, one an "undisturbed" control (designated UC) where no equipment or persons traversed plots during wood–moving, and "disturbance" controls (designated DC). In the latter, all wood on the plot was pushed or moved to an extent that emulated the disturbance on the manipulated wood–load sites. The eighth treatment was the imposition of 40 t/ha of tree "crowns" onto plots (40H). The 40H treatment was deemed interesting because silvicultural practices often involve the felling of a red gum, removal of the bole for timber use, and the deposition of the crown for up to three years before harvesting the main branches for firewood. Thus, fallen timber in these production forests often is in the form of crowns. Existing timber was removed from these plots and fresh crowns deposited. There were four replicate plots for each treatment, apart from 0L, of which there were six. In all manipulated plots, timber was evenly distributed over the whole ha (100 m x 100 m). The middle 50 m x 50 m part of each plot was marked with metal stakes and formed the focus for mammal surveys (i.e. ensuring a "buffer" around the sampling area of 0.75 ha). A total of 1000 t of timber was repositioned during this operation, requiring eight persons for ten days, hydraulic tandem trailers, a bulldozer, semi–trailer and a log–harvesting machine (MAC NALLY, 2001). The timber was moved in late March 2000.

Small–mammal surveys. Sampling schedule

Our original plan was to conduct two survey rounds per annum for three years. The first survey in each year was scheduled to be in the post-breeding phase, usually before June, while the second survey round was to coincide with the breeding period, usually from September to December. The first two surveys (year 1) were to be prior to wood–load manipulations ("pre–impact" measurements), while the latter four (years 2 and 3) were to be after the experimental changes ("post–impact" measurements). Several changes were made to the schedule. First, the fourth round of surveys in late 2000 was to be conducted in October (breeding season) but forest–management staff introduced an "environmental flow" to supplement an earlier, small, natural flow to stimulate germination of River Red Gums, which inundated much of the study area for three months (October–December). This prevented surveys until early 2001. In the first survey of 2001 (January), there was a pronounced increase in densities of antechinuses (ca 10–fold), which prompted us to increase the survey rounds to five for 2001 (January, April, July, September, November). A survey was also performed in 2002 (January). Thus, there were nine survey rounds (each of 5 d), two of which were pre–impact and the remaining seven were post–impact.

Small–mammal surveys. Sampling method

At each of the 34 sites, 10 Type A Elliott box traps (33 x 10 x 9 cm) were set at 7 m intervals along the diagonal of the middle 50 m x 50 m part of each plot. To provide protection for animals, each trap contained cotton wadding and was placed inside an open plastic bag. The traps were baited with a mixture of peanut butter, rolled oats and honey and checked twice daily for a period of 5 d. Captured animals were identified, classified sexually and individually marked by using ear notching. Other survey methods, such as nocturnal spotlight searches, had previously been shown to be ineffective (MAC NALLY et al., 2001). Our trapping procedures were approved both by the university's Animal Ethics Committee and by the Victorian Department of Natural Resources and Environment.

Critical data

Four sets of data are analysed. The first three are measurements of captures of different individuals in each plot in each sampling period. One data set is for females, another for males and the third is the two combined. The fourth data set is the total numbers of individuals trapped on each plot in each survey period. Total trappings were regarded as an indicator of intensity of use of sites. Many individuals, especially breeding males, are very mobile and may be transient over 1 ha spatial scales (the size of our plots). Thus, total trappings, which include re–trappings of individual animals, may provide different information to total densities of individuals.

Analyses

The data consisted of an array of 34 sites by nine survey periods, two of which were before the manipulation and seven afterwards. A Bayesian–based Poisson model was employed to analyse these data. The method involves estimation of the joint posterior probability distribution of model parameters with the data (GELMAN et al., 1995). Most of the data were small, non–negative values (< 10), so the use of a "counts" distribution like the Poisson seemed reasonable. The model is:

$$Y_{j(i)k} \sim \text{Poisson}(\mu_{j(i)k})$$

$$\log(\mu_{j(i)k}) = \beta_i \delta_k \pi_{j(i)} + \alpha_i (1-\delta_k) \pi_{j(i)} + \sigma_j + \sigma_{jk}$$

$$\gamma_i = \alpha_i - \beta_i$$

The *Y*s are the observed numbers of the Yellow–footed Antechinus in plot *j* in survey *k*, with the *j*(*i*) indicating that site *j* belongs to treatment *i*. The *Y*s are assumed to be Poisson–distributed, random samples from variables with "true" population means μ. The βs model mean pre–manipulation densities in the eight treatments, while the αs perform the same role for post–manipulation densities. Thus, the difference between the αs and βs(γs) are the experimental effects of each treatment, and are, therefore, the most important parameters describing the impact of the experimental manipulations. The δ are 1 for pre–manipulation surveys and 0 for post–manipulation surveys. The πs are elements of a matrix that identify the site with its treatment. The σ_j are site random effects, while the σ_{jk} are site–repeated–survey random effects (BRESLOW & CLAYTON, 1993).

The WinBUGS Bayesian analysis program (version 1.3, SPIELGELHALTER et al., 2000) was used. WinBUGS uses the Metropolis–Hastings algorithm to construct the joint posterior distribution of the model parameters. Normal priors for the β and α coefficients were used. Means and standard deviations for the prior distributions were derived from information gathered from our previous, non–experimental, survey work, which involved similar trapping intensities in sites ranging up to 60 t/ha (MAC NALLY et al., 2001). Thus, values for priors for the pre–manipulation means (βs) were all taken from values for the surveys at sites with loads of 32.5 t/ha (closest to the mean of 27 t/ha for pre–manipulation wood loads). Priors for post–manipulation means (αs) were derived from values for woodloads most similar to the post–manipulation woodloads. Thus, the prior for 0L was the mean (and standard deviation) of the survey sites with 1.4 t/ha, while the corresponding sources for other *a*s were: 20L—19.5 t/ha, 40L and 40H—44.9 t/ha, 60L and 80L—60.2 t/ha, and UC and DC—32.5 t/ha. In results of all analyses, means and medians of posterior distributions of parameters were similar, indicating symmetric probability distributions.

Contrasts between specific treatments or combinations of treatments can be computed during the course of the modelling. Five such contrasts were considered. MAC NALLY et al. (2001) reported that fallen-timber loads exceeding ca 40 t/ha may be preferred by the Yellow–footed Antechinus, so specific contrasts were used between means after manipulation for treatments with < 40 t/ha (i.e. 0L and 20L) and others with loads ≥ 40 t/ha (40L, 60L, 80L). Therefore, the first contrast was between the mean of the 40L, 60L and 80L treatments and the mean of the 0L and 20L treatments. A second contrast was between the controls, UC and DC (both after manipulation), to explore whether the manipulation disturbance influenced numbers of the Yellow–footed Antechinus. The third contrast sought to test whether the type of wood debris (logs vs crowns) was important, so 40H was contrasted with 40L (both after manipulation). The fourth and fifth contrasts tested differences in means before and after manipulation for the 40L–80L treatments and for the 0L–20L treatments respectively.

Results

The γ–coefficients indicate whether there are marked changes between the pre–manipulation and post–manipulation densities of Yellow–footed Antechinuses in each treatment. The contrasts allow resolution of some pre–experimental hypotheses regarding how the manipulations would influence densities.

Counts of individual females

For females, the model accounted for 36% of the null deviance (i.e. constant–only model) by using 18 parameters (eight before [β] and eight after [α] means, plus two random effects parameters). There were large increases in post–manipulation densities compared to pre–manipulation values for five treatments: 20L, 40L, 60L, 80L and the undisturbed control, UC (all mean differences > 0.8, table 1; fig. 1A). While 95% credible intervals for only 40L and 80L excluded zero, much of the probability mass for the γ–coefficients for the other three treatments was concentrated in the positive domain (table 1).

Contrasts suggested that the mean (over the seven post–manipulation survey rounds) of the ≥ 40 t/ha log treatments exceeded that of the ≤ 20 t/ha log treatments (contrast 1, table 1),

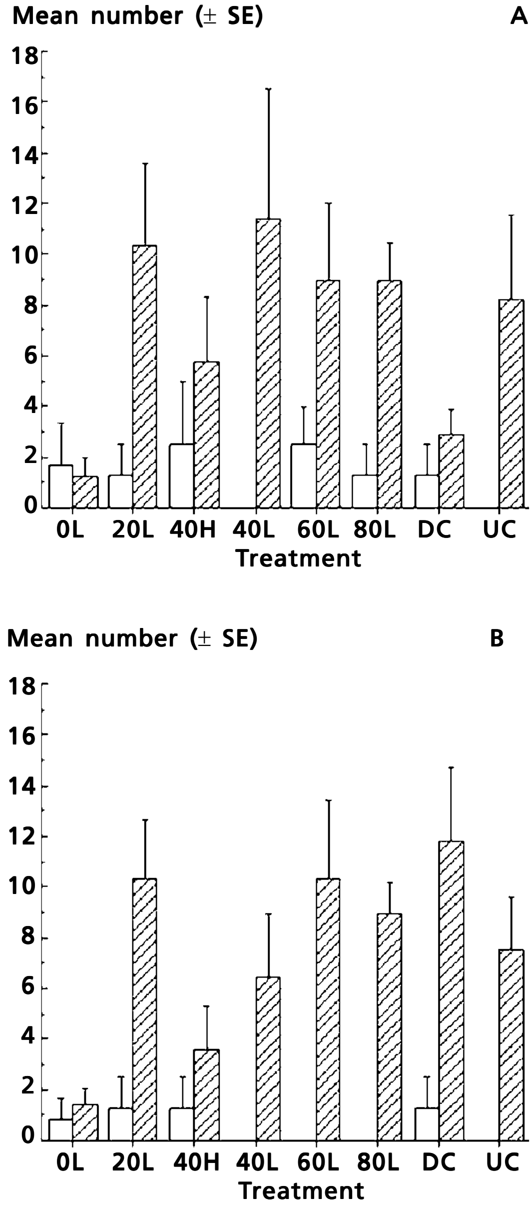

Fig. 1. Mean (± SE) densities of females (A) and males (B) *Antechinus flavipes* as a function of experimental treatment. Open columns: means prior to manipulation (2 rounds); hatched columns: mean following manipulation (7 rounds).

Fig. 1. Densidades medias (± error estándar) de hembras (A) y machos (B) Antechinus flavipes *en función del tratamiento experimental. Columnas blancas: valores medios previa manipulación (2 tomas de datos); columnas rayadas: valores medios después de la manipulación (7 tomas de datos).*

Table 1. Critical parameter details for the Bayesian analysis of numbers of individual females of the Yellow–footed Antechinus: P. Parameter or contrast; 95%. 95% credible interval.

Tabla 1. Detalles de los parámetros críticos para el análisis bayesiano de los números de individuos hembra de ratón marsupial de pies amarillos: P. Parámetro o contraste; 95%. Intervalo de confianza del 95%.

P	Description	Mean ± SD	95%
γ_1	Change in 0L	0.37 ± 0.89	–1.11, 2.26
γ_2	Change in 20L	0.82 ± 0.45	–0.04, 1.77
γ_3	Change in 40H	0.28 ± 0.54	–0.73, 1.41
γ_4	Change in 40L	1.05 ± 0.52	0.09, 2.05
γ_5	Change in 60L	0.93 ± 0.60	–0.15, 2.29
γ_6	Change in 80L	1.36 ± 0.71	0.17, 2.98
γ_7	Change in DC	0.13 ± 0.61	–0.98, 1.42
γ_8	Change in UC	0.92 ± 0.55	–0.11, 2.04
σ_j	Site random effect	0.38 ± 0.12	0.18, 0.61
σ_{jk}	Site–survey round random effect	1.31 ± 0.38	0.63, 2.15
Deviance (Null)	Model fit (Null model fit)	277 ± 21 (433)	236, 316
Contrast 1	Post mean (40L: 80L) – post mean (0L: 20L)	0.38 ± 0.17	0.07, 0.70
Contrast 2	Post mean UC vs post mean DC	0.52 ± 0.19	0.16, 0.90
Contrast 3	Post mean 40L – post mean 40H	0.58 ± 0.30	0.04, 1.13
Contrast 4	Post mean (40L: 80L) – pre mean (40L: 80L)	0.64 ± 0.15	0.37, 0.94
Contrast 5	Post mean (0L: 20L) – pre mean (0L: 20L)	0.31 ± 0.14	0.03, 0.58

that female antechinuses avoided disturbed areas that were not otherwise affected (UC vs DC, contrast 2, table 1), that female antechinuses discriminated positively between logs and crowns (40L vs 40H, contrast 3, table 1), that there were more female antechinuses in the ≥ 40 t/ha log treatments following manipulation than preceding it (contrast 4, table 1), but the change in ≤ 20 t/ha log treatments following manipulation was only half as great (contrast 5, table 1), i.e. 0.31 vs 0.64 (table 1).

Counts of individual males

The model accounted for 39% of the null deviance. There were large increases in post–manipulation densities compared to pre–manipulation values for four treatments: 20L, 60L, 80L and the disturbed control, DC (all mean differences > 0.58, table 2; fig. 1B). However, none of the 95% credible intervals excluded zero (table 2) indicating a less pronounced response than those of females.

Results of contrasts suggested that only three "effects" were important for males. As with females, males appeared to avoid crowns compared with numbers in log areas (table 2). Means in the ≥ 40 t/ha log treatments following manipulation were greater than in the period preceding it (contrast 4, table 1), and, again, the change in ≤ 20 t/ha log treatments following manipulation was just over half as great (contrast 5, table 1), i.e. 0.28 vs 0.46 (table 2).

Counts of individual females and males combined

For females and males together, the model accounted for 57% of the null deviance. There were large increases in post–manipulation densities compared to pre–manipulation values for five treatments: 20L, 40L, 60L, 80L and the

Table 2. Critical parameter details for the Bayesian analysis of numbers of individual males of the Yellow–footed Antechinus: P. Parameter or contrast; 95%. 95% credible interval.

Tabla 2. Detalles de los parámetros críticos para el análisis bayesiano de los números de individuos machos de ratón marsupial de pies amarillos: P. Parámetro o contraste; 95%. Intervalo de confianza del 95%.

P	Description	Mean ± SD	95%
γ_1	Change in 0L	–0.06 ± 0.35	–0.74, 0.62
γ_2	Change in 20L	0.62 ± 0.43	–0.14, 1.52
γ_3	Change in 40H	0.02 ± 0.47	–0.90, 0.94
γ_4	Change in 40L	0.44 ± 0.48	–0.47, 1.36
γ_5	Change in 60L	0.72 ± 0.48	–0.18, 1.69
γ_6	Change in 80L	0.69 ± 0.50	–0.27, 1.67
γ_7	Change in DC	0.59 ± 0.41	–0.23, 1.41
γ_8	Change in UC	0.50 ± 0.41	–0.30, 1.35
σ_j	Site random effect	0.73 ± 0.17	0.39, 1.07
σ_{jk}	Site–survey round random effect	1.67 ± 0.34	1.09, 2.39
Deviance (Null)	Model fit (Null model fit)	276 ± 26 (456)	228, 327
Contrast 1	Post mean (40L: 80L) – post mean (0L: 20L)	0.21 ± 0.15	–0.10, 0.51
Contrast 2	Post mean UC vs post mean DC	–0.40 ± 0.30	–1.02, 0.17
Contrast 3	Post mean 40L – post mean 40H	0.24 ± 0.17	–0.08, 0.58
Contrast 4	Post mean (40L: 80L) – pre mean (40L: 80L)	0.46 ± 0.13	0.20, 0.72
Contrast 5	Post mean (0L: 20L) – pre mean (0L: 20L)	0.28 ± 0.13	0.02, 0.55

undisturbed control, UC (all mean differences > 1.4, table 3). 95% credible intervals for all five of these treatments excluded zero by large margins (> 0.33, table 3).

There were substantially more antechinuses in the ≥ 40 t/ha log treatments following manipulation than preceding it (contrast 4, table 3), but changes in ≤ 20 t/ha log treatments following manipulation, although clearly greater than zero, nevertheless were half as great (contrast 5, table 3), i.e. 0.73 vs 1.50 (table 3). These values correspond to an added 0.73 and 1.50 antechinuses per site per sampling interval following manipulation in the ≤ 20 t/ha and ≥ 40 t/ha log treatments respectively.

Total trappings of females and males combined

The model accounted for 73% of the null deviance. There were large increases in post-manipulation trappings compared to pre-manipulation values for six treatments: 20L, 40L, 60L, 80L DC and UC (all mean differences > 1.8, table 4). While the 95% credible interval for 40H included zero, its mean was > 0.9 and much of the probability mass was for positive values for γ (table 4). There is reasonable evidence for a substantial decrease in numbers of trappings in the 0L treatment (mean = –1.54, table 4).

Once again, there were substantially more antechinuses active (as measured by total trappings) in the ≥ 40 t/ha log treatments following manipulation than preceding it (contrast 4, table 4), but changes in ≤ 20 t/ha log treatments following manipulation, although in excess of zero, nevertheless were less than half as great (contrast 5, table 4), i.e. 0.98 vs 2.28 (table 4). This difference appears to be substantial given that the mean of Contrast 1 is 1.07 and very little probability mass is associated with non-positive values (table 4). There is little

Table 3. Critical parameter details for the Bayesian analysis of numbers of individuals (females plus males) of the Yellow–footed Antechinus: P. Parameters or contrast; 95%. 95% credible interval.

Tabla 3. Detalles de los parámetros críticos para el análisis bayesiano de los individuos (hembras y machos) de ratón marsupial de pies amarillos: P. Parámetro o contraste; 95%. Intervalo de confianza del 95%.

P	Description	Mean ± SD	95%
γ_1	Change in 0L	–0.82 ± 0.45	–1.67, 0.62
γ_2	Change in 20L	1.41 ± 0.58	0.33, 2.56
γ_3	Change in 40H	0.54 ± 0.61	–0.60, 1.79
γ_4	Change in 40L	1.90 ± 0.77	0.50, 3.60
γ_5	Change in 60L	1.67 ± 0.71	0.36, 3.18
γ_6	Change in 80L	2.15 ± 0.79	0.68, 3.90
γ_7	Change in DC	0.99 ± 0.59	–0.15, 2.22
γ_8	Change in UC	1.56 ± 0.63	0.43, 2.87
σ_j	Site random effect	0.80 ± 0.10	0.62, 1.03
σ_{jk}	Site–survey round random effect	0.87 ± 0.28	0.38, 1.46
Deviance (Null)	Model fit (Null model fit)	312 ± 23 (732)	270, 360
Contrast 1	Post mean (40L: 80L) – post mean (0L: 20L)	0.55 ± 0.36	–0.18, 1.23
Contrast 2	Post mean UC vs post mean DC	0.17 ± 0.48	–0.83, 1.11
Contrast 3	Post mean 40L – post mean 40H	0.61 ± 0.54	–0.45, 1.64
Contrast 4	Post mean (40L: 80L) – pre mean (40L: 80L)	1.50 ± 0.25	0.99, 2.02
Contrast 5	Post mean (0L: 20L) – pre mean (0L: 20L)	0.73 ± 0.27	0.22, 1.27

compelling evidence that disturbance affected total trappings (contrast 2; table 4), but there is possibly a marginal increase in total trappings in 40L compared with 40H treatment sites (contrast 3; table 4).

Discussion

Experimental outcomes

The four "slices" of the data (tables 1–4) indicated similar responses by the antechinuses to the wood manipulation. The major observation is that wood loads exceeding 20 t/ha —providing these are in log and large–bough form— are associated with higher densities of Yellow–footed Antechinuses. It is clear that post–manipulation densities generally exceeded those before manipulation. Greater relative increases in densities and activity occurred at high wood–loads (80L) than at lower ones (e.g. 20L). That is, more antechinuses on average were captured on the 34 ha once the timber was rearranged. This effect may reflect the influence of two factors.

The first possibility is that the spatial concentration of fallen timber on the 34 monitored plots attracted antechinuses from surrounding, low–load areas. There was 28% more fallen timber on the 34 plots after manipulation compared to before manipulation (1176 t vs 918 t), so an increase in antechinus numbers is not inconsistent with this change. The concentration of fallen timber into several high-load areas (four separate ha each of 80 t/ha, 60 t/ha, 40 t/ha) also may contribute differentially to an overall "attractiveness" of the 34 ha involved, compared with having the timber more thinly spread over the entire 34 ha.

Another possible factor that we believe may be important relates to the influence of the

Table 4. Critical parameter details for the Bayesian analysis of numbers of captures (females plus males) of the Yellow–footed Antechinus: 95%. 95% credible interval.

Tabla 4. Detalles de los parámetros críticos para el análisis bayesiano de los números de capturas (hembras y machos) de ratón marsupial de pies amarillos: P. Parámetro o contraste; 95%. Intervalo de confianza del 95%.

P	Description	Mean ± SD	95%
γ_1	Change in 0L	–1.54 ± 0.55	–2.66, –0.34
γ_2	Change in 20L	1.97 ± 0.77	0.60, 3.56
γ_3	Change in 40H	0.91 ± 0.72	0.45, 2.31
γ_4	Change in 40L	2.61 ± 1.07	0.72, 4.89
γ_5	Change in 60L	2.03 ± 0.79	0.55, 3.62
γ_6	Change in 80L	2.73 ± 0.98	0.99, 4.82
γ_7	Change in DC	1.87 ± 0.88	0.28, 3.78
γ_8	Change in UC	3.49 ± 1.29	1.33, 6.42
σ_j	Site random effect	1.125 ± 0.12	0.92, 1.39
σ_{jk}	Site–survey round random effect	0.80 ± 0.31	0.37, 1.57
Deviance (Null)	Model fit (Null model fit)	283 ± 24(1037)	238, 329
Contrast 1	Post mean (40L: 80L) – post mean (0L: 20L)	1.07 ± 0.53	–0.01, 2.09
Contrast 2	Post mean UC vs post mean DC	0.35 ± 0.71	–1.03, 1.67
Contrast 3	Post mean 40L – post mean 40H	0.75 ± 0.82	–0.86, 2.24
Contrast 4	Post mean (40L: 80L) – pre mean (40L: 80L)	2.28 ± 0.39	1.50, 3.01
Contrast 5	Post mean (0L: 20L) – pre mean (0L: 20L)	0.98 ± 0.38	0.23, 1.68

supplemented flood, or "environmental flow", introduced in late 2000 by forest–management personnel. In other River Red Gum forests such as Barmah, to the east along the Murray River (see MAC NALLY et al., 2001), forest flooding alters the taxonomic composition and densities of forest–floor and fallen–timber–dwelling invertebrates once the floodwaters recede. Relatively large–sized carabid beetles and suites of active hunting spiders seem to favour these conditions (BALLINGER & YEN, in press; BALLINGER et al., in press), and these invertebrates may be actively sought by the antechinuses (STATHAM, 1982). Flood recession also is associated with blooms of grasses, sedges and forbs (unpublished obs.), which may extend the time for which the forest floor habitats are suitable for this new retinue of invertebrates.

It was surprising that antechinuses responded strongly to the 20L–treatment, with effects ranging between 60% (individual females) and 90% (individual males) of the 80L treatment. We attach less significance to the latter figure because males, when common (i.e. breeding season), tend to range relatively widely in search of females. This is reflected by the low site-fidelity of most males within trapping sessions compared with females (unpublished obs.). Whether the 20L treatment effect remains strong once the longer–term effects of the artificial flooding have decayed remains to be seen.

Results of this study also showed that large logs and branches are important to the antechinuses because the 40H, or "crowns", treatment, was relatively unattractive to the animals. Females particularly avoided these plots compared with 40L plots, so that the current management practices that effectively provide much of the "new" fallen timber in the form of crowns probably are not advantageous to the Yellow–footed Antechinus. Provision of fallen boles and the large limbs is needed.

There appeared to be a gender–based difference in responses to disturbance. Such a difference was not expected, but females appeared to shun control plots that had been extensively disturbed but that were otherwise unaffected *vis–à–vis* fallen–timber loads (i.e. UC vs DC contrast, table 1). Males did not show such a response, apparently being oblivious to the disturbance (UC vs DC contrast, table 2). The response by females in the DC plots was surprising because the 20L treatments, which had similar woodloads (20 vs 27 t/ha) and a similar level of disturbance, produced results differing little from the UC treatment (table 1). We suspect that these differences will dissipate over longer time–frames and that responses of females to the disturbances (i.e. UC vs DC) will decline as the time since the manipulation was performed becomes longer than a couple of generations.

From a species-management perspective, it is important that density effects such as those we have described for loads m 40 t/ha be translated into improved reproductive performance (MARGULES & PRESSEY, 2000). Further studies in the next three years of the Yellow–footed Antechinus in this experimental system are planned, focusing especially on genetic relationships and spatial patterns of occurrence of individual animals, and on breeding success as a function of wood load.

Habitat restoration

Despite many decades of attempting to relate either occurrence or reproductive success to habitat elements (SCOTT et al., 2002), definitive experimental demonstrations of the impact of differences in habitat–structural elements on biodiversity are rare. As outlined in the Introduction, many such elements (especially vegetation) are difficult to manipulate quantitatively. In other words, are the purported treatments actually perceived by the focal organisms in the way that the experimenter intended? We are eager for other conservation ecologists to conduct similar experiments to ours to provide a more general experimental footing for the role of fallen timber (as an exemplar of habitat elements) in the sustainable management of forest and woodland biodiversity. The precision with which fallen timber can be manipulated, and the extent of natural forested areas around the globe, make this an appealing element with which to experiment.

Goals for habitat restoration can be set at various levels, including limiting further degradation, "rehabilitation", and target–setting for states arbitrarily defined as "improved", "desirable" or "natural" (HOBBS & NORTON, 1996; LAKE, 2001). In relation to the current study, what would "natural" conditions be like for the floodplains forests *vis–à–vis* fallen timber? This refers to conditions prior to European settlement > 200 y ago because aboriginal Australians have been present on the continent for 40,000 years. While aboriginal Australians influenced many characteristics of landscapes, their impacts almost certainly were much less severe than those of Europeans (CRABB, 1997). Determining historical levels for many habitat variables has proved to be problematic. For fallen–timber loads, few documentary sources for determining pre–European settlement levels exist (PARKINSON & MAC NALLY, 2000), so measurements at isolated sites at which exploitation is or has been difficult or impossible due to access and geographic obstructions is the best available option. MAC NALLY et al. (in press a) estimated that current loads averaging ca 20 t/ha may be a little as one–sixth of loads during pre–settlement times.

There is little prospect of returning to pre-settlement levels because the supply of timber is much reduced. The total area of forest is much less, trees generally are smaller, and a high extraction rate for human use (≥ 250,000 t/y) continues. If harvesting were stopped immediately, the average rate of fallen–timber–load increase would be perhaps ca 1 t/ha–y, requiring more than a century for levels to return to pre–European levels given natural decay and other losses.

An alternative to using pre–impact levels *per se* is to address directly biodiversity or species–management objectives (MAC NALLY et al., 2001, in press a). Different organisms may have different "optimum" wood–loads. Our survey program suggested that the Yellow–footed Antechinus occurred in greater densities at sites with fallen–timber loads exceeding 40–50 t/ha (MAC NALLY et al., 2001), although that figure is higher than suggested from the experimental results presented here. However, a wood–dependent, near–threatened species of bird, the Brown Treecreeper *Climacteris picumnus*, showed a clear response to the manipulations with higher densities above 40 t/ha (MAC NALLY et al., in press b). This bird is likely to benefit substantially from an increase in wood loads from the current ca 20 t/ha to something in excess of 40 t/ha. However, the "consensus" between the two taxa is high overall, suggesting that ≥ 40 t/ha is a reasonable management basis. An increase of 20 t/ha on average is much more likely to be an operationally, socially and politically feasible target within a few decades than is the ≥ 100 t/ha amount suggested by comparisons between current and pre–settlement values.

Acknowledgments

We gratefully acknowledge the support of the Australian Research Council through Grant Nos F19804210 and A19927168. We thank Andrew Bennett, Sam Lake, Gordon Sanson and Mario Díaz for either reading the manuscript or contributing to parts of the work. Suggestions by Philip Dixon of the Department of Statistics, Iowa State University, greatly helped the analyses presented here. Murray Thorson, Ray Harrower, Keith Cherry, Amber Parkinson and Lawrie Conole all assisted in the work. The North–western Region of the Victorian Department of Natural Resources and Environment (Robert Price) was especially co–operative in performing the manipulation.

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