



Bombs, fire and biodiversity: Vertebrate fauna occurrence in areas subject to military training



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ABSTRACT

Military training areas (MTAs) cover 6% of the earth's land surface, but the impact on biodiversity of weapons use in MTAs remains largely unknown. We quantified the effects of military training on vertebrates in a 5-year study at Beecroft Weapons Range in south-eastern Australia by contrasting the occurrence of birds, mammals and reptiles between 24 sites within an area subject to repeated weapons use and a matched set of non-impacted sites. Species richness of mammals and reptiles was similar within versus outside the impact area, although many individual species responded to fire, which occurred more frequently in impacted sites. Bird species richness, the occurrence of larger-bodied and migratory bird species, and the occurrence of most individual bird species, was reduced within the impact area. Many bird species that displayed low prevalence in impacted sites also declined over time across the whole study area. Differences in biota between the impact and non-impact areas were detectable after controlling for the effects of recent fire, suggesting that weapons use impacted vertebrates through mechanisms additional to altered fire regimes.

Overall, our data indicated that Beecroft Weapons Range maintained considerable biodiversity value despite prolonged military use. Hence, MTAs have the potential to make a substantial contribution to conservation outside the formal protected area network. However, managers of MTAs need to explicitly state their environmental objectives. This is because management practices may be different if the aim is to maximize species richness rather than to secure populations of particular species.

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1. Introduction

An estimated 2.5% of the world's GDP is allocated to defence spending (SIPRI 2014). Training of an estimated 28 million defence personnel worldwide often takes place on specifically designated areas, hereafter termed Military Training Areas (MTAs). Zentelis and Lindenmayer (2015) estimated that MTAs cover at least 1% of the earth's terrestrial land surface and possibly as much as 5–6%. In Australia, MTAs cover an area of approximately 18 million ha, which is approximately 2.3% of the continent (Zentelis and Lindenmayer 2015). MTAs often encompass a wide range of ecosystem types because of requirements to train defence personnel under different environmental conditions (Aycrigg et al. 2015). MTAs therefore have the potential to make a significant contribution to biodiversity conservation if they are managed in environmentally-appropriate ways (Hills 1991; Zentelis and Lindenmayer

2015; see also Stein et al. 2008). However, empirical investigations of the conservation value of MTAs are rare (Jentsch et al. 2009; Fiott 2015). Moreover, few studies have quantified the impacts of military training on biodiversity. This is despite the fact that the maintenance of biodiversity and environmental integrity are among the primary objectives for the management of MTAs in many jurisdictions globally (e.g., Gazenbeek 2005; Department of Defence 2014). In the study reported here, we sought to address knowledge gaps associated with the impacts of military training on biodiversity using a 5-year empirical study of birds, mammals and reptiles at Beecroft Weapons Range in south-eastern Australia. This area has been subject to military training for >150 years, much of it repeated bombing from naval ships.

Our overarching question was: **What are the impacts of military training on vertebrate fauna?** Answering this apparently simple question is more complex than initially appears (Fig. 1) because, conceptually, the impacts of military training may manifest in several ways. First, there may be direct impacts on animals such as being struck by ordnance or they may be stimulated to flee through noise and nearby physical disturbance. Second, there may be indirect effects on animals such

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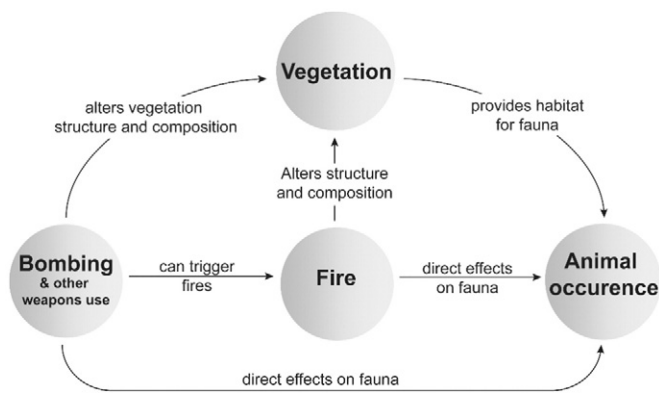


Fig. 1. Conceptual model of the potential inter-relationships between military training, fire, vegetation structure, and vertebrate fauna. The strength of both direct and indirect effects may be mediated by life-history attributes of impacted fauna.

as the occurrence of fires that are triggered by bombing and the use of other weapons. Fires can directly kill animals (Bell et al. 2001; Thonicke et al. 2001; Keith et al. 2002) or indirectly affect their occurrence by altering vegetation structure and habitat suitability (Whelan 1995; Swan et al. 2015). Third, weapons use can physically modify vegetation structure (without fire occurring) and this also can effect habitat suitability for fauna (Fig. 1).

To answer our overarching question about the effects of military training on birds, mammals and reptiles, we developed three postulates to compare the species richness and the occurrence of individual species in these vertebrate groups within versus outside areas subject to weapons use.

- **Postulate #1.** The vertebrate fauna inhabiting sites within the “impact area” subject to repeated weapons use would be depauperate relative to that on sites located outside the impact area. The effects of military training would be reflected by marked differences in standard measures of biodiversity such as species richness and the occurrence of individual species (Fig. 1). This postulate was based on elements of various disturbance theories which suggest that species other than early successional specialists may be eliminated from, or be rare in, places subject to disturbances that are recurrent, frequent and of high-intensity and/or high severity (reviewed by Pulsford et al. 2016). We also might expect to observe differences in population trajectories between the impact and non-impact areas as reflected by an interaction between impact area and year. This was because of differences in the type and prevalence of recurrent disturbances between the impact and non-impact areas, consistent with succession theory (Pulsford et al., 2016).
- **Postulate #2.** Differences in vertebrate fauna within and outside the impact area can be explained, in part, by differences in the prevalence of fire between the two areas (as reflected by fire regime variables such as time since fire and number of past fires) (Fig. 1). This postulate was based on past work in similar vegetation types in the broader region which has indicated that fire regime variables can have significant impacts on groups such as birds (Lindenmayer et al. 2008b; Lindenmayer et al. 2016b) and mammals (Lindenmayer et al. 2016a).
- **Postulate #3.** Differences in vertebrate fauna within and outside the impact area can be explained by the performance filtering hypothesis (Mouillot et al. 2012). This hypothesis predicts the gain or loss of species with particular functional traits from areas subject to environmental change (Newbold et al. 2013; Lindenmayer et al. 2015; Tilman 2001; Schleuter et al. 2010; Hidasi-Neto et al. 2012). We tested this postulate only for birds as it was the sole taxonomic group we studied with sufficient species richness and functional diversity to test trait-based hypotheses. We explored relationships between disturbance by military training and key life history attributes such as

movement patterns given that migratory taxa are known to be sensitive to perturbations (Runge et al. 2014). We also quantified relationships between disturbance and body size, diet and the substrates used for foraging given well known links between some of these traits and extinction proneness (Lindenmayer and Fischer 2006) and/or links with environmental change (Luck et al. 2012).

Understanding the factors which influence biodiversity within MTAs is important for the development of best practice management of these globally extensive, and likely environmentally important, areas of land (Lawrence et al. 2015; Zentelis and Lindenmayer 2015). This study therefore makes a significant contribution toward the objectives of better quantifying the impacts of military training within MTAs and assisting better management of environments subject to this kind of land use.

2. Methods

2.1. Study area

We conducted this study at the Beecroft Weapons Range (35°03' S, 150°49' E) which is a ~4200 ha area of Beecroft Peninsula located ~135 km south of Sydney on the south coast of New South Wales, south-eastern Australia (Fig. 2). Beecroft Weapons Range has a temperate maritime climate with an average monthly rainfall of 103 mm (SD = 21 mm), and average minimum and maximum air temperatures for January (summer) and July (winter) of 18–24 °C and 9–15 °C, respectively (Bureau of Meteorology 2016).

Beecroft Weapons Range is managed by the Department of Defence and it contains a ~2000 ha area (see Fig. 2), hereafter termed the “impact area”, that has been used regularly for weapons training since the 1800s (Welbourne et al. 2015). This area is often closed to public access for periods of several days to several weeks during which there is testing of a wide range of ordnance including ship-based naval gun fire, air to ground missiles, and small weapons (e.g. rifles, grenades and other kinds of hand-held armaments). The impact area is also used for demolition training.

The Beecroft Weapons Range has been subject to repeated fires over the past 38 years (Fig. 2). These fires are either triggered by bombing or are prescribed fires intentionally used as a means of reducing the risk of wildfire escaping the training area. Sites (as defined below) have been subject to up seven fires in the past four decades (see Fig. 2). There is a significant difference in the average number of fires per site over the past 38 years within versus outside the impact area ($F_{1,38} = 11.12$, $P = 0.002$) (0.81 in non-impact area sites, 2.38 in impact area sites, standard error of difference = 0.47). In addition, the average time since fire was 16 years inside the impact area and 28 years outside it ($F_{1,38} = 12.02$, $P = 0.001$).

2.2. Study design

Our study comprised 40 sites, with a site defined as a 100 m long transect. A total of 24 sites was located within the impact area (subject to military training) with the remaining 16 sites outside the impact area (Fig. 2). All sites were dominated by heathland comprising shrubs such as heath banksia *Banksia ericifolia*, scrub she-oak *Allocasuarina distyla*, dagger hakea *Hakea teretifolia*, and tea tree *Leptospermum* spp. (Skelton and Adam 1994).

We identified the appropriate location for each of our 40 sites by careful inspection of maps, on-the-ground field reconnaissance, and consultation with staff from Beecroft Weapons Range. The site locations were approved by the Officer in Charge at Beecroft Weapons Range and the Defence Environment team. Each of the 24 sites within the impact area was cleared of unexploded ordnances in January 2010 (see Fig. A1).

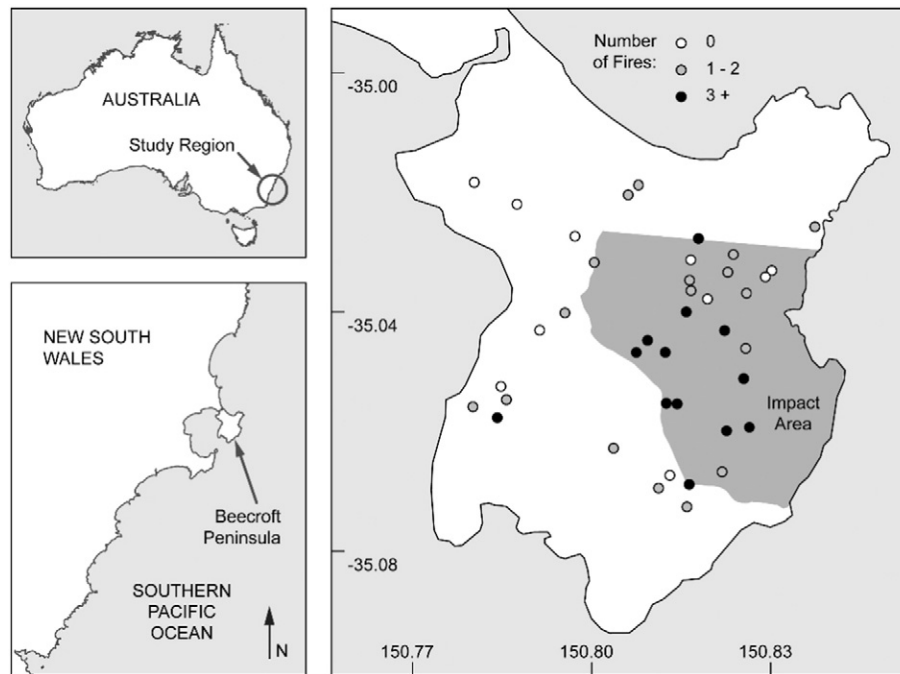


Fig. 2. Site placement within Beecroft Weapons Range. The shaded part of the right panel is the impact area subject to repeated weapons use. Circles correspond to sites within and outside the impact area (see text). Colours show the number of fires that have occurred at each site since 1978.

2.3. Fauna surveys

2.3.1. Birds

We surveyed birds by completing four five-minute point interval counts (sensu Pyke and Recher 1983) in late September each year from 2010 to 2014 at the 20 m and 80 m permanent points placed along the 100 m transect established at each of our 40 sites. Each site was surveyed at least twice, on a different day, by a different observer to reduce day effects on detection and overcome potential observer heterogeneity problems (Cunningham et al. 1999; Field et al. 2002). Thus, a total of 20 min of point interval counts was completed at each site in each of 40 field sites in each of the five years of our study. We recorded all birds seen or heard and assigned observations to different distance classes from a point – 0–25 m, 25–50 m, 50–100 m, and > 100 m.

Our survey protocol was specifically designed to quantify site occupancy and for our statistical analyses (see below) we did not assume that individual counts at the two points on the same site were independent. In addition, we limited our analyses to data gathered for those birds detected within 50 m of a plot point on a given transect. To account for known sources of variation in our surveys in the most appropriate and feasible manner we: (i) surveyed multiple points per site (local spatial heterogeneity), (ii) surveyed on multiple days (temporal heterogeneity) and (iii) used multiple observers (observer heterogeneity) (Cunningham et al. 1999; Lindenmayer et al. 2009).

2.3.2. Mammals

To survey mammals, we established markers at 0 m, 20 m, 40 m, 60 m, 80 m and 100 m points along the 100 m transect at each of the 40 sites in our study. Trapping infrastructure at each site was as follows:

- We placed an Elliott aluminium box trap (10 cm × 10 cm × 30 cm; Elliott Scientific Equipment, Upwey, Victoria) at 10 m intervals along the transect, giving 10 small box traps per site.
- We placed a small wire cage trap (20 × 20 × 50 cm) at the 20 m, 40 m, 60 m and 80 m points along the transect giving a total of four small wire cage traps per site.

- We placed a large wire cage trap (30 × 30 × 60 cm) at the 0 m and 100 m points of the transect giving a total of two large wire cage traps per site.

Our trapping protocols involved opening Elliott traps and cage traps for three consecutive nights at each of our 40 sites in summer each year from 2010 to 2014. We baited all traps with a mixture of peanut butter and rolled oats. Elliott traps and cage traps in which an animal had been captured were wiped clean, re-baited, and re-positioned where the initial capture had taken place.

2.3.3. Reptiles

To survey reptiles, we set out three kinds of artificial substrates at the 20 m and 80 m points along the permanent transect established at each of the 40 sites in our experiment. These substrates were four large wooden sleepers (railroad ties), four roof tiles, and two stacked 2 m × 2 m sheets of corrugated iron. These substrates were searched in spring and summer in each survey year.

2.4. Vegetation surveys

Vegetation surveys were completed in 2014 by the same observer (CM). We measured vegetation at the 20, 40, 60, 80 and 100 m points along each transect to gather covariates for use in modelling of the response of birds, mammals and reptiles to military training and fire. At each point, we recorded the maximum height of the vegetation and estimated the percentage cover of vegetation at five height classes: 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm and 80–100 cm. Due to the widespread presence of unexploded ordnance throughout the impact area, we were restricted to measuring vegetation within one metre of each side of our transects.

2.5. Collation of bird life history attributes

We compiled data on bird species traits to address our third postulate (see Introduction) on links between temporal changes in species' identities within the impact area and particular kinds of life-history

attributes. We summarized data on body mass and life history traits (movement, diet, and foraging substrate) (Handbook of Australian and New Zealand Birds 1990–2007; BirdLife Australia 2014). These traits are thought to reflect the ability of species to respond to environmental change (Luck et al. 2012).

2.6. Statistical analysis

Prior to analysis of faunal data, we tested for effects of different forms of disturbance (fire and military training activities) on vegetation structure. To achieve this, we fitted linear mixed models to vegetation height and percentage vegetation cover data at various heights above the ground, using our three disturbance variables (impact vs non-impact area, time since fire, and number of fires) as predictors. For our percent cover response variables, we divided each value by 100 to form proportions, then logit-transformed them to restrict values to between zero and one. We used a square root transformation on our 'maximum vegetation height' covariate. We ran a single model for each response variable, with each model allowing linear combinations of all three predictors, but not allowing interactions between them. We also included 'site' as a random effect to account for multiple vegetation measures recorded at each site (i.e. at different points along a given transect).

We defined species richness for a given group of vertebrates as the sum of species observed in a given site in a given year. We modelled these data by fitting a single Poisson generalized linear mixed model (GLMM) (Bates et al. 2014) to data on all observed species for each taxon; i.e. for 56 bird, 12 mammal, and seven reptile species. The predictors used were: whether or not a site was in the impact area, the number of years since the start of the study, the interaction between year and impact, the logarithm of the number of years since the last fire, and the total number of fires on record for that site. Vegetation measures were investigated but discarded because of their very limited value in explaining the observed results.

For our individual species models, we customized our statistical approach for each taxon, as necessitated by the properties of our data. For reptile and mammal species, observations consisted of abundance data (counts), which we modelled using hierarchical generalized linear models (HGLMs) to account for potential non-Gaussian error structure of this kind of data (Lee et al. 2006). We used a Poisson distribution with a log link for the fixed effects, and fitted 'site' as a random effect using a Gamma distribution with a log link. We ran these models for all mammals and reptiles for which 40 or more individuals were recorded and which were detected in >20 site-survey combinations over the five-year duration of our study (Table A1).

For birds, our data were the 'detection frequency' of each species; i.e. the proportion of surveys in which each species was detected per site per year. We used GLMMs to fit a quasi-binomial model with a logit link to these data, again including 'site' as a random effect. We restricted our analyses to the 21 individual bird species (Table A2) detected >25 times and in >17 site-survey combinations over the five-year duration of our study.

In addition to analyses of species richness for all three taxa, our bird assemblage was sufficiently large to allow functional analysis to determine whether bird species responses to disturbance were mediated by their traits. We used logistic mixed models to assess every two-way interaction between each of our four trait variables (body mass, movement, diet, and substrate) and impact area and year. Our model included site and species as random effects. We omitted singletons and doubletons from this analysis, as well as the uncommon raptors that had functionally-rare life history attributes, leaving 48 species for analysis. We omitted analyses of relationships between traits and fire regime variables. This was because fire regime variables had no significant effects on bird species richness.

3. Results

3.1. Differences in vegetation attributes inside and outside the impact area

We found that the overall height of the vegetation was significantly ($P < 0.05$) lower in the impact area than outside it. In addition, vegetation cover was significantly greater in areas that had not been recently burned (Fig. A2). There were no significant differences in the percentage cover of any vegetation height classes between the impact and non-impact areas. There were significant effects of time since fire and the number of fires on overall vegetation height and vegetation cover at all measured heights above the ground (Table A3).

3.2. Assemblage-wide responses to military training, fire and vegetation cover

Bird species richness was significantly lower within versus outside the impact area (coefficient = -0.32 , S.E. = 0.09 , $P < 0.001$; Fig. 3), but was not related to any of the fire variables. Bird species richness also declined significantly over time (coefficient = -0.11 , $P = 0.01$), but there was no significant interaction between year and impact ($P = 0.78$). Conversely, there were no significant relationships between the species richness of mammals or reptiles and impact area, time, or their interaction. Instead, both groups showed significant variation in richness in response to time since fire, but in opposing directions – reptile richness was highest in recently burned sites (coefficient = -0.11 , $P = 0.034$), while mammal richness was highest in long unburned vegetation (coefficient = 0.30 , $P < 0.001$; see Table A4). The number of fires did not have a significant effect on the occurrence of any of the vertebrate groups (Table A4).

3.3. Individual species responses to military training, fire and vegetation cover

Analysis of individual species occurrences was possible for 21 of the 56 species of birds, four of the 12 species of reptiles, and five of the seven species of mammals detected in this study. Of the 30 species with sufficient data for modelling, 16 exhibited significant differences in detection frequency or abundance within versus outside the impact area. All of these species were birds, with the detection frequency of 12 species being significantly lower within the impact area than outside it (Fig. 4), and four significantly more common within the impact area. No mammal or reptile species showed significant differences in abundance between the impact and non-impact areas.

Fourteen species exhibited marked differences in detection frequency or abundance over time, with only two of these being consistently positive (Brown Antechinus and Long-nosed Bandicoot), meaning that declines were more common than increases among the species that we studied. For seven of these species, differences in detection frequency or abundance over time varied between the impact and non-impact areas (Fig. 4). For example, there was evidence of a significant negative interaction effect between year and impact for the Southern Emu-wren, Variegated Fairy-wren and Bush Rat, implying that declines in these species were restricted to the impact area (see Table A5 for details). Notably, two species of native birds (the Eastern Yellow Robin and the Fan-tailed Cuckoo) and two exotic mammals – the Black Rat and House Mouse, exhibited the opposite response and increased over time within the impact area (Fig. 4c). Further, the effects of the impact zone unadjusted for any of the other predictors (Fig. A3) were very similar to those for impact shown in Fig. 4a. Thus, whilst the effects of time and fire are important, they do not fully explain the effects of military training impact.

In addition to effects of time and impact, three mammal species (Black Rat, Bush Rat and Brown Antechinus) were more frequently captured in locations that were long unburnt (Fig. 4d) with the last of these species also being less common in frequently burned sites (Fig. 4e). The

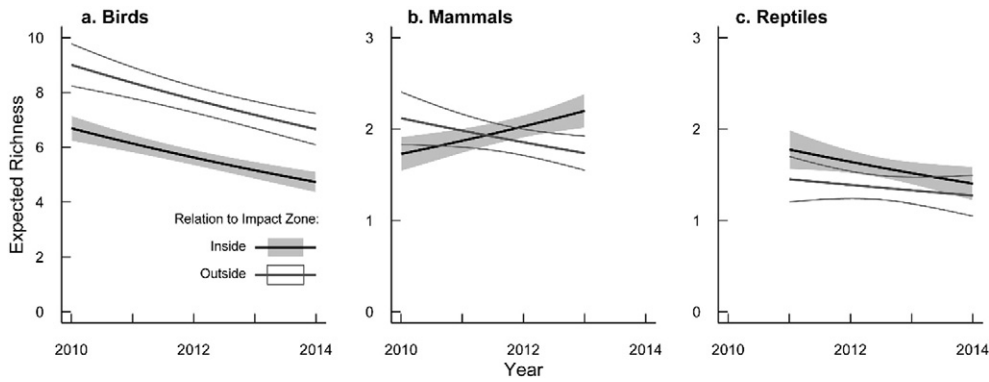


Fig. 3. Change in expected richness of three animal taxa over time, within and outside of the impact area.

House Mouse was the only mammal species to benefit from frequent or recent fire, being most often captured in frequently burned sites. We found that the Delicate Skink and the Weasel Skink were more common in recently burned locations, although the Weasel Skink also was common in areas subject to fewer fires.

3.4. Trait-based analyses

We determined whether bird species responses to disturbance by military training were mediated by their traits. The models for the four traits we examined showed lower bird occurrence within the impact area than outside it (Fig. 5), and lower occurrence at the end of the study period than at the beginning (Table A6). However, each trait showed distinct patterns of response to impact and time. Specifically, birds with larger body mass were less common on average than small birds (coefficient = -0.52, $P = 0.027$), but larger-bodied birds also were less likely to be found within the impact area (coefficient of the interaction between impact and body mass = -0.33, $P < 0.001$; Fig. 5a). Similarly, there was no difference in the probability of observing migratory versus sedentary birds outside the impact area ($P = 0.4$), but sedentary bird species were much more common within the impact area than migratory bird species (coefficient = 0.84, $P < 0.001$; Fig. 5b). Trait analyses exploring diet revealed that only nectarivores exhibited

a significant response to the impact area (coefficient = -0.57, $P = 0.001$; Fig. 5c). Finally, understorey-dwelling birds were more common overall than ground- or canopy-dwelling species, but differences in occurrence between the impact and non-impact areas were significant only for canopy-dwellers (Fig. 5d).

4. Discussion

We completed an empirical study of the impacts of military training on biodiversity. We found evidence for marked differences in the species richness and occurrence of vertebrate biota in sites inside versus those outside the military training impact area, particularly for birds. These effects remained present despite controlling for differences in time since fire and the number of fires that had affected each survey location, suggesting that weapons use had effects on vertebrates through mechanisms other than increases in the occurrence of fires (e.g. physical impacts, noise or other unmeasured factors).

4.1. Is the fauna inhabiting the impact area depauperate relative to that outside the impact area?

We postulated that the fauna inhabiting the impact area at Beecroft Weapons Range would be depauperate relative to the non-impact area.

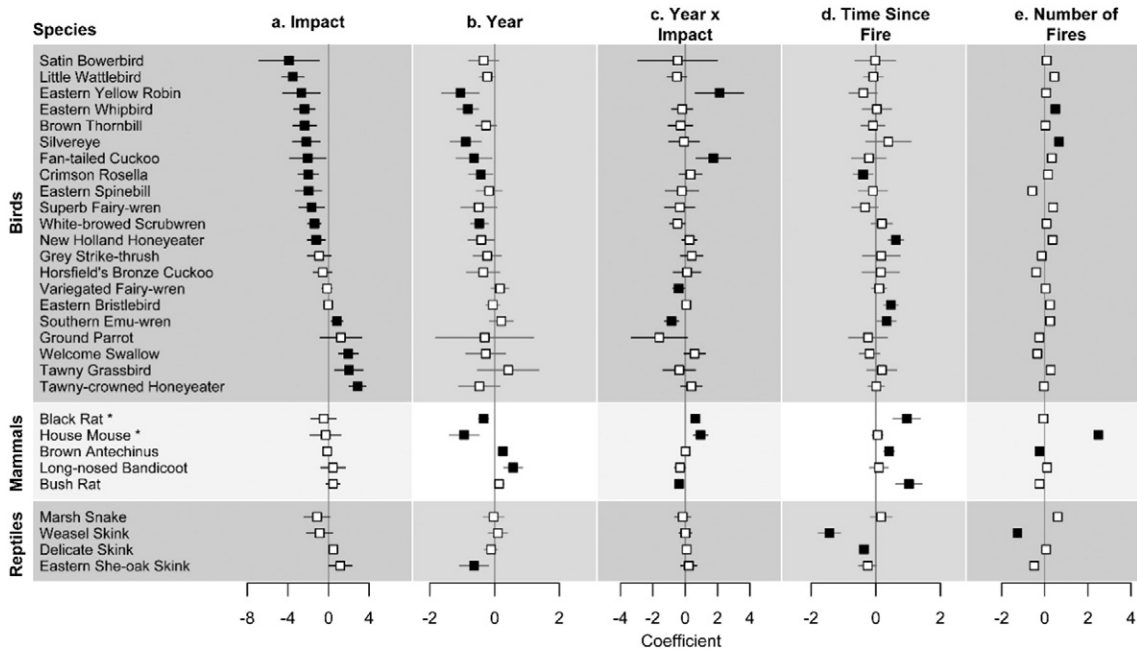


Fig. 4. Effect of predictor covariates on the detection frequency (birds) or abundance (mammals and reptiles) at Beecroft Weapons Range. Filled squares show those effects whose 95% confidence intervals (horizontal lines) do not overlap zero. * denotes exotic species. Scientific names are given in Tables A1 and A2.

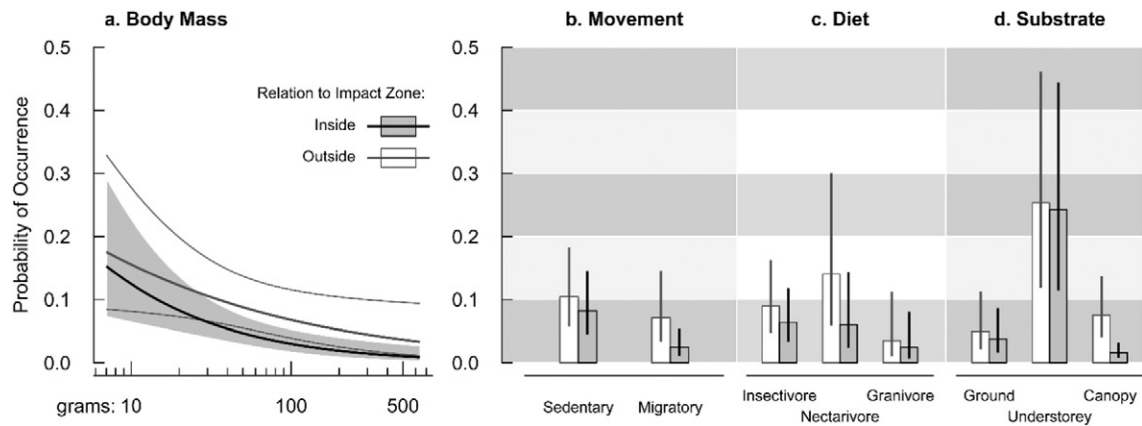


Fig. 5. Change in probability of observation of bird species in relation to traits.

This prediction was only partially upheld because of marked inter-group and inter-specific responses (Figs. 3 and 4). For example, overall bird species richness was lower in the impact area, as were the detections of most individual species. However, the detection frequencies of two bird species of conservation concern - the Eastern Bristlebird and the Ground Parrot - were similar inside and outside the impact area. As evidence of yet further contrast, neither mammal nor reptile species richness was depressed within the impact area.

Several inter-related factors may, in part, explain some of the differences in biota within versus outside the impact area. First, sites within the impact area were subject to, on average, three times more fires than sites outside the impact area and fire effects may have been reflected by the responses of some taxa to time since fire effects. Second, there were significant differences in vegetation cover within versus outside the impact area (Fig. A2, Table A3). Such differences may have influenced habitat suitability. Third, the extensive body of work on succession theory indicates that, over time, there can be marked temporal changes in occurrence of species in perturbed areas associated with the time elapsed since the last disturbance as often mediated by temporal changes in habitat suitability (Swanson et al. 2011; reviewed by Pulsford et al. 2016).

The differences between sites within and outside the impact area were prevalent despite including two key fire regime variables in our models (*viz*: time since fire and the number of fires). This indicates that military training was affecting vertebrates through mechanisms other than increases in the occurrence of fire. These mechanisms could include direct physical impacts, noise disturbance, or other, unmeasured indirect effects (e.g. changes in habitat patch sizes, prey abundance etc.).

4.2. Can differences in the fire regime explain differences in the fauna inside and outside the impact area?

Although fire regime variables did not explain the effects of military training on bird species richness, the occurrence of many mammals and reptiles, and some birds, was associated with differences in fire regime variables. Time since fire effects were prominent for mammals and reptiles, but in opposing ways. Mammal species richness and several individual species of mammals were most likely to be recorded on sites characterized by a relatively long time since fire, whereas reptile species richness exhibited the opposite effect as did individual species such as the Delicate and Weasel Skinks. We suggest that relationships between fire, vegetation structure and habitat requirements of animals is the likely driver of these results. Fire can have large impacts on vegetation structure and plant species composition (Franklin et al. 2002; Haslem et al. 2011), which are major predictors of habitat suitability for a wide range of animals (MacArthur and MacArthur 1961; Morrison et

al. 2006; Woinarski 1999). For example, many studies have demonstrated the importance of vegetation cover for small mammals (e.g. Catling and Burt 1995; Whelan et al. 2002; Banks et al. 2011) and the reduced levels of cover with recent fire (Table A3) is likely to erode habitat suitability for small mammals. Conversely, high levels of cover can create unsuitable thermal microclimatic environments for reptiles and this may, in turn, explain reduced level of species richness and the occurrence of individual species for this group with increasing time since fire. An alternative explanation is that reptiles used our artificial substrates because other natural sites were consumed by fires. For this group, higher numbers of captures may not equate to greater abundance.

In contrast to our results for mammals and reptiles, we found no relationships between time since fire and bird species richness. Moreover, only four of 21 individual bird species exhibited time since fire effects (one negative and three positive; Fig. 4). The relative paucity of time-since-fire effects was unexpected given the well documented effects of this explanatory variable in many other studies of birds (Smucker et al. 2005; Saab et al. 2007; Pons and Clavero 2009) including those in similar (and nearby) ecosystems to the ones which featured in this investigation (e.g. Lindenmayer et al. 2008b; Lindenmayer et al. 2016b). At least two possible reasons may explain the relative paucity of time since fire effects for birds. First, there may be scale issues for birds because, unlike many reptile and small mammal species, most bird species are mobile and can readily move between burned and unburned areas. The size of fires at Beecroft Weapons Range are mostly small in size compared with other areas as weapons use starts localised fires that are quickly contained by land managers. Second, work in similar ecosystems elsewhere in eastern Australia, has shown that some aspects of the fire regime such as fire severity can have more substantial effects on birds than time since fire (Lindenmayer et al. 2008b; Lindenmayer et al. 2014). However, data on fire severity were unavailable for this study.

We found that the occurrence of one species of conservation concern, the Eastern Bristlebird, did not differ significantly between the impact and non-impact areas (Fig. 4), although it was more likely to be recorded on long unburned sites (Table A5). These findings are broadly consistent with recent work on the species in nearby areas which show the species can readily recolonize burned areas but is most abundant in long unburned locations (Lindenmayer et al. 2016b). The persistence of this species in fire-prone places like coastal heathland may be associated with baiting for feral predators such as the Red Fox (*Vulpes vulpes*). The species may be vulnerable to predation in recently burned areas where vegetation cover has been removed. Indeed, work elsewhere suggests the existence of inter-relationships between hunting efficiency of invasive predators and the removal of vegetation cover following fire (McGregor et al. 2014).

4.3. Are differences in biodiversity inside and outside the impact area explained by differences in life history attributes?

An increasing number of studies is demonstrating associations between biotic responses to the environment and traits or life history attributes (e.g. (Mouillot et al. 2012; Newbold et al. 2013; Lindenmayer et al. 2015)). Our analyses were confined to data on birds and revealed several trait-based responses. First, larger-bodied bird species were less likely to occur in areas subject to military training (Fig. 5). One possible explanation for this result might be associated with the amount of a bird's territory that is disturbed by repeated bombing and the ability to tolerate such kinds of recurrent perturbation. Larger bodied birds have larger territories than smaller species (Gill 1995; Handbook of Australian and New Zealand Birds 1990–2007) and repeated weapons use may have a proportionately greater effect on effective territory size thereby influencing the ability of such taxa to persist within the impact area.

A second key outcome from our work was that relative to sedentary bird species, migratory taxa were less common within the impact area than outside it (Fig. 5). These findings suggest that species that travel long distances to breeding habitat may avoid places subject to repeated disturbance; in this case the use of weaponry. The basis for such sensitivity remains unclear but our findings are broadly congruent with those of other studies worldwide which suggest that highly mobile bird species can be sensitive to the effects of disturbances (Runge et al. 2014). We also uncovered other life history trait associations, where nectivorous and canopy-feeding birds were less prevalent in the impact than the non-impact area. It is possible that these effects were due to the effects of repeated disturbance on vegetation in the impact area, with disturbance reducing vegetation height and potentially also food availability for nectarivores. Notably, flower production (and hence nectar availability) increases with increasing time since fire in key heathland plant species such as *Banksia* spp. in our study area (Zammit and Westoby 1987; Bradstock and O'Connell 1988).

4.4. Other effects

Our analyses revealed significant declines in detection frequency or abundance of ten species over time, with only two species increasing over time (Fig. 4a). In addition, there was a significant negative linear time trend for bird species richness. The reasons for these temporal effects remain unclear, although for some species, there appears to be a link with military training as indicated by a significant negative interaction between year and impact area, in which declines were confined to the impact area (Fig. 4a). Two exotic small mammal species (the Black Rat and House Mouse) are often associated with highly disturbed areas and they both exhibited a positive interaction between impact area and year. We suggest that the observed temporal changes in some vertebrate taxa at Beecroft Weapons Range (including increases of exotic species) warrant careful continued monitoring with a plan for altered management action if trends continue.

4.5. Key caveats

We have observed marked differences in the richness and occurrence of vertebrates inside versus outside the area subject to military training activities. As we have studied only one military training area (leading to a lack of replication and a lack of randomness in the selection of the impact area), it is possible (although unlikely) that the differences we observed were confounded by pre-existing differences in the survey sites. While not ideal, this study design is largely unavoidable in the investigation of the impacts of military training as activities such as bombing must be contained to specially controlled areas for safety and logistical reasons.

4.6. Implications for management

The primary role of MTAs is training of defence personnel. However, important secondary environmental values need to be explicitly incorporated into the management of such areas (e.g. Gazenbeek 2005; Department of Defence 2014; Lawrence et al. 2015). A fundamental part of integrating military training and environmental management objectives is to quantify the impacts of military training on environmental values. However, the answer to the overarching question which motivated this study: What are the impacts of military training on biodiversity? – was complex because of the highly variable responses of different groups of biota and different species. Some species responded positively, others negatively, and yet others exhibited largely neutral responses to military training activities (Fig. 4). Nevertheless, our empirical investigation indicated that MTAs can be important environments for a range of biota, including species of conservation significance (see also Aycrigg et al. 2015). This was demonstrated in our study through the occurrence of species of conservation concern such as the Eastern Bristlebird and Ground Parrot in both the impact and non-impact areas. Indeed, for groups such as reptiles and mammals, species richness was similar inside and outside the impact area. Hence, Beecroft Weapons Range maintains considerable biodiversity value despite prolonged military training in the area. Moreover, given our results coupled with the size of the MTA estate globally, areas managed by defence forces have the potential to make a substantial contribution to conservation outside the formal protected area network.

We found that some native bird species were significantly less likely to be detected within the impact area versus outside it, while others were more likely to be detected inside the impact area (Fig. 4). We therefore suggest that marked differences in biotic responses between species and between vertebrate groups demands that managers of MTAs (in this case, the Australian Department of Defence) explicitly state the objectives of management. This is because the kinds of management targeted for a given area may be different if the overarching aim is to maximize overall species richness versus if the aim is to secure populations of individual species.

Achieving secondary (environmental conservation) objectives on areas where military training is the primary land use can be challenging and is complicated by inter-species and inter-group differences in response to disturbance. One approach to maintaining biodiversity values in MTAs will be to ensure that such areas are large enough to support patches of vegetation in different stages of recovery following perturbation as well as some places that are exempt from weapons use or other kinds of training that may alter vegetation cover or have other effects such as increasing the prevalence of fire. This recommendation corresponds to the general land and resource management principle of “don't do the same thing everywhere” (see Lindenmayer et al. 2008a). This principle therefore applies equally to land subject to military training as it does to other kinds of disturbance regimes such as those subject to fire (including prescribed burning), livestock grazing and forestry.

A further conservation issue revolves around the intensity of use of military training areas. That is: Is the optimal trade-off between military training and environmental values achieved by low intensity weapons use across a large area or high intensity use in a small area (leading to potential “sacrificial zones”)? Weapons use will continue in large parts of defence estate in Australia and elsewhere around the world and the answer to this key question remains unknown but an important one to address.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.10.030>.

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