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Corresponding author:

Bronwyn Hradsky
Quantitative and Applied Ecology Group
School of Biosciences
University of Melbourne
VIC 3010 Australia
Email: hradskyb@unimelb.edu.au

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Responses of invasive predators and native prey to a prescribed forest fire

Bronwyn A. Hradsky*, Craig Mildwaters, Euan G. Ritchie, Fiona Christie, and Julian Di Stefano

School of Ecosystem and Forest Sciences, University of Melbourne, Creswick VIC 3363 Australia (BH, CM, FC, JDS)

Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood VIC Australia 3125 (ER)

Fire shapes biome distribution and community composition worldwide, and is extensively used as a management tool in flammable landscapes. There is growing concern, however, that fire could increase the vulnerability of native fauna to invasive predators. We developed a conceptual model of the ways in which fire could influence predator-prey dynamics. Using a before-after, control-impact experiment, we then investigated the short-term effects of a prescribed fire on 2 globally significant invasive mesopredators (red fox, *Vulpes vulpes*, and feral cat, *Felis catus*) and their native mammalian prey in a fire-prone forest of southeastern Australia. We deployed motion-sensing cameras to assess species occurrence, collected predator scats to quantify diet and prey choice, and measured vegetation cover before and after fire. We examined the effects of the fire at the scale of the burn block (1,190 ha), and compared burned forest to unburned refuges. Pre-fire, invasive predators and large native herbivores were more likely to occur at sites with an open understorey, whereas the occurrence of most small and medium-sized native mammals was positively associated with understory cover. Fire reduced understory cover by more than 80 %, and resulted in a 5-fold increase in occurrence of invasive predators. Concurrently, relative consumption of medium-sized native mammals by foxes doubled, and selection of long-nosed bandicoots (*Perameles nasuta*) and short-beaked echidnas (*Tachyglossus aculeatus*) by foxes increased. Occurrence of bush rats (*Rattus fuscipes*) declined. It was unclear if fire also affected the occurrence of bandicoots or echidnas, as changes coincided with normal seasonal variations. Overall, prescribed fire promoted invasive predators, while disadvantaging their medium-sized native mammalian prey. Further replication and longer-term experiments are needed before these findings can be generalized. Nonetheless, such interactions could pose a serious threat to vulnerable species such as critical-weight-range mammals. Integrated invasive predator and fire management are recommended to improve biodiversity conservation in flammable ecosystems.

Key words: Australia, critical weight range mammal, diet, ecological synergy, *Felis catus*, fire, functional response, mesopredator, predator prey interactions, *Vulpes vulpes*

**Correspondent:* hradskyb@unimelb.edu.au

Fire shapes the distribution of biomes and composition of communities worldwide (Bond and Keeley 2005; Pastro et al. 2014), and is extensively used as an ecological management tool in flammable landscapes (Bowman et al. 2009; Penman et al. 2011). Fire primarily influences fauna through its effects on vegetation structure and composition (Banks et al. 2011; Conner et al. 2011), and a central tenet of the habitat accommodation model is that species succession post-fire is driven by vegetation change (Fox 1982; Monamy and Fox 2000). Yet, although associations between ground-dwelling fauna and vegetation structure in fire-affected landscapes are well documented (e.g., Torre and Diaz 2004; Santos and Cheylan 2013; Swan et al. 2015), the mechanisms that underlie these relationships have rarely been quantified experimentally (Driscoll et al. 2010; Griffiths and Brook 2014; although see Zwolak et al. 2012; Leahy et al. 2015).

One potentially important driver of faunal responses to fire is predation. Predators strongly influence the structure and function of many ecological communities (Ritchie and Johnson 2009), and there are several non-exclusive pathways by which fire could affect predator-prey relationships. Firstly, fire can directly kill predators (Cross et al. 2015) or prey (Garvey et al. 2010), and so alter their relative abundances (Fig. 1–Pathways 1 and 2, respectively; hereafter P1, P2). Most fire-effects on fauna, however, are mediated by post-fire changes in vegetation structure and composition (Monamy and Fox 2000; Banks et al. 2011; Fig. 1–P3). By affecting the availability of food or other habitat components, fire can indirectly influence prey distribution, abundance or behavior (Gureja and Owen-Smith 2002; Letnic et al. 2004; Zwolak et al. 2012; Fig. 1–P4). Changes in refuge availability can also alter prey vulnerability to predators (Fig. 1–P5), and hence the per-capita impact of a predator upon prey species (Fig. 1–P6). For example, a loss of understory cover after fire may enable existing predators to hunt more effectively (Conner et al. 2011; Leahy et al. 2015). Changes in prey availability, hunting efficacy and vegetation structure may also affect habitat suitability for the predator (Fig. 1–P7 and 8), and hence predator distribution, abundance, or activity (Fig. 1–P9). For example, predators may be attracted by or intensify their use of recently burned habitats if prey are highly abundant or more vulnerable to predation (Ogen-Odoi and Dilworth 1984; Barnard 1987; Letnic et al. 2004; McGregor et al. 2014; McGregor et al. 2016). Conversely, predators may avoid recently burned areas if prey abundance is low (McGregor et al. 2014) or if they are unable to hunt effectively without cover (Eby et al. 2013). Fire-related changes in the availability of alternative prey may also cause predators to target prey species that remain relatively available (Green and Sanecki 2006; Dawson et al. 2007; Fig. 1–P10). The net changes in total predation pressure can have a top-down effect on prey behavior, abundance, or distribution post-fire (Conner et al. 2011; Arthur et al. 2012; Leahy et al. 2015; Fig. 1–P11).

An increase in prey vulnerability to predation after fire may benefit rare or threatened predators such as swift foxes (*Vulpes velox*—Thompson et al. 2008) and Florida panthers (*Puma concolor coryi*—Dees et al. 2001). However, there is growing concern that fire and invasive predators could have synergistically negative impacts on native fauna (Fisher et al. 2014; Doherty et al. 2015; Ziembicki et al. 2015). Invasive predators have a disproportionately large impact on native prey (Salo et al. 2007), and there is mounting evidence from tropical savannas in Australia that invasive predators are attracted to, and hunt more effectively in, burned habitat (e.g., McGregor et al. 2014; Leahy et al. 2015; McGregor et al. 2016). Thus far, however, little is known about how fire affects the relationships between invasive predators and native prey in structurally complex, mesic ecosystems (although see Green and Sanecki 2006; Arthur et al. 2012).

We used a before-after, control-impact experiment to investigate the short-term effects of a prescribed fire on 2 invasive predators (red fox, *Vulpes vulpes*, and feral cat, *Felis catus*) and their native mammalian prey in a eucalypt forest of southeastern Australia. We predicted that, prior to the fire, understory cover would be 1) negatively associated with occurrence of invasive predators, and 2) positively associated with the occurrence of native mammalian prey species. Fire consumes understory vegetation, potentially increasing habitat suitability for invasive predators and making native mammals more vulnerable to predation. Therefore, we further predicted that 3) the occurrence of invasive predators would increase after the fire, and 4) predators would increase their relative consumption or selection of native mammals. Finally, we predicted that 5) the occurrence of native mammals would decrease after the fire.

Prescribed fires in this landscape are generally patchy (e.g., Sitters et al. 2015), and unburned patches within the impact (burned) block might provide important post-fire refuges for native mammals (Robinson et al. 2013; Swan et al. 2016). To investigate to importance of burn patchiness, we tested predictions 3 and 5 at 2 spatial scales. The coarse 'block scale' corresponded to the impact block (1,190 ha), and so was consistent with the scale of fire management in the region (DEPI 2013). The finer 'intra-burn scale' distinguished between changes in species occurrence at burned and unburned sites within the impact block.

MATERIALS AND METHODS

Study area and design.— Our study was conducted within the Otway Ranges, southeastern Australia (38°24′ S, 144°1′ E). The locality has a moderate climate: maximum daily temperatures average 13°C in winter and 23°C in summer. Rainfall averages approximately 1,000 mm per annum, with the majority falling in winter (www.ala.org.au; BOM 2014). Overstory vegetation is dominated by messmate stringybark (*Eucalyptus obliqua*) and narrow-leaved peppermint (*E. radiata*); midstory species include prickly Moses (*Acacia verticillata*) and hop goodenia (*Goodenia ovata*). In wetter areas, Austral bracken (*Pteridium esculentum*) and forest wire grass (*Tetrarrhena juncea*) form a dense understory. Foxes and feral cats are the largest terrestrial predators in the region.

The impact block was a 1,190-ha area of forest designated for burning, while the control block was an equivalent area approximately 10 km away with broadly similar topography and vegetation (Fig. 2). We were unable to replicate our study at the scale of the fire due to burn-schedule constraints, and so our results are specific to the study location. The distance between the control and impact blocks was a compromise between attaining similar environmental conditions and spatial independence. Invasive predators are capable of travelling long distances (Carter et al. 2012), but we marked several foxes at the impact block as part of a separate study and found no evidence of movement between blocks (B. Hradsky, unpublished data). Home ranges of foxes and feral cats in this region are usually less than 7 km in length (Hradsky 2016), and so we considered that populations of predators at the control block were unlikely to be affected by the treatment. Prior to our study, both blocks were burned in a 1983 wildfire. Approximately 11 % of the impact block also burned in a prescribed fire in 1991.

Within each block, we selected 54 sites using a stratified random sampling design. Sites were distributed in clusters of 3 (gully, mid-slope, and ridge; Fig. 2). Clusters were at least 200 m apart, while sites within clusters were separated by an average distance of 112 m (range: 28 – 316 m). We surveyed invasive predators, native mammals, and vegetation at these sites, but collected predator scats throughout the blocks. We surveyed both blocks prior to the burn (January to April 2013). Land managers conducted a prescribed fire at the impact block 6 – 10 May 2013, burning approximately 60 % of the area (Fig. 2), and we repeated all surveys as soon as access was permitted (late May – July 2013). During the post-fire surveys, we recorded whether sites at the impact block had been burned or remained unburned.

Occurrence of native mammals and invasive predators.—We surveyed fauna at each site using a Reconyx Hyperfire HC500 motion camera (Reconyx, Holmen, Wisconsin), which captures images of passing animals using a passive infrared motion detector and near-infrared flash. At each site, we fastened 1 camera to a tree at a height of 30 cm and faced it toward a bait station 1.6 m away. The bait station comprised 5 tea-strainers (each containing a mixture of peanut butter, golden syrup, oat, and pistachio essence), and was tied to a picket approximately 30 cm above the ground. We removed understory vegetation between the camera and bait station to ensure animals were clearly visible. Cameras were set to maximum sensitivity, programmed to record images continuously while movement was detected, and took 5 photographs per trigger. Cameras were deployed for 25 full days at each site.

Two researchers (BH and CM) independently identified all fauna from the camera-trap photographs, and double-checked any discrepancies in species identification. Species were considered to occur at a site if they were recorded at least once during the camera-trap survey period. Changes in occurrence between surveys may reflect a change in the species' distribution, abundance, or activity.

Understory cover.— We surveyed understory cover at each site along two 10-m transect lines, centered on the camera-mount point and oriented north-south and east-west, respectively. At 2-m intervals along these transects, we recorded the presence or absence of vegetation 20 – 50 cm above the ground using a height pole, and then divided the summed presences by 12 (i.e., the total number of points) to estimate proportional cover. We considered this height category to be the most indicative of fire-related changes in understory vegetation structure as dead vegetation often remains close to the ground after fire, whereas taller vegetation may be unaffected by low-severity fire.

Diets of predators.— We collected predator scats during systematic searches along roads and tracks, as well as opportunistically while conducting other fieldwork. We focussed our collection on fresh scats (based on odor, weathering, and color) and commenced post-fire scat collection 3 weeks after the fire. Scats were fresh-frozen in individual bags and sent to an expert (Barbara Triggs, Genoa, Australia) who analyzed scat contents according to the methods of Brunner and Coman (1974). Mammal remains were identified to species level where possible, and other animal items were sorted to class level. Vegetable matter was sorted into fruit and seeds, and other plant matter. The proportion of each scat comprising each prey item was estimated visually, and the dry weight of each scat was measured to 0.1 g.

Effects of understory cover and fire on occurrence of invasive predators and native mammals (predictions 1, 2, 3, and 5).—We used generalized linear mixed models (GLMMs) with logit-link functions and binomial errors to test these predictions. To evaluate the associations between understory cover and species occurrence (predictions 1 and 2), we compared models of each fixed predictor (*understory cover* and *block*) alone to the additive, interactive, and null models. To test the effects of the fire on species occurrence (predictions 3 and 5), we compared changes in occurrence at the impact block to changes at the control over the same period. The fire effect corresponded to the interaction between *time* and *treatment*, where *time* had 2 levels (before [B] and after [A]) and *treatment* either had 2 levels (for the block scale analysis: control [C] and impact [I]) or 3 levels (for the intra-burn scale analysis: control, impact-unburned [I_u] and impact-burned [I_b]). In each case, we compared support for the interactive model (occurrence ~ time × treatment) to support for the additive (occurrence ~ time + treatment) and null (occurrence ~ 1) models.

We used Akaike's Information Criterion corrected for small sample size (AICc) and associated Akaike model weights to assess the level of support for competing models: the model with the lowest AIC is the best in the set, others within 2 AIC units also have substantial support, and those with Δ AIC 4 – 7 have considerably less support (Burnham and Anderson 2002).

The random structure in the GLMMs accounted for the repeated temporal measurements and spatial nesting in our design. To determine the most appropriate random structure for each species' model set, we fitted the full fixed model (all possible fixed effects and their interactions) and compared the level of support for models with different (or no) random structures using AICc (Zuur et al. 2009). The candidate random structures were *cluster* for predictions 1 and 2, and *cluster*, *site*, and *site within cluster* for predictions 3 and 5. Results of random structure selection are presented in Supplementary Data S3. We used the highest-ranked random structure to compare the fixed models, as described above. If the model with no random structure was selected, fixed models were run as generalized linear models (GLMs).

As a measure of GLMM fit, we generated conditional and marginal R^2 (Nakagawa and Schielzeth 2013) using the package MuMIn (Barton 2016). Marginal R^2 was used as the measure of fit for GLMs. We ran GLMMs in lme4 (Bates et al. 2015) and GLMs in the base package of R version 3.3.0 (R Core Team 2016).

Camera-trapping data on invasive predators (foxes and feral cats) were fairly sparse, and both species showed similar responses to understory cover and fire (Fig. 3, Supplementary Data S1). We therefore used the combined occurrence of invasive predators (foxes and feral cats) at each site to test predictions 1 and 3.

We tested the predictions relating to the occurrence of native mammals (predictions 2 and 5) for 1 small (body mass ~100 g: bush rat, *R. fuscipes*), 2 medium (0.6 – 5 kg: long-nosed bandicoot, *Perameles nasuta*, and short-beaked echidna, *Tachyglossus aculeatus*) and 1 large (>10 kg: swamp wallaby, *Wallabia bicolor*) terrestrial native mammal species. Other native mammals recorded at a sufficient number of sites to analyze occurrence comprised less than 4 % of biomass consumed by foxes and so were not regarded as primary prey species. Likewise, other species preyed upon by foxes were not detected at a sufficient number of sites to conduct formal analyses. Lists of all species detected by cameras and in scats are provided in Supplementary Data S1 and S2, respectively.

To test whether data met the assumption of independence, we generated spline correlograms of Moran's I for the residuals of the top-ranked models, using the package ncf (Bjornstad 2016). For most models, the 95 % confidence interval around Moran's I substantially overlapped zero at the minimum distances between adjacent sites, indicating that the model structure adequately accounted for any spatial autocorrelation in the response variable. However, models of echidna responses to fire at both scales showed some evidence of positive autocorrelation at ~ 1,000 m. We therefore included cluster as a random factor in the fixed model comparisons for echidnas, which decreased the autocorrelation but had very little influence on model ranks or estimates.

We generated overall and survey-specific detectability estimates (p) for each species to estimate the probability that the species was truly absent when not detected by camera traps (α) and to check whether α was influenced by fire (which could confound apparent changes in occurrence). We calculated α as $1 - (1 - p)^n$, where n is the number of repeat survey days (n = 25 for each survey period). To estimate survey-specific α, we ran a single-season occupancy model for the before period and another single-season occupancy model for the after period, using the R package unmarked (Fiske and Chandler 2011). Multi-season models require estimates of colonization and extinction rates and failed to estimate variance for some taxa. Overall α was > 0.75 for all taxa except short-beaked echidnas (Supplementary Data S4). Detectability of echidnas was very low for all treatments post-fire, presumably because activity drops during winter torpor. Fire did not affect α for invasive predators, bush rats, echidnas, or swamp wallabies; detectability of bandicoots may have declined in burned areas post-fire, but pre- and post-fire confidence intervals overlapped substantially (Supplementary Data S4).

Effects of fire on diets of predators and prey selection (prediction 4).— Prey accumulation curves generated in EstimateS 9.1.0 (Colwell 2013) indicated that samples of fox scat from each survey period adequately represented dietary diversity. Scat analysis showed that cats consumed native mammals (including common ringtail possums, *Psuedocheirus peregrinus*, and long-nosed bandicoots, *Perameles nasuta*), insects, and reptiles; however, too few cat scats were collected to adequately estimate diets of cats.

We present data on diets of foxes as the proportion of biomass consumed comprising each prey type. This method adjusts for differences in the digestibility of different prey and so provides the best approximation of diets of carnivores (Klare et al. 2011). We estimated biomass consumption of each prey type during each sampling period by multiplying the dry weight of each scat containing the item by the proportion of the scat comprising the item and the relevant conversion factor, summing these biomasses across all scats in the sample, and dividing by the total fresh biomass of all prey items, as per Goszczynski (1974). Item-specific conversion factors are provided in Supplementary Data S5.

To quantify selection of prey by foxes, we used Ivlev’s electivity index (Ivlev 1961) to compare the proportion of biomass consumed to prey availability (estimated as the proportion of sites where the species occurred). The effect of fire on consumption and selection corresponded to the change at the impact block relative to the change at the control, i.e., (IA -

IB) - (CA - CB). To estimate uncertainty around each value, we used PopTools 3.2 (Hood 2009) for Microsoft Excel to resample scats and occurrences of prey with replacement, and then calculated new estimates using the resampled data. We repeated this procedure 10,000 times and used the resulting distributions to derive the averages and 95 % confidence intervals. Note that Ivlev's electivity index, like most other measures of prey selection, has limitations when prey items are rare and the relative availability of prey items differs between samples (Lechowicz 1982) – thus, the precise magnitude of changes in prey selection should be interpreted with caution.

To facilitate comparison with other studies, we also assessed how fire affected the frequency of occurrence of prey items in fox scats. Detailed methodologies of all diet analyses are provided in Supplementary Data S6.

Our study did not involve contact with the study species as data were collected using remote survey techniques (motion-sensing cameras and scat samples). All research was conducted with the approval of the Victorian Department of Environment and Primary Industries (research permit numbers 10005514 and 10006882).

RESULTS

Pre-fire relationships between invasive predators and understory cover (prediction 1).—Prior to the fire, invasive predators were more likely to occur at sites with an open understory, and at the control block (Fig. 3; Table 1). Neither predator species was detected at sites with >75 % understory cover. Although the best model indicated a consistent relationship between occurrence of predators and understory cover across the study area, there was some evidence (ΔAICc = 1.3) that the association between predator occurrence and understory cover was stronger at the control than impact block (Table 1).

Pre-fire relationships between native mammals and understory cover (prediction 2).— Pre-fire, occurrence of bush rats was positively associated with understory cover at the impact block, but not at the control (where occurrence was higher overall; Fig. 4a; Table 1). Occurrence of long-nosed bandicoots was positively associated with understory cover, and was higher at the control than impact block (Fig. 4b); the additive and interactive models received similar support (Table 1). The best model of occurrence of echidnas showed a positive association with understory cover at both blocks, but all models explained only a small proportion of variance (Fig. 4c; Table 1). Occurrence of swamp wallabies was negatively related to understory cover at both blocks, but slope of this relationship differed between blocks (Fig. 4d; Table 1).

Effects of fire on understory cover.—The fire at the impact block burned 36 of the 54 survey sites (67 %). Understory cover at these sites declined from a mean (lower 95 % confidence limit, upper 95% confidence limit) of 0.59 (0.51, 0.67) to 0.12 (0.06, 0.18). Over the same period, cover remained relatively constant at the impact-unburned sites: before—0.73 (0.67, 0.79); after—0.60 (0.52, 0.68), $n = 18$; and at the control: before—0.62 (0.56, 0.68), after—0.53 (048, 0.60), $n = 54$.

Effects of fire on occurrence of invasive predators (prediction 3).— Occurrence of invasive predators increased at both the block and intra-burn scale after the fire, relative to the control (Fig. 3). This fire-effect was driven by a large increase in occurrence of predators at burned sites post-fire, and so was more clearly supported at the intra-burn scale (Akaike weight = 0.90 versus 0.66; Table 2). Occurrence of foxes and feral cats at burned sites increased to 1,500 % and 600 % of pre-fire levels, respectively, remained unchanged at unburned sites within the impact block, and increased to a lesser degree at control sites (to 300 % and 118 % of pre-fire levels, respectively; Fig. 3).

Effects of fire on diets of invasive predators (prediction 4).— The proportion of biomass consumed by foxes that comprised medium-sized native mammals more than doubled at the impact block after the fire, whereas the proportion comprising large native mammals nearly halved, relative to changes at the control block (Fig. 5). Consumption of small native mammals by foxes, and consumption of all native mammals as a group, however, were not affected. Among the minor dietary items, consumption of fruits and seeds increased and consumption of introduced mammals and insects declined (Fig. 5). The effects of fire on the frequency of prey occurrence in scats were similar to the effects on biomass consumption, but differed in magnitude for items such as insects and fruit that occurred frequently but only comprised a small proportion of total biomass (Supplementary Data S2).

After the fire, consumption of echidnas by foxes increased substantially, as did selection of echidnas and bandicoots by foxes (Fig. 5). There was some evidence that consumption of bandicoots by foxes also increased, and that consumption and selection of wallabies by foxes decreased, but confidence limits overlapped zero (Fig. 5). Consumption of bush rats by foxes remained low post-fire (4 % of biomass consumption).

Effects of fire on occurrence of native mammals (prediction 5).—There was some evidence that occurrence of bush rats declined as a result of the fire (Fig. 4a). The fire-effect model was more strongly supported at the block than intra-burn scale (model weight = 0.63 versus 0.49). At both scales, the *P*-value of the interaction term was <0.10 (Table 2).

It was unclear whether fire affected occurrence of long-nosed bandicoots as the additive and interactive models received similar support at both scales (Table 2). Long-nosed bandicoots were detected at 7 (19 %) burned sites pre-fire but only 1 burned site (3 %) post-fire (Fig. 4b). Occurrence of short-beaked echidnas declined to very low levels at both blocks post-fire (Fig. 4c), making it impossible to determine whether fire affected occurrence of echidnas (Table 2).

Swamp wallabies were widespread, particularly at the impact block (Fig. 4d). The best-ranked model at both scales did not include a fire effect; however, there was some evidence for a fire-related decline at the block scale (ΔAICc = 0.7; Table 2; Fig. 4d).

DISCUSSION

Disturbance processes such as fire have the potential to interact synergistically with invasive predators, compounding threats to native fauna (Didham et al. 2007; Doherty et al. 2015). Our study is among first to experimentally and concurrently investigate the effects of prescribed fire on the occurrence, diet, and prey selection of invasive predators, and one of few predator-fire studies to include both temporal and spatial controls (see also Conner et al. 2011; Cross et al. 2015). The prescribed fire promoted invasive predators and decreased habitat suitability for native mammals such as long-nosed bandicoots and bush rats by reducing understory cover. This resulted in an increase in occurrence of invasive predators at burned sites, and a switch in diet of red foxes from large to medium-sized native mammals. Our evidence that fire exacerbates the impacts of invasive predators on medium-sized native mammals concurs with recent findings from tropical savanna ecosystems (e.g., McGregor et al. 2014; Leahy et al. 2015). Such interactions between threatening processes are highly concerning given the historic vulnerability of Australia’s critical-weight-range (35 – 5,500 g) mammals to extinction (Burbidge and McKenzie 1989; Chisholm and Taylor 2010). However, the short duration and un-replicated nature of our design means that further experiments and longer-term monitoring are required before our results can be generalized to other situations.

As we predicted, the occurrence of invasive predators in unburned forest was negatively associated with understory cover, and increased greatly at burned sites post-fire.

This indicates that the fire increased habitat suitability for foxes and feral cats by reducing understory cover (Fig. 1– P3, P7, and P8). Red foxes and feral cats can hunt more effectively in open habitats (Cerveny et al. 2011; McGregor et al. 2015). In addition, predators are sometimes able to exploit the edges of dense habitat more effectively than the interior (Chalfoun et al. 2002). For example, feral cats and foxes select for edges between open and dense habitats (McGregor et al. 2014; Hradsky 2016), and predation of deer fawns by red foxes increases when forest is fragmented by farmland (Panzacchi et al. 2009). Patchy 'pyrodiverse' burning is often thought to benefit biodiversity (Parr and Andersen 2006), and unburned patches within larger burns may provide ecological refuges for native fauna (Robinson et al. 2013). However, targeted use of edges by invasive predators could greatly diminish the protective value of small unburned patches of vegetation for native fauna. The influence of the size, distribution, and structure of unburned patches on post-fire predation rates needs further investigation.

The occurrence of foxes and feral cats did not increase at unburned sites within the burn block, indicating that fire caused a highly localized shift in predator activity. Similarly, only swift foxes (*Vulpes velox*) whose core home ranges overlapped a burn block foraged and denned more intensively in burned areas after a prescribed fire (Thompson et al. 2008). The increase in occurrence of foxes at the control block over the same period is likely to be due to the dispersal season for foxes (April – June; B. Hradsky, pers. obs.), illustrating the importance of a controlled experimental design.

Our predictions that native mammals would prefer dense understory vegetation and become more vulnerable to predators after fire received nuanced support. Prior to the fire, small- and medium-sized native mammals generally had positive associations with understory cover, but a large herbivore, the swamp wallaby, preferred more open sites. These patterns accord with the post-fire switch in diet of foxes from large to medium-sized native mammals.

In particular, consumption of echidnas and bandicoots by foxes increased against background declines in their occurrence, whereas selection of swamp wallabies by foxes decreased.

These changes in the diet of foxes indicate that fire increased the vulnerability of medium-sized native mammals to fox predation (Fig. 1– P5) or decreased the availability of alternative, larger prey (Fig. 1– P10). Small and medium-sized native mammals such as bandicoots and native rodents are highly dependent on dense vegetation for shelter, selecting habitats with high understory cover even when food resources are greater or competition is lower elsewhere (Spencer et al. 2005; Dexter et al. 2011). Similarly, Arthur et al. (2012) found a positive correlation between shrub cover and population recovery of bandicoots after fire. In contrast, swamp wallabies might be more able to detect or escape foxes in burned, open forest. In an African savanna, for example, lions (*Panthera leo*) avoided burned areas despite high herbivore abundance, presumably because of lower hunting success (Eby et al. 2013). Consumption of small native mammals by foxes remained low (≤ 10 %) throughout the study, perhaps indicating that these species were not preferred prey. Further research into fire-effects on diet of feral cats is needed, as feral cats often selectively prey upon this size class (Kutt 2012).

Evidence for our final prediction that occurrences of native mammals would decline post-fire as a result of changes in habitat suitability (Fig. 1–P4) or increased predation pressure (Fig. 1–P11) was equivocal. The fire was likely to have caused a decline in the occurrence of bush rats, particularly at burned sites – a finding consistent with their preference for high understory cover and changes in abundance observed in a concurrent trapping study (Fordyce et al. 2016). Long-nosed bandicoots were extremely rare at burned sites after the fire, but they also were relatively uncommon at burned sites prior to the fire and declined between survey periods at the control block, reducing our capacity to distinguish a fire-effect from temporal and spatial heterogeneity. Similarly, occurrence of short-beaked echidnas declined substantially at all sites (presumably as a result of winter torpor), making it impossible to distinguish a fire effect. In contrast, occurrence of swamp wallabies remained high, and there was little evidence for a fire-related decline in this species.

The uncertainty around our final prediction may be partly due to the limitations of species-occurrence data. Unfortunately, it was unfeasible to estimate the density or abundance of such a broad suite of species concurrently. However, presence-absence data may obscure some important fire effects. For example, responses of predators to fire can occur over short time-scales, vary with severity of fires or prey abundance, or involve shifts in individual activity within home ranges rather than long-term changes in distribution (Thompson et al. 2008; McGregor et al. 2014; McGregor et al. 2016). Similarly, native mammals may exhibit relatively subtle behavioral responses to fire (Stawski et al. 2015; Fordyce et al. 2016). Higher-resolution approaches such as GPS tracking and mark-recapture studies could provide additional insights into the effects of fire on the survival and behavior of key species.

The ultimate impact of a fire-related increase in predation will depend on its duration, extent, and the degree to which populations are top-down regulated, i.e., whether changes cause a net loss (or gain) in populations through additive mortality. For example, an increase in predation could simply compensate for other sources of mortality, such as starvation, if prey are primarily bottom-up regulated (Prevedello et al. 2013). Additional experiments including replicate burn blocks and longer-term monitoring are needed before generalizing our results, and experimental manipulations of food resources and abundance of native and invasive predators, as well as fire, are required to disentangle the relative importance of these different drivers (e.g., Morris et al. 2011).

Nonetheless, the capacity of fire to promote invasive predators and increase the vulnerability of medium-sized native mammals to foxes is highly concerning. Predation by invasive red foxes and feral cats, and inappropriate fire regimes are major drivers of declines in Australia’s native mammals (Woinarski et al. 2015). Interactions between threatening processes can exacerbate the risk of species extinction, and require a sophisticated approach to management (Didham et al. 2007; Doherty et al. 2015). If predation by invasive species limits recovery of native fauna after fire, integrated management of fire and invasive predators may be essential for biodiversity conservation in flammable forest ecosystems.

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SUPPLEMENTARY DATA

Supplementary Data S1.—Mammal species occurrence at control and impact sites before and after prescribed fire, Otway Ranges, Australia.

Supplementary Data S2.—Effect of prescribed fire on frequency of occurrence of prey items in red fox (*Vulpes vulpes*) scats, Otway Ranges, Australia.

Supplementary Data S3.—Random effect selection for generalized linear mixed models.

Supplementary Data S4.—Estimated probabilities that species were truly absent when not detected on camera traps over the 25-day survey period.

Supplementary Data S5.—Conversion factors used to calculate biomass of food in red fox (*Vulpes vulpes*) diet.

Supplementary Data S6.—Procedure for estimating biomass consumption, prey occurrence, and prey selection from red fox (*Vulpes vulpes*) scat samples.

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TABLES

Table 1. Effects of understory cover and block on occurrence of predators and prey in unburned forest, Otway Ranges, Australia. *Cover* is continuous; *block* has 2 levels - control (C) and impact (I); ΔAICc is the difference in Akaike's Information Criterion adjusted for small sample size between the model and the best model, Akaike weight is the likelihood of the model being the best in the set; R^2 is the proportion of variance explained by model. For all taxa, the model with no random effect received the strongest support and so models were run as generalized linear models.

Response variable	Fixed model	Δ AICc	Akaike weight	R^2
Invasive predators	cover + block	0.0	0.58	0.24
	cover × block	1.3	0.31	0.21
	block	4.2	0.07	0.15
	cover	5.6	0.04	0.12
	null	10.3	0.00	0.00
Bush rat	cover × block	0.0	0.90	0.30
	cover + block	5.4	0.06	0.23
	block	6.3	0.04	0.19
	null	22.6	0.00	0.00
	cover	22.7	0.00	0.02
Long-nosed bandicoot	cover + block	0.0	0.45	0.13
	cover × block	0.5	0.36	0.16
	block	1.9	0.18	0.09
	cover	7.0	0.01	0.04
	null	8.4	0.01	0.00
Short-beaked echidna	cover	0.0	0.37	0.07
	cover × block	0.6	0.28	0.13
	cover + block	1.0	0.23	0.08
	null	3.2	0.07	0.00
	block	4.2	0.04	0.01
Swamp wallaby	cover × block	0.0	0.87	0.71
	cover + block	4.0	0.12	0.29
	cover	10.3	0.01	0.18
	block	11.4	0.00	0.15
	null	17.5	0.00	0.00

Table 2. Responses of invasive predators and native mammals to prescribed fire, Otway Ranges, Australia, derived from generalized linear (mixed) models. The fire burned approximately 60 % of the impact block, while the control block remained unburned. Analyses were conducted at 2 scales: block and intra-burn. At the block scale, predictor variables were time (before and after), and treatment (tr: control and impact). At the intra-burn scale, predictor variables were time (before and after) and treatment (tr: control, impact-unburned (Iu) and impact-burned (Ib)). At both scales, models with an interaction term assess the effect of the prescribed fire on species occurrence (relative to changes at the control). Parameter estimates for the effect of fire are shown with standard errors (*SE*) and statistical significance (*P*). Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc), and model support is indicated by Akaike weights. Model fit is indicated by R^2m (fixed effects only) and, if applicable, R^2c (full model including random structure).

Species	Scale	Fixed model	Estimate ± *SE*	*P*	Δ AICc	Akaike weight	R^2m	R^2c
Invasive predators	Block	tr × time	1.27 ± 0.72	0.077	0.0	0.66	0.19	-
		tr + time			1.3	0.34	0.13	-
		null			19.0	0.00	0.00	-
	Intra-burn	tr × time	Iu: -0.81 ± 1.14	0.477	0.0	0.90	0.25	-
			Ib: 2.14 ± 0.90	0.017				
		tr + time			4.3	0.10	0.18	-
		null			25.1	0.00	0.00	-
Bush rat	Block	tr × time	-1.50 ± 0.89	0.090	0.0	0.63	0.35	0.65
		tr + time			1.0	0.37	0.33	0.62
		null			40.3	0.00	0.00	0.58
	Intra-burn	tr + time			0.0	0.51	0.36	0.60
		tr × time	Iu: -0.75 ± 1.11	0.501	0.1	0.49	0.39	0.65
			Ib: -1.86 ± 0.97	0.054				
		null			46.2	0.00	0.00	0.58
Long-nosed bandicoot	Block	tr × time	-1.14 ± 0.71	0.111	0.0	0.58	0.24	-
		tr + time			0.7	0.42	0.19	-
		null			30.8	0.00	0.00	-
	Intra-burn	tr + time			0.0	0.60	0.25	-
		tr × time	Iu: -1.09 ± 0.88	0.212	0.8	0.40	0.34	-
			Ib: -1.61 ± 1.16	0.166				
		null			35.7	0.00	0.00	-

Short-beaked echidna	Block	tr + time			0.0	0.73	0.33	0.34
		tr × time	0.43 ± 1.10	0.697	1.9	0.27	0.33	0.34
		null			30.5	0.00	0.00	0.00
	Intra-burn	tr + time			0.0	0.88	0.34	0.34
		tr × time	Iu: 0.59 ± 1.38	0.670	4.1	0.12	0.34	0.34
			Ib: 0.27 ± 1.33	0.837				
		null			29.0	0.00	0.00	0.00
Swamp wallaby	Block	tr + time			0.0	0.59	0.1	-
		tr × time	-0.85 ± 0.70	0.252	0.7	0.41	0.14	-
		null			9.9	0.00	0.00	-
	Intra-burn	tr + time			0.0	0.71	0.1	-
		tr × time	Iu:-0.05 ± 1.07	0.966	1.9	0.28	0.15	-
			Ib: -1.31 ± 0.92	0.156				
		null			7.9	0.01	0.00	-

FIGURE CAPTIONS

Fig. 1. Conceptual model of the interactions between fire, habitat, predators, and prey.

Fig. 2. Site layout at impact and control blocks, Otway Ranges, Australia. Black dots show camera-trapping sites, arranged in clusters of 3 across adjacent gully, midslope, and ridge with 54 sites (18 clusters) per block. Gray shading indicates areas burned in a prescribed fire (May 2013); black lines indicate roads.

Fig. 3. Associations with understory cover pre-fire, fire at a block scale, and fire at an intra-burn scale for occurrence of (a) invasive predators combined, (b) red foxes (*Vulpes vulpes*), and (c) feral cats (*Felis catus*), Otway Ranges, Australia. There were 54 control and 54 impact sites. Surveys were repeated before and after a prescribed fire in May 2013; 36 of the impact sites burned, 18 remained unburned. Logistic regression curves in the first column were fitted using the top-ranked model for invasive predators. Shading and error bars indicate 95 % confidence limits.

Fig. 4. Associations with understory cover pre-fire, fire at a block scale, and fire at an intra-burn scale for 4 species of native mammal, Otway Ranges, Australia. Logistic regression curves in the first column were fitted using the top-ranked model. Shading and error bars indicate 95 % confidence limits. Sample sizes are as per Fig. 3.

Fig. 5. Effect of fire on biomass consumption and prey selection by red fox (*Vulpes vulpes*), Otway Ranges, Australia. Numbers represent the estimated percentage of prey biomass consumed by red foxes at control and impact blocks block before (B) and after (A) fire. The fire-effect is the change at the impact block relative to change at the control: positive values

indicate an increase post-fire, negative values a decrease. Error bars indicate 95 % confidence limits. Only taxa consumed at both blocks are shown; selection was only calculated for species for which occurrence data were available.