



Peak hour in the bush: linear anthropogenic clearings funnel predator and prey species

STUART J. DAWSON,^{1,*}  PETER J. ADAMS,¹ KATHERINE E. MOSEBY,²
KRIS I. WADDINGTON,³ HALINA T. KOBRYN,¹ PHILIP W. BATEMAN⁴ AND
PATRICIA A. FLEMING¹ 

¹*Environmental and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia 6150 (Email: stuart.dawson102@gmail.com),* ²*University of New South Wales, Sydney, New South Wales,* ³*Buru Energy Limited, Perth, Western Australia,* and ⁴*Department of Environment and Agriculture, Curtin University, Bentley, Western Australia, Australia*

Abstract Linear clearings, such as roads and tracks, are an obvious anthropogenic feature in many remote environments, even where infrastructure is sparse. Predator species have been shown to prefer moving down linear clearings, and therefore, clearings could increase predation risk for other species. We investigated whether tracks cleared for seismic surveys are preferentially used by predators and herbivores in a landscape inhabited by bilbies (*Macrotis lagotis*), a vulnerable species of conservation concern. We used a paired camera trap array to investigate the use of cleared seismic lines at four time points after clearing (1 month, 3 months, 7 months, 48 months) by six mammal species. Bilbies, cattle (*Bos indicus/B. taurus*), dingoes (*Canis familiaris*), feral cats (*Felis catus*) and agile wallabies (*Macropus agilis*) preferred to use seismic lines compared with adjacent undisturbed vegetation for almost all surveys, while spectacled hare wallabies (*Lagorchestes conspicillatus*) avoided them. Bilbies and agile wallabies showed similar temporal activity patterns on and off seismic lines but feral cats, dingoes and cattle used seismic lines at different times of day to control areas. We also investigated microhabitat selection by spool tracking individual bilbies. Bilbies selected a route through vegetation that was more open than surrounding vegetation. While spatial and temporal funnelling of bilbies and their predators (especially cats) may increase the frequency of encounter between the two, it is important to note that bilbies were active at significantly different times to predators both on and off seismic lines. The identified selection for seismic lines, and changes in spatial and temporal overlap between species, can be used to develop effective management strategies, to minimize potential impacts on native species.

Key words: activity patterns, avoidance, disturbance, linear clearings, roads.

INTRODUCTION

Linear clearings in natural vegetation, such as roads and tracks, are often the only obvious anthropogenic feature in many remote environments where infrastructure is sparse, and once abandoned, these roads and tracks may take longer than 80 years to recover (Bolling & Walker 2000). Such disturbances can create edge effects, disrupt dispersal patterns, isolate populations, aid the spread of weeds and increase human or predator access (Trombulak & Frissell 2000; Fischer & Lindenmayer 2007; Laurance *et al.* 2009). These effects can influence species in different ways, with negative, neutral and positive effects being identified (Cerbocini *et al.* 2015; Fahrig & Rytwiniski 2009; Forman 2003; Laurance *et al.* 2009; Scott *et al.* 2006; see Taylor & Goldingay 2010 for Australian review)

One of the key concerns involving linear clearing is the effect on predator–prey relationships. Prey vulnerability is defined in terms of two parameters: the frequency of encounter between predator and prey, and the ease of capture (Pastorok 1981; Greene 1986); any factor that modifies the probability of encounter between prey and predator can therefore influence the predation pressure on species. In Canada, wolves (*Canis lupus*) use linear clearings for movement, increasing the predation risk for caribou (*Rangifer tarandus caribou*) close to those features (Latham *et al.* 2011). The resulting avoidance of linear clearings by caribou results in functional habitat loss (Latham *et al.* 2011).

In Australia, the response of predator species to linear clearings has been well studied. The dingo (*Canis familiaris*, a naturalized predator (Jackson *et al.* 2017)) and red fox (*Vulpes vulpes*, an introduced predator) often use linear features such as roads and tracks for movement, with both species following tracks for over 500 m (Mahon *et al.* 1998; Read &

*Corresponding author.

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Eldridge 2010). Similarly, feral cats (*Felis catus*) are more likely to be recorded on linear features such as roads, creeks, treelines, dune crests or at the edge of patches than in a patch interior (Bengsen *et al.* 2012; McGregor *et al.* 2014; Pastro 2013; see Doherty *et al.* 2015 for review).

By contrast with studies on predator species, the behavioural response of introduced and native herbivore guilds to linear clearings is not well understood (Bond & Jones 2014). Despite rangelands covering 80% of the Australian mainland, there have been few studies investigating the response of domestic cattle (*Bos indicus/B. taurus*) to linear clearings. In America, cattle have been recorded using logging tracks for movement throughout the landscape (Roath & Krueger 1982). Similarly, two didelphid marsupials in South America use plantation rows to orient their movements, using rows as guidelines for navigation between habitat fragments (Prevedello & Vieira 2010), as have mice in Italy (Sozio *et al.* 2013). Where data on Australian native mammalian herbivore are available, it often suggests that roads and tracks have a 'barrier effect', with many species avoiding roads (Goosem 2004; Laurance *et al.* 2009; Taylor & Goldingay 2010). Responses of native animals of different species to linear clearing are highly variable, and identifying and understanding responses by animals therefore warrant scientific investigation.

The majority of published research on behavioural responses of animals to linear clearings has dealt specifically with roads (Forman & Alexander 1998; Trombulak & Frissell 2000; Forman 2003; Van der Ree *et al.* 2015), usually defined as permanent or semipermanent access pathways, sealed or unsealed, that receive some degree of maintenance. By contrast, seismic lines are temporary tracks (used for <6 months), during a seismic survey for petroleum, then left to recover. Seismic surveys have been occurring in Australia for over 40 years, often covering a large area (~20 000 ha). Recovering seismic lines are therefore common features across much of remote Australia. Seismic lines differ from the majority of roads by virtue of their extensive and broad spatial nature (a grid pattern with lines ~250 m apart), but they are usually not maintained and are therefore generally more temporary in nature. Therefore, the responses of animals to seismic lines likely differ from their interactions with roads (e.g. Cerboncini *et al.* 2015).

We investigated the use of seismic line clearings by predator and prey species at a site in the West Kimberley, north-west Australia, where there has been extensive anthropogenic disturbance through live-stock grazing, and recently at a localized scale, seismic surveys. Populations of the medium-sized, nocturnal greater bilby (*Macrotis lagotis*) were present at these sites. These marsupials have suffered a

dramatic range contraction after European colonization of Australia (Southgate 1990a; Woinarski *et al.* 2014). Introduced predators (feral cat and red fox) have been identified as a key factor threatening the bilby, along with cattle grazing and inappropriate fire regimes (Pavey 2006; Woinarski *et al.* 2014). Understanding whether linear clearings increase predation risk for bilbies is therefore key to wildlife management of these disturbed areas (May & Norton 1996; Goosem 2004).

We used a paired camera trap array to investigate the activity patterns of six species, on and off seismic lines. Firstly, we tested whether there was differential use of seismic lines compared with adjacent undisturbed vegetation. We predicted that predators and cattle were more likely to use seismic lines as part of movements across the landscape towards and away from water or to access hunting sites, while herbivores (macropods) and bilbies would more likely avoid the clearings. We synthesized the camera data with microhabitat selection for two individual bilbies using spool tracking. Secondly, we compared temporal activity patterns on and off the seismic lines, to identify changes in behaviour associated with seismic line use. Thirdly, we compared use of seismic lines at sites cleared at different times as the lines recovered and passively revegetated. Lastly, an unplanned fire at one site allowed us to opportunistically test the effect of removal of all vegetation on the selective use of seismic lines.

METHODS

Study sites

The West Kimberley region, in the north-west of Western Australia, has a tropical, monsoonal climate, with an annual average of 500 mm of rainfall during November to April (Appendix S1). 'Pindan' vegetation, typical of the west Kimberley and Dampier Peninsula (Kenneally *et al.* 1996), was dominant across all three sites.

Three populations of bilbies were surveyed in this study: the Grass-seed population (GSP), Judi population (JP), and Kurrajong population (KP) which was surveyed twice (Appendix S2). The three sites were selected as they were the only bilby populations in the area. Bilbies are not evenly distributed throughout the areas they occupy; rather, they exist in small isolated populations and as such may be considered independent. A fire burnt GSP on day 85 of the survey, consuming all understory vegetation. At all sites, seismic surveys had been carried out, involving clearing ~4-m-wide tracks, in a grid pattern, separated by approximately 250 m

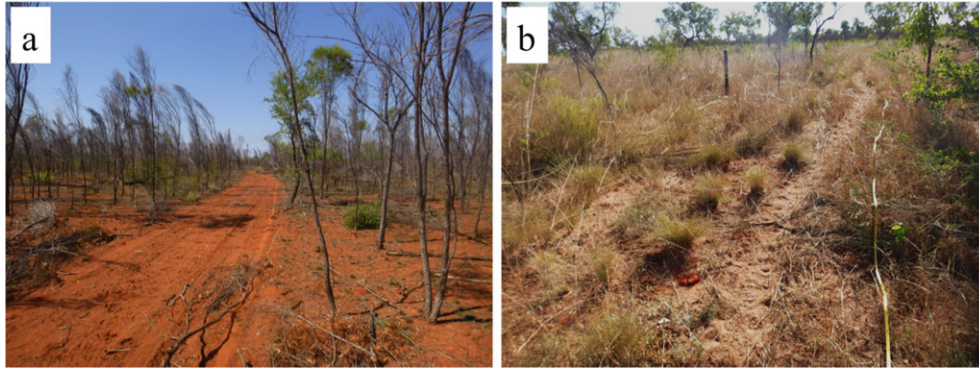


Fig. 1. Examples of variation in vegetation across sites. (a) JP, showing a 3 mo seismic line, and the associated *Acacia* woodland, characteristics of both JP and KP. (b) is GSP, showing a 48-month seismic line, and the associated grassland. Note the presence of a 'cattle track' in GSP. [Colour figure can be viewed at wileyonlinelibrary.com]

(Appendix S1 and S2). Two populations (KP and JP) were located during clearing, and GSP was cleared prior to the commencement of the study; therefore, no populations were monitored prior to clearing. Seismic lines used in this study were in various stages of recovery, ranging from no vegetation on the track at 1 month post-clearing to minor differences to the surrounding vegetation at 48 months post-clearing (Fig. 1, Buru Energy Ltd., unpub. data, 2016). The sites were subject to cattle grazing, and all seismic lines showed signs of cattle use, evidenced by tracks, scats and sightings.

Camera trapping

Four surveys were undertaken between June 2015 and August 2016. A camera trap array was made up of paired cameras, with one camera positioned on a seismic line (seismic station), and another camera ~20 m from the seismic line in adjacent vegetation (control station). The extent of each survey was determined by the area occupied by bilbies (estimated by the extent of burrows), with cameras spaced to cover the full extent of the burrows. Therefore, the spacing between camera pairs along seismic lines ranged between 50 and 150 m (Appendix S1 and S2). Cameras were not baited and positioned at a height of 400 mm on a metal stake. Each camera station had a small area to the front cleared of grass in order to minimize interference with the camera function. Cameras on seismic lines were designed to face approximately 22.5° to the track, in a southerly direction, to avoid glare from the sun triggering the camera. Four camera models were used as follows: three Reconyx models (HC500, HC600 and PC900) and Scoutguard SG860C (white flash model). Cameras were paired 'on' and 'off' track by type to avoid treatment bias due to camera model.

The duration of camera deployment was determined by the availability of cameras, seasonal access to the sites and the need to survey multiple sites for replication, resulting in differences in effort between surveys. KP1 was surveyed for 40 days, JP for 65 days, KP2 for 91 days and GSP for 85 days before fire, and 40 days post-fire (Appendix S2). In addition, there was variation within surveys in total trap effort between treatments (seismic and control) due to individual camera's memory or batteries being exhausted or physical disturbance (i.e. being moved or knocked to the ground) (Appendix S2). 'Disturbed' cameras still took photographs; however, the altered field of view (and resulting detection probability) warranted exclusion. We standardized trap data by the number of camera nights (one camera open for 24-h period) by either calculating a trap rate (captures per day), or for analyses which required actual numbers of captures (chi-square test; χ^2); differences in trap effort were standardized by multiplying the raw captures of one survey by a correction factor proportional to the difference in trap nights (e.g. 20 captures in 20 days in A and 20 captures in 19 days in B. Therefore, we multiplied trap captures in B by 1.052 to correct for trap effort).

For each photo capture, we identified the time, species present and approximate distance from the camera (using known landmarks). Visibility was greater on seismic lines due to reduced vegetation cover; therefore, the depth of view of each control site was estimated and animals captured beyond this distance on the paired seismic line camera were discarded (0.007% of total captures). Captures of the same species were considered independent if they were obviously different individuals, or separated by more than 10 min. Large groups of highly gregarious species (cattle and agile wallabies) were considered as a single capture. Only feral cats could be identified to individual (identification performed using pelage).

Spool tracking

Spool tracking is a simple and well used method of investigating habitat use, especially for small species (Glen & Dickman 2006; Prevedello & Vieira 2010). Two bilbies were trapped overnight from their burrow. Trapping was undertaken in June and July 2015 at GSP (13 nights). Occupied burrows (identified based on camera trap monitoring and sign on the sand apron) were trapped using the 'burrow trap' method (McGregor & Moseby 2014). Traps were baited with rolled oats and peanut butter and were left for a maximum of two consecutive nights. Bilbies had a ~230 m length of nylon spool (mass = 6 g) attached to their tail using 'Leukoplast' tape, with the loose end of the thread tied to nearby vegetation. Once processed, the animal was released back into the burrow in which it was caught. When it emerged from the burrow the following night (at least 10 h later), it was assumed to be acting 'normally'; therefore, the movement trail should not show escape behaviour.

Following the spool the day after release, the density of vegetation the animal moved through was recorded every 2 m using a touchpole. The number of vegetation intercepts was recorded for three height brackets (0–10 cm, 10–30 cm and 30–100 cm). Two 'control' paths were similarly measured: a 'path control' 1 m to the side of the thread and a 'compass control', taken on straight-line transects starting at the burrow on cardinal compass bearings and not moving more than the maximum straight-line distance that the spool went from the burrow (Fig. 4). Care was taken when sampling vegetation not to push down any grasses on the transect (changing the measurements gained by the touch pole). The path used was recorded using a handheld GPS.

Statistical analyses

Only the six most commonly caught species were included in statistical analysis (cattle, dingo, cats, bilbies, agile wallabies and spectacled hare wallabies). To test for use or avoidance of seismic lines, a chi-square test was conducted on the standardized number of captures on seismic and control cameras. Expected values were calculated by assuming equal probability of captures on both treatments. Tests were conducted for each individual survey (pooling camera data within each treatment within a survey) and then also for the data overall (pooling camera data within each treatment across all surveys). To test for the frequency of 'capture strings' (i.e. animals following a seismic line and being captured on

adjacent cameras), we identified incidents of captures of the same species on adjacent cameras of the same treatment, within 1 h.

We tested for changes in the proportion of captures on seismic lines across the four times since clearing using a chi-square test, with expected values calculated assuming there was no difference across the four time points. The post-fire period at GSP was excluded from this analysis. Spectacled hare wallabies were also excluded from this analysis as they were present at only one site.

To identify temporal patterns in activity for the five most common species (spectacled hare wallabies were excluded as they were found at only one site), and compare between species and across treatments, we used the timestamp record from all captures in the *Overlap* package version 0.2.6 (Meredith & Ridout 2014). *Overlap* uses nonparametric kernel density curves using a default smoothing parameter to characterize the probability density distribution of the activity pattern of each species. The smoothing parameter ($1/c$) is the inverse of the von Mises kernel (corresponding to a circular distribution) concentration parameter (c). For each species pair, we calculated the total overlap (Δ) as the measure of overlap between the two species' estimated distributions, ranging from 0 (no overlap) to 1 (total overlap). Three estimators are available for use in the package; we used Δ_4 when the smaller sample size in the pair was greater than 75, and Δ_1 when the smaller sample size in the pair was less than 50 (Meredith & Ridout 2014). We estimated 95% confidence intervals from 10 000 smoothed bootstrap samples, after correcting for the bootstrap bias. For each comparison of temporal patterns (comparing species, or comparing treatments), a Mardia–Watson–Wheeler test for homogeneity was conducted in the *circular* package version 0.4-7 (Agostinelli & Lund 2013). This test detects difference in the mean angle of circular temporal data, which is representative of temporal peaks in activity. This test requires a minimum of 10 observations and assumes no repeat data. Captures were therefore pooled across the four surveys for the temporal analyses, and captures recorded at identical times were adjusted by 0.86 seconds [overlap accepts 24 h time on a 0 (00:00:00) – 0.99999 (23:59:59) scale, meaning an adjustment of 0.00001 resulted in 0.86 s]. All statistical tests of temporal patterns were conducted using R version 3.3.2.

We monitored GSP pre- and post-fire (for 85 and 40 days, respectively), comparing selection between seismic and control stations pre- and post-fire using a chi-square test. Expected values were calculated assuming equal probability of capture between treatments and prefire/post-fire.

RESULTS

Response to seismic lines

In total, 3068 separate trap events of 28 species were recorded over 10 610 trap days from 822 648 images (Appendix S3). Of the 120 captures of cats, 93.64% were identified to individual, with a total of 15 individuals and an average of 5.25 (SD = 2.22) individual cats in each population (range: 3–8). An asymptote was reached for 3 of the four surveys, suggesting all individuals present during the survey had been recorded. Cats were the only species for which number of individuals could be estimated.

In descending order of frequency of observations, agile wallabies, cattle, bilbies, cats and dingoes were

trapped on seismic line stations more than control stations (Fig. 2). Spectacled hare wallabies were trapped on control stations significantly more than on seismic line stations (Fig. 2).

Two species were commonly seen on multiple consecutive cameras moving down a seismic line; cattle (45.5% of total captures were as a string) and dingoes (39.7% of total captures were as a string), with strings of greater than two captures recorded (12.7% for cattle; 12.3% for dingoes). Recording the same species on multiple consecutive cameras in control areas was much less common (4.3% for cattle; nil for dingoes) (Fig. 4). Less commonly seen in string captures, were bilbies (17.9% of captures) and agile wallabies (13.4% of captures), again with a greater likelihood of string captures on seismic line stations than for control stations. Cats were seldom seen on consecutive cameras (Fig. 3),

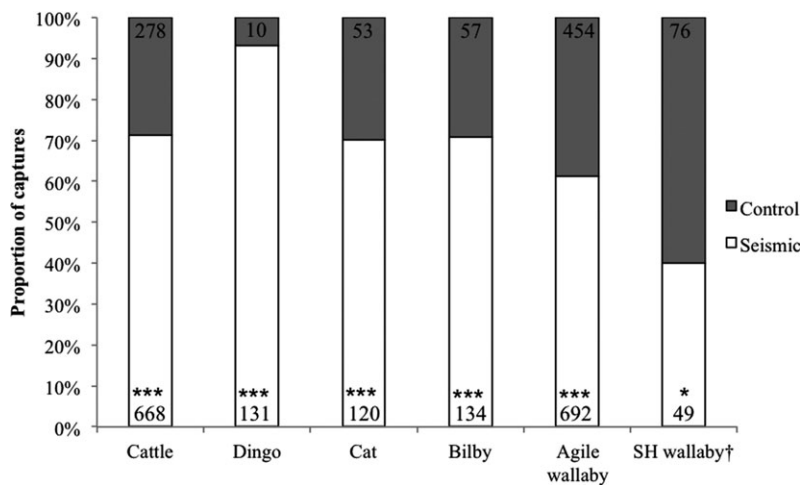


Fig. 2. The proportion of captures in each site, pooled across all four surveys. n in each treatment indicated in each bar. ‘†’ indicates species found at only one site. * indicates $P < 0.05$. *** indicates $P < 0.001$.

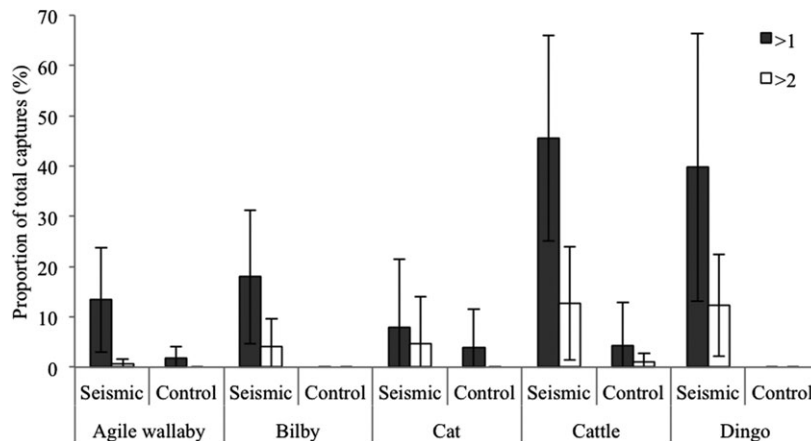


Fig. 3. The proportion (%) of total captures that were part of a ‘string’ of captures of differing length (>1, and >2). Error bars represent standard deviation.

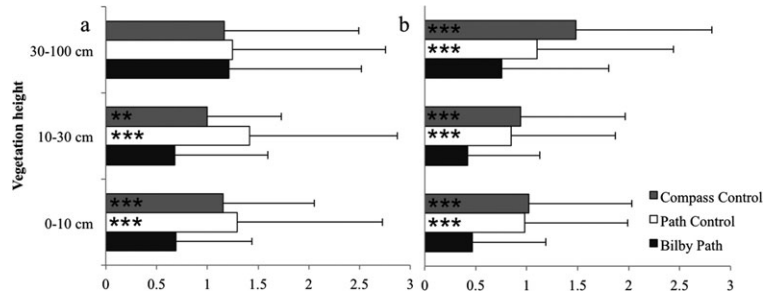


Fig. 4. The vegetation density, measured as number of intercepts of touch pole, at three height brackets, at 2-m intervals along the bilby path, path control and four compass controls. Bilbies *a* and *b* are labelled accordingly. Error bars are standard deviation. Significance was calculated by comparison with bilby path. ** indicates $P < 0.01$. *** indicates $P < 0.001$.

except in the GSP surveys, where 27.9% of captures on seismic line stations were part of a string, compared to 15.4% on control sites (Fig. 3).

Spool tracking

Two bilbies were caught and spool-tracked, resulting in 320 m (128 m and 192 m) of movement being recorded. Both animals ('a' and 'b') showed selection for a more open path at the 0–10 cm level (a: $\chi^2 = 18.11$, $P < 0.001$, b: $\chi^2 = 26.32$, $P < 0.001$) and the 10–30 cm level (a: $\chi^2 = 25.04$, $P < 0.001$, b: $\chi^2 = 20.50$, $P < 0.001$); however, only one animal showed selection at the 30–100 cm level (b: $\chi^2 = 57.62$, $P < 0.001$), a height which would be above the animal (Fig. 4). The path taken by both animals was also more open than the compass control transects, at both the 0–10 cm (a: $\chi^2 = 12.04$, $P < 0.001$, b: $\chi^2 = 29.49$, $P < 0.001$) and 10–30 cm levels (a: $\chi^2 = 6.78$, $P < 0.05$, b: $\chi^2 = 27.63$, $P < 0.001$), with one animal also showing selection for more open movement paths at the 30–100 cm level (b: $\chi^2 = 91.97$, $P < 0.001$).

Time since clearing

Agile wallabies and bilbies showed significant changes in microhabitat selection between the four times since clearing, encapsulated in the four surveys (agile wallabies: $\chi^2 = 144.68$, $P < 0.001$; bilbies: $\chi^2 = 22.54$, $P < 0.001$) (Fig. 5). At 1 month post-clearing, 78% of bilby captures were on seismic lines, which fell to 60% at 7 months, but then rose to 81% at 48 months. The proportion of agile wallaby captures on seismic lines declined with time since clearing from 90% of captures on seismic lines at 1 month to 41% of captures at 48 months. Cattle ($\chi^2 = 6.76$, $P = 0.08$), cats ($\chi^2 = 3.26$, $P = 0.35$) and dingoes ($\chi^2 = 2.89$, $P = 0.44$) showed no difference in the proportion of captures on seismic lines across the 4 surveys; all three consistently selected for seismic lines (Fig. 5).

Temporal activity patterns on and off seismic lines

Native prey species showed no significant difference in activity times between seismic lines and control

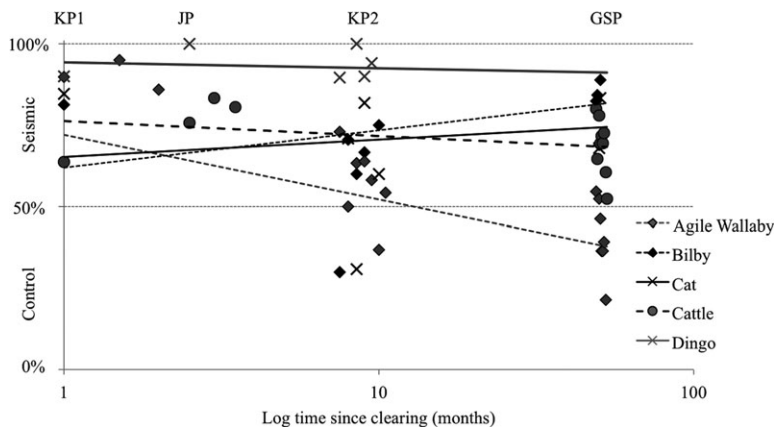


Fig. 5. Percentage of captures at seismic and control sites over time since clearing, for the species found in all four surveys. Markers indicate trap proportions pooled into 30-day bins. Trend lines of predators are shown in solid lines, herbivores in small dashed lines and cattle in large dashed lines. Only 30-day bins with more than 10 captures in total were plotted.

areas (bilbies $W = 0.46$, $P = 0.79$; agile wallabies $W = 0.18$, $P = 0.91$). Conversely, predator species and cattle showed significant differences in activity times between treatments (cats: $W = 10.92$, $P < 0.01$; dingoes: $W = 6.45$, $P < 0.05$; cattle: $W = 11.44$, $P < 0.01$).

All species in the current study were nocturnal or crepuscular; regardless of high levels of overlap,

however, the majority of species were active at different times to each other (Fig. 6, Appendix S4). The only exceptions were cats and dingoes in control areas, and cats and cattle in control areas, which showed no significant difference in peak activity times, although this result may be an artefact of low sample sizes of those species/treatment combinations ($n = 53$ captures of cats and $n = 10$ for dingoes at control stations).

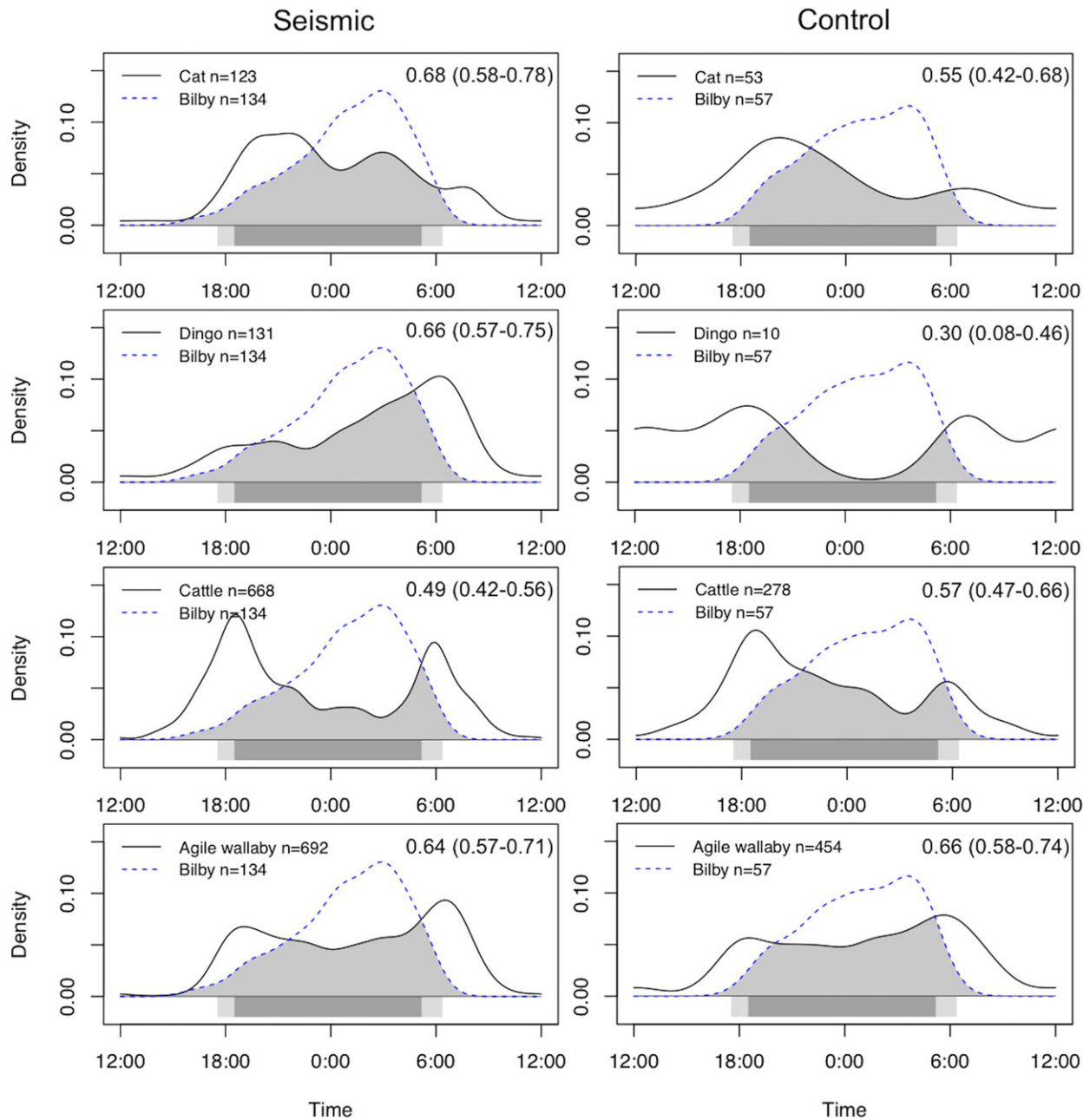


Fig. 6. Temporal patterns in activity between bilbies (dotted line) and other study species. Area under both curves shaded in grey. Grey bars below x-axis s indicate hours of darkness, with the light grey buffers indicating season changes in sunrise and sunset. Values in the top right hand corner of each graph represent the proportion overlap in temporal activity (with 95% confidence intervals in brackets).

Bilbies had the lowest overlap with all other species across both treatments, with significant differences in activity times (Appendix S4). Bilbies showed greater temporal overlap with herbivorous species (agile wallaby and cattle) at control stations than on seismic lines, but showed greater temporal overlap with predator species (dingo and cat) on seismic lines compared with control stations (Fig. 6, Appendix S4).

Effect of fire on the selective use of seismic lines

The capture rate during the survey period after the fire at GSP was reduced for bilbies (94% reduction, $\chi^2 = 35.10$, $P < 0.001$), cats (78% reduction, $\chi^2 = 12.93$, $P < 0.001$), dingoes (84% reduction, $\chi^2 = 4.34$, $P < 0.05$) and spectacled hare wallabies (85% reduction, $\chi^2 = 36.56$, $P < 0.001$). There was no significant difference in capture rate before and after fire for cattle and agile wallabies. Due to the reduction in capture rates, statistical tests could only be conducted for data on cats, cattle and agile wallabies. Cattle showed significant selection for seismic lines both before (73% of captures on seismic lines, $\chi^2 = 57.50$, $P < 0.001$) and after fire (64% of captures on seismic lines, $\chi^2 = 21.71$, $P < 0.001$). There was an increase in the capture rate of cattle for control stations post-fire ($\chi^2 = 3.40$, $P < 0.05$), resulting in the strength of selection being weaker post-fire. Cats showed strong selection for seismic lines before fire ($\chi^2 = 9.86$, $P < 0.01$), but no significant selection post-fire ($\chi^2 = 0.29$, $P = 0.658$). Agile wallabies showed no selection before fire ($\chi^2 = 1.11$, $P = 0.22$), but significant avoidance of seismic lines post-fire ($\chi^2 = 6.876$, $P < 0.01$).

DISCUSSION

Our study shows that bilbies, cats, dingoes, cattle and agile wallabies are funnelled on seismic lines at both a spatial and temporal scale. The only species that avoided seismic lines was spectacled hare wallabies. Individual bilbies selected for the most open route while moving through the undergrowth, explaining the observed selection for seismic lines. The use of seismic lines by bilbies and agile wallabies varied with the age of clearing, while cats, dingoes and cattle consistently used the lines as they recovered over time, and cattle movements are likely to have kept the paths relatively clear of vegetation. Removal of the grassy understorey by fire caused a dramatic decrease in capture rate of all species except cattle, which were unaffected by the removal of vegetation and continued to use the seismic lines in preference to adjacent paths through the bush.

Response to seismic lines

Five of the six species in the current study selected for seismic lines. While this result corroborates previous studies on predators in Australia (Mahon *et al.* 1998; Robley *et al.* 2010; Bengsen *et al.* 2012; Pastro 2013; Read *et al.* 2015), it is unexpected for native herbivores. Generally, studies of the effect of linear clearing on native herbivores have focused on roads with traffic and have identified a 'barrier effect', where animals avoid a linear disturbance (Goosem 2004; Laurance *et al.* 2009; Taylor & Goldingay 2010); none have identified selection for linear clearing by such species in Australia. The use of linear clearings by small mammals has been identified previously in other regions (Prevedello & Vieira 2010).

Cattle showed strong selection for seismic lines, quantifying anecdotal records for rangeland cattle throughout northern Australia. Similarly, studies from America have identified road use by cattle (Roath & Krueger 1982). The use of seismic lines by cattle may maintain their open structure and hinder regrowth of vegetation along the lines. Their continued use of these paths may therefore sustain the impact of seismic clearings.

Dingoes and cats both showed selection for seismic lines in the current study, supporting previous published studies that these predators show preference for open, cleared tracks (Mahon *et al.* 1998; Read & Eldridge 2010; Robley *et al.* 2010). The incursion of predators using roads for access is one of the consequences of the creation of linear clearings (May & Norton 1996; Forman & Alexander 1998; Trombulak & Frissell 2000). The additional selection for seismic lines by bilbies and agile wallabies suggests that the creation of seismic lines has funnelled both predator and prey species into a reduced movement corridor, which may increase the chance of encounter, thereby increasing predation risk for these prey species (Pastorok 1981).

By contrast with the other species, we recorded spectacled hare wallabies significantly avoided seismic lines overall. This difference could reflect their antipredator responses. Spectacled hare wallabies require shelter sites in close proximity to feeding areas in order to remain hidden from predators (cats and dingoes) (Ingleby & Westoby 1992). We hypothesize that spectacled hare wallabies (1.6–4.5 kg) (Menkhorst & Knight 2010) avoid seismic lines to remain within cover, and studies of the closely related rufous hare wallaby (*Lagorchestes hirsutus*) indicate that they retreat to cover when disturbed (McLean *et al.* 1996). By comparison, the larger agile wallaby (9–27 kg) (Menkhorst & Knight 2010) appears to rely on speed for escape rather than remaining hidden, and therefore, rather than aiding concealment, dense understorey would be an obstruction to escape. Similar

differences in antipredator responses with body size have been noted for tammar wallabies (*Macropus eugenii* 6–10 kg, which uses understory as cover and forages close to vegetation) and western grey kangaroos (*Macropus fuliginosus* 28–54 kg forage in the centre of clearings and perceive vegetation as an obstruction) (Blumstein & Daniel 2002). The behaviour of bilbies is therefore interesting, because despite their small size (1.1–2.5 kg), these animals appear to rely on escape running rather than use of cover for protection, and they select to use linear clearings for movement.

Spool tracking

The unexpected selection of seismic lines by bilbies is congruent with their microhabitat selection recorded during spool tracking. Bilbies selected vegetation that was more open than surrounding vegetation at heights relevant to their stature (0–10 cm and 10–30 cm categories), both at a fine scale (compared to the vegetation within 1 m) and at a broader scale (compared to available habitat). This indicates that, during natural movement patterns, bilbies selected an open route for movement. This corroborates with anecdotal observations that bilbies show limited ability to avoid vegetation during escape running (Moseby pers. obs.), making selection of a more open route beneficial for survival. Additionally, the path control of both animals spool-tracked was more open than the compass control, indicating that they selected both a more open area to move through, and a more open path within that area to travel along. It is important to note that given the small sample size, these results are only considered in the context of the broader camera trapping data presented in the current study.

In addition to broader scale preference for open understory recorded for bilbies (Southgate 1990b), the use of open ‘runways’ through the understory for movement has been shown in other species (Tasker & Dickman 2001; Prevedello & Vieira 2010). The use of runways is likely to be a preference for ease of movement, as creating a new path through a grassy understory would be energetically expensive. Bilbies use multiple burrows throughout their home range during the night and will retreat to a burrow if startled (Johnson & Johnson 1983). Regular use of the same open routes throughout the night might increase the efficiency and speed with which they can find, and retreat to, a burrow. In addition, regular use may keep such routes more open.

Time since clearing

Cats, dingoes, cattle and bilbies showed a consistent selection for seismic lines over time, even as

vegetation regrows and the seismic line become less distinguishable from the adjacent vegetation (Fig. 1). Large, hard-hooved mammals are likely to disrupt topsoil and trample vegetation (Dunne *et al.* 2011) more than smaller, native herbivore species. The high levels of use of seismic lines by cattle throughout the study may hinder the recovery of vegetation on seismic lines. Surveys of sentinel sites spread across the exploration lease indicate that vegetation cover on seismic lines is slightly lower than control sites after 4 years, and cattle tracks are present on seismic lines at many sites (Buru Energy Ltd., unpub. data, 2016). Agile wallabies selected for seismic lines soon after clearing, but the strength of selection faded over time.

Temporal patterns

Native prey species (bilbies and agile wallabies) showed no difference in activity times between treatments (presumably because they use them as part of their foraging activities) while predator species and cattle showed a significant difference in activity times between treatments. Bilbies were strictly nocturnal with a peak in activity at around 3 a.m., similar to the patterns reported in previous studies (Johnson & Johnson 1983). Given the activity patterns of bilbies did not change between treatments, a higher overlap between bilbies and their predators on seismic lines is likely due to a shift in the spatiotemporal patterns of dingoes and cats. On seismic lines, cats show a small peak in activity at 3 a.m., corresponding to the peak activity time of bilbies. Such temporal funneling of species on seismic lines may affect the vulnerability of prey species to predation (Pastorok 1981). However, an important caveat is that while temporal overlap between bilbies and cats was greater on seismic lines than in control areas, there were still significant differences in overall activity times for these two species across both treatments. As such, we believe that the relationship between bilby and cat activity times should not be considered a causal relationship.

Predators and cattle may use seismic lines for different activities compared with control areas and therefore show activity at different times. Dingoes and cats have large home ranges (Moseby *et al.* 2009) and are likely to be using seismic lines as movement pathways and control areas for hunting or sheltering. For example, dingoes are highly nocturnal/crepuscular on seismic lines, while activity in control areas is largely diurnal. This may represent two discrete behaviours: movement on seismic lines, and shelter during the hot daytime hours in control areas, where cover is more plentiful, consistent with previous studies (Thomson 1992).

Effect of fire

The removal of vegetation at GSP by fire dramatically reduced the capture rate of all species except cattle and agile wallabies. Cattle still showed strong selection for seismic lines after fire, in the absence of vegetation, indicating that the use of the seismic line is at least partly independent of the vegetation. This suggests that cattle follow tracks using cues other than vegetation in their daily routine movement away from, and returning to water (Lange 1969). We recorded a reduction in the capture rate of cats, but no selection or avoidance of seismic lines by cats after fire. This suggests that the primary reason for selection of seismic lines by cats was for ease of movement through the understory, the removal of which enabled them to move 'randomly' through the landscape, independent of seismic lines. Although they were still present at this site post-fire, agile wallabies avoided seismic lines after fire. With no difference in vegetation between treatments after fire (both were bare), this avoidance is possibly explained by an avoidance of disturbance by cattle.

Removal of the grassy understory by fire appears to have resulted in reduced activity of bilbies, dingoes and spectacled hare wallabies, with dramatic reduction in capture rates. The removal of cover is likely to make small herbivore species more susceptible to predation (Conner *et al.* 2011) which may explain their avoidance of the area. Complete removal of the understory is likely to remove food items, making the area unattractive for herbivores. Even though bilbies are reported to use fire-promoted plant species (Southgate & Carthew 2007), these plants can take months to germinate and grow, depending on rainfall. Burnt areas are also likely to be less favoured by dingoes for diurnal rest sites or hunting.

Methodology and limitations

A limitation of this study was that we were not able to identify how many individuals contributed to the activity data recorded at each site. Bilbies are found in isolated groups, which generally contain less than three individuals (Johnson 1989). Bilby populations were not randomly selected, as all populations exposed to seismic clearing during the study period were included. Therefore, as this study examined three populations, it is likely that the camera trapping component represents the habitat selection of less than 10 individuals. Similarly, the spool tracking data from two individuals are a small sample size. However, the consistency of the selection for a more open route (from both spool tracking and camera trapping) suggests that the observed patterns are ecologically meaningful. The only species for which individuals could be reliably identified from photos was cats. We

recorded 3–8 individual cats across the 4 surveys, making a total of 15 cats. Despite these arguably low numbers of individuals, the experimental design was such that it enabled direct comparison of activity patterns between seismic lines and adjacent control sites and is therefore independent of requiring population density estimates (see Burton *et al.* 2015).

The timeline of the study precluded individual populations being monitored over more than 7 months, with different populations being used to represent different time since clearing. As such, variability between sites may influence the habitat selection at each. We believe that the consistency of response shown by numerous species indicates that the behaviour is representative of the wider population.

Because we were not able to estimate bilby population density, or calculate any measure of the persistence of bilby populations, no comment can be made regarding the direct effect of funnelling bilbies onto seismic lines on their predation risk. Long-term studies of bilby population exposed to cats and linear clearing are required to identify impacts. However, we note that the discontinuous distribution of these species across the landscape would make it very difficult to obtain sufficient statistical power to quantify this relationship.

Another issue that we noted was the temperature dependence of camera data and therefore its influence on temporal patterns. Camera traps detect animals using a passive infrared (PIR) sensor, which identifies heat differential, that is a body (animal) is hotter or colder than the ambient temperature. When the body temperature of the animal is close to the ambient temperature, the chance of triggering the camera is reduced (Meek *et al.* 2012). We therefore expect that we captured less diurnal activity using our camera traps due to hot daytime temperatures reducing the detection probability of cameras. This should not influence conclusions made regarding the difference between seismic lines and control stations, but may somewhat underestimate diurnal activity records.

Seismic camera sites were 'connected' by a seismic line, while control cameras had no such connection to each other. Dingoes, cattle and bilbies were seen in 'strings' of captures more commonly on seismic lines. This indicates that animals followed seismic lines for long distances (>100 m), which has been recorded previously (Mahon *et al.* 1998; Read & Eldridge 2010; Robley *et al.* 2010). While this may suggest a degree of spatial autocorrelation of cameras on seismic lines and resulting pseudoreplication, it actually illustrates the very point of the current study.

CONCLUSIONS

The current study shows that spatial and temporal overlap of bilbies, cats, dingoes, cattle and agile

wallabies is greater on seismic lines than in control areas, a finding that was consistent throughout the recovery process recorded (with the exception of agile wallabies). By contrast, spectacled hare wallabies avoided seismic lines. The removal of vegetation by fire removes the selection of seismic lines by cats and causes agile wallabies to avoid them, while having no impact on the selection by cattle. The strong selection for seismic lines by cattle and the resulting potential effects on vegetation recovery suggest that further research should be conducted into the impact of cattle use on seismic line recovery.

Previous studies of predator–prey relationships around seismic lines have identified use of the lines by wolves, causing avoidance by caribou (in response to an increased predation risk), resulting in functional habitat loss (Latham *et al.* 2011). In contrast, the current study identifies selection for seismic lines by prey species. The spatial and temporal funnelling of bilbies (a vulnerable species) and cats may increase the frequency of encounter, which in turn may increase the vulnerability of bilbies to predation. The impact of landscape level disturbances, such as fire, on feral cats, has recently been brought to light (McGregor *et al.* 2014, 2017). Similarly, understanding the effects of clearing on feral cats, and the native species that they threaten, is key to informing management strategies. We suggest investigation of the efficacy of feral cat management targeted areas subject to clearing for seismic surveys may inform potential threat mitigation strategies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 The location of study sites in relation to Australia, the local west Kimberley region, and each other.

Appendix S2. Information pertaining to each survey.

Appendix S3. A summary of capture statistics for the current study.

Appendix S4. The degree of overlap in temporal activity patterns between all combinations of the five

species found in all surveys, with the 95% confidence intervals in brackets.