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Bioturbation by a reintroduced digging mammal reduces fuel loads in an urban reserve

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Abstract. Digging animals may alter many characteristics of their environment as they disrupt and modify the ground's surface by creating foraging pits or burrows. Extensive disturbance to the soil and litter layer changes litter distribution and availability, potentially altering fuel loads. In many landscapes, including peri-urban areas, fire management to reduce fuel loads is complex and challenging. The reintroduction of previously common digging animals, many of which are now threatened, may have the added benefit of reducing fuel loads. We experimentally examined how the reintroduction of a marsupial bandicoot, quenda (*Isoodon fusciventer*), altered surface fuel loads in an urban bush reserve in Perth, Western Australia. Foraging activities of quenda (where they dig for subterranean food) were substantial throughout the reserve, creating a visibly patchy distribution in surface litter. Further, in open plots where quenda had access, compared to fenced plots where quenda were excluded, quenda foraging significantly reduced litter cover and litter depth. Similarly, estimated surface fuel loads were nearly halved in open plots where quenda foraged compared to fenced plots where quenda were absent (3.6 cf. 6.4 Mg/ha). Fire behavior modeling, using the estimated surface fuel loads, indicated the predicted rate of spread of fire were significantly lower for open plots where quenda foraged compared to fenced plots under both low (29.2 cf. 51.4 m/h; total fuels) and high (74.3 cf. 130.4 m/h; total fuels) fire conditions. Although many environments require fire, including the bushland where this study occurred, fire management can be a considerable challenge in many landscapes, including urban bushland reserves, which are usually small and close to human infrastructure. The reintroduction of previously common digging species may have potential value as a complimentary tool for reducing fuel loads, and potentially, fire risk.

Key words: *bandicoot; ecosystem engineer; fire management; fire regime; plant–animal interactions; quenda; reintroduction.*

INTRODUCTION

Animals that regularly dig for food or create burrows and whose soil turnover activities affect the availability of resources for other organisms are often considered ecosystem engineers (Jones et al. 1994). Through soil displacement, digging animals can enhance many ecosystem functions (Davidson et al. 2012, Fleming et al. 2014), including increased water infiltration, altered soil nutrients, altered microbial properties and enhanced seedling recruitment (James et al. 2010, Eldridge et al. 2016, Valentine et al. 2018) all of which are likely to influence vegetation and landscape structure (Whitford and Kay 1999). Furthermore, animals that disrupt the surface litter layer through their behaviors have recently been implicated in altering fuel loads (Nugent et al. 2014, Hayward et al. 2016, Smith et al. 2016). In this study, we examine the effect of digging activities of an Australian marsupial bandicoot, quenda (*Isoodon fusciventer*), on surface fuel loads, following their reintroduction in an urban bushland reserve.

The mechanisms by which animals can directly alter fuel loads include herbivory and through the production of bare ground. Fire and herbivory are important, interacting disturbances (van Langevelde et al. 2003), with herbivory playing a recognized role in altering fuel loads (Waldram et al. 2008, Leonard et al. 2010). However, less is understood about how the creation of bare ground by animals alters fuel loads. Although the nature of fire spread and intensity is complex, the surface fuel layer is an important determinant of fire behavior and releases much of the energy during a fire (Sullivan et al. 2012). Small scale variations in the surface fuel layer can alter fire behavior (Atkins and Hobbs 1995, Thaxton and Platt 2006) with discontinuities in the surface fuel layer impeding the spread of a low intensity fire (Gould et al. 2011).

Animals can create bare ground that may alter surface fuel loads and fire behavior in many ways. Through wallowing, foraging, nesting and burrowing, animals can

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reduce surface fuel layers. For example, American bison (*Bison bison*) were shown to create numerous deep wallows without vegetation that had an impact on reducing fire spread in North American grasslands (Knapp et al. 1999). In some situations, a combination of behaviors act in concert; for instance, Hierro et al. (2011) found that herbivory and the creation of burrows by the South American viscacha (*Lagostomus maximus*) acted like a fire-break around active burrows. Nest building by an Australian megapode, Malleefowl (*Leipoa ocellata*), involves gathering large amounts of litter into mounds, with fire behavior modeling suggesting that the bare ground around mounds can reduce fire intensity (Smith et al. 2016).

Digging for subterranean food or creating burrows may also modify the surface litter layers. In Australia, many of the medium-sized marsupials regularly dig (Fleming et al. 2014), potentially reducing fuel loads (Martin 2003, Hayward et al. 2016), via the mechanical effect of soil mixing and covering litter with soil, which may also enhance litter decomposition. At a landscape scale, animals contribute collectively to surface heterogeneity and patchiness by soil disturbance (Whitford and Kay 1999), potentially maintaining both open areas and areas of denser vegetation, that are important for long unburnt habitat refuges (Parr and Andersen 2006). The loss, decline and range contraction of many of Australia's medium-sized digging mammals (Fleming et al. 2014), predominantly attributed to predation from introduced cats (*Felis catus*) and red foxes (*Vulpes vulpes*; Woinarski et al. 2015), is likely to have drastically altered the surface heterogeneity of Australian landscapes.

Fuel load reduction in forest ecosystems, particularly in Mediterranean climates, is of increasing importance because of a higher incidence of fire weather due to climate change (Enright et al. 2015). Contemporary prescribed burning aims to manage fuel loads and fuel structure to mitigate effects of wildfire and has been used in Australia since the 1950s (Burrows and McCaw 2013), although anthropogenic fire has been used in Australia for thousands of years, typically creating patchy mosaics of different aged vegetation (Hassell and Dodson 2003). The cessation of traditional Aboriginal burning practices and altered fire management (Bowman 1998, Abbott and Burrows 2003), coupled with the loss of many digging mammals, means fuel loads are likely to be higher and more homogenous in contemporary times.

Reestablishing populations of digging mammals has been proposed as a potential tool for managing the risks of wildfire (Johnson et al. 2018). Translocations of previously common mammals occur throughout Australia providing an opportunity to collect information on altered fuel loads. Seminal research in this field was conducted by Hayward et al. (2016) in semiarid habitat at Scotia reserve (>64,000 ha) in southeastern Australia. Their research showed that litter mass, cover, and predicted fire spread were lower inside fences where three threatened digging mammals, the bilby (*Macrotis lagotis*), boodie (*Bettongia lesueur*), and woylie (*B. penicillata*), had been reintroduced during the previous 10 yr (Hayward et al. 2016). We contribute to this research area by examining surface fuel loads in an urban reserve, in a fire-prone Mediterranean climate, within a short time (<4 yr) of the reintroduction of a single digging mammal species.

In urban and peri-urban reserves with remnant native vegetation that is close to human habitations and infrastructure, fire management is challenging and often has competing interests (Gill and Stephens 2009, Driscoll et al. 2010). From a human safety perspective, there is a desire to minimize fuel loads in reserves to reduce the risk of wildfire (Gibbons et al. 2012). From a conservation management perspective, there may be a desire to maintain older post-fire-aged habitat to cater to the resource requirements of some wildlife, such as endangered Carnaby's Cockatoos (*Calyptorhynchus latirostris*; Valentine et al. 2014). Further, urban reserves typically also have the added goal of engaging people with nature (Standish et al. 2013). The ability of native digging mammals to reduce fuel loads may offer the advantage of a complementary fire management strategy. However, as most urban reserves are isolated and small, they may not support multiple species reintroductions where the reintroduced species use similar resources, and it is unknown if a single reintroduced digging mammal species can influence fuel load characteristics.

We examined if the translocation of quenda to an urban reserve of banksia woodlands in Perth, Western Australia, could alter surface fuel loads. Banksia woodlands are composed of a sclerophyllous layer of low trees (or tall shrubs) dominated by one or more *Banksia* spp., often interspersed with emergent *Eucalyptus* spp. and a species-rich understorey of sclerophyllous shrubs, sedges, and herbs. Due to ongoing threats, including habitat clearing, invasive species, and fire regime changes, the banksia woodlands in our study area are part of a threatened ecological community listed as Endangered under federal legislation through the *Environment Protection and Biodiversity Conservation Act 1999* (Threatened Species Scientific Committee 2016). These banksia woodlands are considered some of the most flammable woodlands in Australia (Burrows and Abbott 2003) and to reduce the risk of wildfire to human settlement, prescribed burning is undertaken (Wilson et al. 2014), though it remains a management challenge.

Although previously common throughout south-western Australia, due to a combination of threats, including habitat loss and predation by foxes and cats, quenda had declined throughout much of their range by the 1940s (Abbott 2008). Previous research indicates that the quenda's foraging habits of digging for subterranean prey turns over large amounts of soil (~4 Mg per individual annually; Valentine et al. 2013) and can alter soil and litter properties that subsequently influence seedling recruitment and growth (Valentine et al. 2017, 2018).

Our research explores (1) whether the digging activity of quenda altered microhabitat characteristics that influence surface fuel loads and (2) whether the microhabitat changes created by quenda could influence predicted fire behavior.

Materials and Methods

Study site

The study took place at Craigie Bushland (bushland is an Australian term for a remnant parcel of native vegetation), a 53-ha urban reserve approximately 20 km north of Perth, Western Australia (Appendix S1: Fig. S1). The reserve is considered to be an important remnant of bushland containing good condition habitat (Bush Forever site #303; Government of Western Australia 2000) of the endangered Banksia Woodlands of the Swan Coastal Plain ecological community (Threatened Species Scientific Committee 2016) and is managed by the City of Joondalup. The reserve is located within the Swan Coastal Plain bioregion (Thackway and Cresswell 1995) mostly on Spearwood dune systems with an open banksia woodland dominated by *Banksia attenuata* and *B. menziesii,* interspersed with jarrah (*Eucalyptus marginata*), tuart (*E. gomphocephala*), and marri (*Corymbia calophylla*). Prominent understorey species include *Xanthorrhoea preissii* and the sedge *Mesomelaena pseudostygia.* The area has not experienced widespread fire for at least 20 yr (K. Armstrong, *personal communication*).

The City of Joondalup constructed a 43.5-ha predator-proof fence in 2010 to exclude introduced cats and foxes from the reserve, although the public can access the site and its walking trails. A reintroduction translocation of 46 quenda occurred in mid-2013 by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA; A. Reaveley, *personal communication*). Few, if any, quenda were thought to occur in the bushland prior to the reintroduction. Since reintroduction, the population of quenda has steadily increased, with estimates indicating between 100 and 120 individuals residing in Craigie Bushland (L. Valentine, *unpublished data*). Quenda, a medium-sized (adults ~800–1,200 g) marsupial endemic to southwestern Australia, are omnivorous, feeding on invertebrates, including earthworms, beetles, and their larvae, as well as underground fungi and plant material. They regularly forage on subterranean fungal fruiting bodies and may play an important role in the dispersal of mycorrhizal fungi (Tay et al. 2018). Quenda are predominantly nocturnal and search for their food via olfaction, creating ~45 distinctive conical foraging pits per night, with each individual turning over nearly 4 Mg of soil annually (Valentine et al. 2013). Foraging pits are on average 7–8 cm deep and 10 cm wide, and have an associated spoil heap of evacuated soil, also known as the ejecta mound (Valentine et al. 2013). At the time of study, quenda were the only digging animals in the reserve. Only three western grey kangaroos (*Macropus fuliginosus*) were known to occur in the reserve, and their impact on plots was anticipated to be minimal.

Influence of quenda on microhabitat

To study the effect of quenda digging on microhabitat, five paired 10 × 10 m plots, with a minimum of 180 m between pairs, were established in April 2014 (Appendix S1: Fig. S1). Locations of paired plots were randomly selected from quenda trapping points established by DBCA along fire-break tracks, with each paired plot located a minimum of 30 m from the track edge and visually matched for broad habitat characteristics. As the plots were constructed ~9 months after quenda were translocated into the bushland reserve, quenda foraging pits were present in all plots initially. Microhabitat measurements (methods described below) taken within 2 weeks of fence erection indicated no significant differences in average litter depth (paired t test, $t_4 = 1.58$; $P > 0.05$) or bare ground created by quenda cover (paired t test, $t_4 = 0.42$; $P > 0.05$) between paired plots. The corner of each plot was marked using galvanized steel markers (One-Steel fence droppers, Cyclone, Perth, Australia; ~94 cm high). One plot in each pair was surrounded by a fence to exclude quenda (with a minimum 0.5-m buffer between the plot and fence) while the other plot remained open and was accessible by quenda. Fences were constructed from Waratah Longlife Blue Netting (1.8 m high × 4.0 cm diameter holes; 1.4 mm wire diameter mesh) and Waratah Galstar Extreme Steel posts (Waratah, Perth, Australia; 180 cm). The wire netting stood ~120 cm above the ground and had a 60 cm skirt that was pinned into the ground with 200-mm weed staples. Although we did not evaluate the effect of the fence itself, we do not believe the fences significantly influenced fuel loads in our study (e.g., by altering wind or run-off of litter) because (1) banksia woodlands are relatively flat, with deep, sandy soils and little water run-off, and (2) we did not visually detect build-up of litter on the fence perimeters and we allowed a buffer zone between the fence and the internal plots to account for subtle effects of the fence on wind movement of litter. At the time of sampling for this study (April–June 2017), the plots had been in place for 3 yr and we did not detect any incursions into the fenced plots (checks on fence integrity every 3 months and visual scans for signs of fresh/new diggings).

To estimate the amount of soil disturbance quenda produce the number of foraging pits were counted within each plot. At Craigie Bushland, quenda were the only digging mammal present and their foraging pits were easy to identify. The exposed soil of the spoil heap for each dig was measured (length and width; cm) using a ruler. As spoil heaps were typically oval, the equation for the area of an ellipse was used to estimate the bare ground for each foraging pit. The amount of bare ground quenda created while foraging (quenda bare ground) was calculated as the sum of each spoil-heap area converted to m^2/plot:

$$\text{quenda bare ground} = \sum \frac{\left(\frac{(\text{spoil heap length cm})}{2}\right) \times \left(\frac{(\text{spoil heap width cm})}{2}\right) \times \pi}{10000}. \qquad (1)$$

To ensure that our estimates of soil exposed by quenda were equitable among plots, we standardized by the proportion of surface area available for digging within each plot. For each plot, we drew the basal area of each digging impediment, such as large shrubs, trees, and fallen logs, within each square meter of the plot boundary on graph paper (1 mm^2 representing 10 cm^2). The resulting map mostly consisted of oval and round shapes requiring the equation for elliptical area. The number of square millimeters occupied by non-oval shapes was manually counted and converted to square meters. The total area of impediments in m^2/plot was subtracted from 100 to obtain total available digging area. We compared the mean number of quenda digs and area of quenda bare ground between fenced and open plots with paired *t* tests using log-transformed values when necessary to satisfy assumptions of normality. All data were analysed using R version 3.4.3 (R Core Team 2013).

The influence of quenda digging on microhabitat composition was measured from five 0.5 × 0.5 m quadrats in each plot (one quadrat in each plot quarter and one in the center of each plot). In each quadrat, we estimated the percentage (%) of litter cover, coarse woody debris, quenda bare ground, bare ground (not identifiably created by quenda), and vegetation (Appendix S1: Fig. S2). Litter depth (nearest mm, with a ruler averaged over three locations within quadrat) and canopy cover (using a hemispherical crown densiometer held at breast height) were also recorded. To analyze the effect of treatment (fenced and open) on quadrat microhabitat response variables, we used linear mixed-effect models in the lme4 package in R (Bates et al. 2015). Paired plot was the only random effect. Wald chi-squared tests were used to estimate *P* values of treatment from the car package in R. A visual inspection of data prior to applying the model showed no apparent deviations from homoscedasticity or normality. Microhabitat percentage data were arcsine transformed prior to analysis to normalize the distribution. Pearson's product moment correlation was used to examine possible correlations between microhabitat variables. When reporting values in the text, we use untransformed mean values with 95% CI.

Assessing surface fuel loads

Fuels can be divided into four main types of layers on their vertical arrangement: canopy, elevated fuel, near surface fuel, and surface fuel (Gould et al. 2011). As digging mammals may alter ground-level microhabitat characteristics, this study focuses on assessing surface fuel loads only. Surface fuels were composed of litter, twigs, bark, and other fine fuel lying on the ground (Gould and Cruz 2012) and were assessed by adapting fuel sampling techniques described in Fontaine et al. (2012) and Ruthrof et al. (2016). To characterize surface fuel loads, the fuel is often sorted into different size categories that represent time-lag fuel classes that indicate the time it takes, under specified conditions, for a fuel particle to lose (or gain) ~63% of the difference between its initial moisture and its equilibrium moisture (Gould and Cruz 2012). Standardized time-lag fuel classes (Gould and Cruz 2012) were adapted in this study and included: 1-h time-lag fuels (<6 mm), 10-h time-lag fuels (6–25 mm), and 100-h time-lag fuels (>25–70 mm); with the combined classes representing total surface fuels.

To estimate biomass of surface fuel loads in plots in a non-destructive manner, we developed a linear regression between litter depth (cm) and litter mass (g) using destructive sampling techniques similar to Fontaine et al. (2012) from outside the plots. In a ~2 ha area surrounding the paired plot locations, we assessed litter loads using 25 × 25 cm quadrats (*n* = 12–14 quadrats paired/plot, total of 65 quadrats) from locations with visibly varying litter cover (e.g., litter cover varying 10–100%). Within each quadrat, litter depth was measured with a ruler (mm, average of three places in the quadrat). The litter was then collected to mineral earth level, placed in paper bags, dried for 48 h at 60°C, weighed (providing total surface fuels, g), sorted into different time-lag fuel size categories (1-, 10- and 100-h), and weighed (g). No samples contained 100-h fuels and this size category was excluded from subsequent analysis. The derived linear regression models between litter depth and surface fuel load consisted of the correct functional form with normally distributed errors and without heteroscedasticity and auto-correlated errors.

We collected information on surface fuels within plots using the point interception method (Elzinga et al. 2001). At the point of intersection every 2 m along the edge and within the interior of each 10 × 10 m plot (*n* = 36 points/plot) we measured microhabitat (percent cover of vegetation, litter, coarse woody debris, and bare ground; and litter depth, mm) in a 25 × 25 cm quadrat. To estimate surface fuel loads within each plot, we used the subset of quadrats (range: 21–27) where litter was recorded as a variable, and inserted the measured values for litter depth (mm) in the derived linear regression models (Eqs. 3 and 4 in *Results*). The resultant value for surface fuel (total and time-lag fuel size categories) in g/quadrat were converted to Mg/ha and standardized in relation to the surface area available for digging within each plot.

Predicting fire behavior

To examine potential changes in fire behavior resulting from quenda digging at Craigie Bushland, we used the McArthur Forest Fire Danger Index (FFDI; McArthur 1967), to evaluate rate of forward spread (ROS) under high and low fire danger conditions according to the McArthur Mk5 Forest Fire Behavior model (Noble et al. 1980). The FFDI using the Keetch-Byram Drought Index (KBDI; Keetch and Byram 1968) for soil moisture component is used for evaluating fire danger in Australia (Lucas 2010, Kumar and Dharssi 2017) and was previously used to assess fire behavior in a large reserve with reintroduced digging mammals in semiarid habitat (Hayward et al. 2016).

Evaluations of the models indicate they may underestimate fire spread by a factor of two to three and perform best when wind speeds do not exceed 12.5 km/h (McCaw et al. 2008). The climate variables we used for calculating FFDI under high and low fire danger conditions (Table 1), included wind speeds <12.5 km/h to increase precision of the predicted forward rate of spread (McCaw et al. 2008). Climate data (Table 1) were collected from nearby Australian Bureau of Meteorology (BOM) weather stations (Swanbourne ID: 94614 and Ocean Reef ID: 009214) for high and low fire danger days. The estimated FFDI for Craigie Bushland based on these variables was 16.99 and 6.69 for the high and low fire danger day, respectively. The ROS was calculated according to Noble et al. (1980), using the fuel mass (Mg/ha) obtained for each plot (above) according to Eq. 2:

$$\mathrm{ROS} = 0.0012 \times \mathrm{FFDI} \times \text{fuel mass}. \qquad (2)$$

To compare surface fuel loads and estimated ROS between fenced and open plots, we used linear mixed-effect models in the lme4 package in R (Bates et al. 2015) with paired plot as a random effect. Wald chi-squared tests were used to estimate P-values from the car package in R. A visual inspection of data prior to applying the model showed no apparent deviations from homoscedasticity or normality.

Table 1. Climate variables used to calculate the Forest Fire Danger Index (FFDI) for Craigie Bushland under low fire danger (Low FD) and high fire danger (High FD) conditions.

Variable	Low FD	High FD	Source
Time	15:00	15:00	
Date	9 Sep 2017	4 Jan 2017	
Temperature	20.9°C	33.3°C	Swanbourne
Annual rainfall	673.2 mm	673.2 mm	Swanbourne
Days since rain	7	7	Swanbourne
Relative humidity	71%	17%	Swanbourne
Temperature (day before)	23.2°C	38.4°C	Swanbourne
Wind speed	11 km/h	7 km/h	Ocean Reef
Perth average Keetch-Byram	5.4 (Sep)	120 (Jan)	Lucas 2010

Notes: Climate data were sourced from nearby Australian Bureau of Meteorology (BOM) weather stations (Swanbourne ID: 009215 and Ocean Reef ID: 009214). Keetch-Byram index (Keetch and Byram 1968) is derived using data between 1974 and 2003 (Lucas 2010).

Results

Influence of quenda on microhabitat

There was a substantial difference in the mean number of quenda digs between treatments, with approximately 17 times the number of digs in the open plots, where quenda had access, compared to the fenced plots, where quenda were excluded ($t_4 = 9.12$, $P < 0.001$; open 161.0 ± 23.8 digs, fenced = 9.2 ± 6.7 digs). All the observed diggings in the fenced plots were created prior to the construction of the fence (3 yr earlier). The area of quenda bare ground was also substantially greater in open plots compared to fenced plots for the raw values ($t_4 = 8.68$, $P < 0.001$; open 2.44 ± 0.46 m^2, fenced = 0.11 ± 0.09 m^2) and once standardized by available digging area ($t_4 = 7.15$, $P = 0.002$; open 2.00 ± 0.48 m^2, fenced = 0.08 ± 0.06 m^2).

Microhabitat assessments indicated that cover estimates for quenda bare ground and litter varied significantly between open and fenced plots (Table 2). Litter cover in the open plots was nearly one-half (48 ± 18.9%; Table 2) that of fenced plots (81.6 ± 8.7%, Table 2). In contrast, the quenda bare ground cover was substantially greater (38.0 ± 20.3%, Table 2) in the open plots compared to the fenced (1.5 ± 7.5%, Table 2). Litter depth was also reduced in the open plots (10.6 ± 5.1 mm, Table 2) compared to fenced plots (25.0 ± 2.2 mm, Table 2). All other microhabitat variables, including vegetation, bare ground, coarse woody debris, and the canopy cover estimates were not significantly different between fenced and open plots (Table 2).

A Pearson's product moment correlation coefficient confirmed a negative relationship between quenda bare ground and litter cover ($r = -0.88$, $n = 50$, $P < 0.0001$), quenda bare ground and litter depth ($r = -0.69$, $n = 50$, $P < 0.0001$), and a positive relationship between litter depth and litter cover ($r = 0.72$, $n = 50$, $P < 0.0001$).

Assessing surface fuel loads

A strong relationship was observed between litter depth and litter mass in bushland outside the paired plots ($r^2 = 0.82$, $P < 0.001$) resulting in correlative equations to predict surface fuel loads inside the plots (Fig. 1) for 1-h fuel (Eq. 3) and total surface fuel (Eq. 4). Heteroscedasticity and nonnormal errors in the data for 10-h fuel resulted in an unreliable model for predicting 10-h fuel mass and was therefore excluded from further analysis. The correlative equations for fuel mass (g per 25 × 25 cm quadrat) were

Table 2. Results of linear mixed-effect models for microhabitat response variables between paired fenced (quenda excluded) and open (quenda accessible) treatments at Craigie Bushland, Western Australia.

Variable and treatment	Coefficient	95% CI	t	χ^2	P
Quenda bare ground (%)				38.38	**<0.0001**
Fenced	0.01	−0.069–0.101	0.35		
Open	0.38	0.178–0.585	6.19		
Bare ground (%)				1.80	>0.05
Fenced	0.02	0.000–0.035	2.21		
Open	0.01	−0.029–0.041	−1.34		
Litter cover (%)				36.80	**<0.0001**
Fenced	0.82	0.737–0.894	20.70		
Open	0.48	0.292–0.670	−6.07		
Vegetation (%)				0.15	>0.05
Fenced	0.12	0.083–0.165	6.10		
Open	0.11	0.016–0.119	−0.38		
Coarse woody debris (%)				0.19	>0.05
Fenced	0.03	0.015–0.050	4.06		
Open	0.02	−0.015–0.056	−1.31		
Litter depth (mm)				97.06	**<0.0001**
Fenced	25.05	22.84–27.27	23.76		
Open	10.56	5.41–15.72	−9.85		
Canopy cover (%)				0.17	>0.05
Fenced	0.65	0.570–0.740	16.91		
Open	0.59	0.421–0.767	−1.36		

Note: Significant differences between fenced and open treatments are highlighted in boldface type.

$$1\text{ h fuel (g)} = 2.52\ (\text{depth(mm)}) - 19.2 \qquad (3)$$

$$\text{Total surface fuel (g)} = 2.70\ (\text{depth(mm)}) - 19.4. \qquad (4)$$

To determine surface fuel loads within the paired plots, we used the average litter depths we recorded during point-intercept sampling of the plots in the equations above (Appendix S2: Table S1). There was significantly more estimated surface fuel in the fenced plots compared to the open plots for both 1-h fuel and total surface fuel load estimates (Table 3, Fig. 2); with open plots, where quenda foraged, containing nearly one-half of the fuel load of fenced plots.

Estimated rate of fire spread

The fire behavior models indicated that the estimated rate of spread was close to 1.8 times faster in fenced plots compared to the open plots. Estimated rate of spread for 1-h fuel and total surface fuel loads was significantly faster where quenda were absent (fenced treatment), compared to where quenda foraged (open treatment) for both high and low fire danger days (Table 3, Fig. 3).

Discussion

This study has demonstrated that foraging activities of quenda in an urban bushland reserve increased bare ground cover while reducing litter cover and depth, and subsequently, reduce surface fuel loads and predicted rate of spread of fire. Where quenda foraged, surface fuel loads were lower and estimated to be nearly one-half (~56%) of the fuel loads observed in plots where quenda were excluded. Under a high fire-danger scenario, the predicted rate of spread of fire in areas with quenda foraging was ~45% lower than the predicted rate of spread of fire in areas where quenda were excluded. These results clearly indicated that digging activities of quenda in urban bushlands have the capacity to alter surface fuel loads and fire spread.

Quenda digging altered microhabitat and fuel loads

There was a large amount of digging activity by the population of quenda in the reserve, which is the main driver for the differences in microhabitat characteristics (e.g., litter depth, litter cover, bare ground, and estimated litter mass) observed between open and fenced plots. We are confident that the results we observed in this study are primarily caused by quenda as (1) quenda were the only digging mammals in Craigie Bushland; (2) we differentiated between quenda-created bare ground and bare ground created by other disturbances (e.g., ants, humans); and, (3) all quenda diggings observed in the fenced plots were created prior to the fence construction. The presence of old quenda digs in the fenced plots indicates that some quenda digs may persist for years after creation, at least 3 yr in our study. Most quenda digs are probably more ephemeral and degraded quickly; and potentially the old digs we observed in the fenced plots were originally larger digs, and hence less likely to be entirely covered by litter fall in the intervening years.

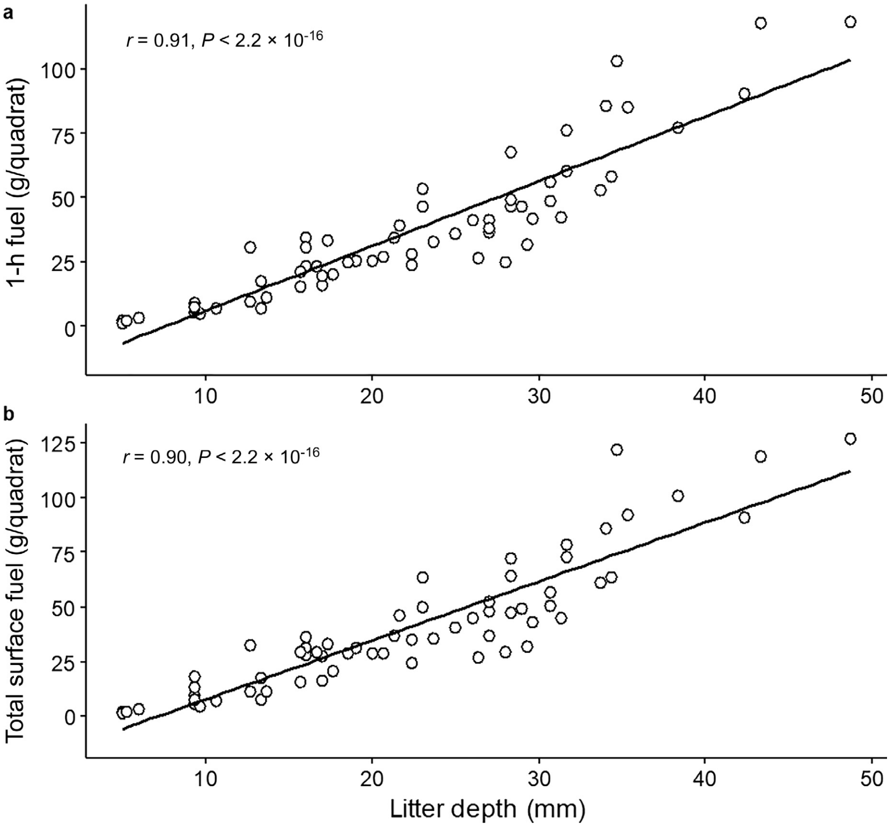

FIG. 1. The relationship between litter mass (g/quadrat) and litter depth (mm) for (a) 1-h fuel and (b) total surface fuels derived from destructive sampling ($n = 64$) at Craigie Bushland, Western Australia.

TABLE 3. Results of linear mixed effects models on estimated fuel loads and rate of fire (ROS) under low and high fire danger (FD) conditions for 1-h and total surface fuel load estimates between fenced (quenda excluded) and open (quenda accessible) treatments at Craigie Bushland, Western Australia.

Variable and treatment	Coefficient	95% CI	t	χ^2	P
1-h fuel					
Fuel load (Mg/ha)					
Fenced	5.8	5.2–6.4	20.4	60.2	<0.0001
Open	3.3	2.0–4.5	−7.8		
ROS low FD					
Fenced	46.9	41.9–51.8	19.0	59.7	<0.0001
Open	26.2	15.9–36.4	−7.7		
ROS high FD					
Fenced	119.0	106.3–131.6	19.0	59.7	<0.0001
Open	66.5	40.3–92.4	−7.7		
Total surface fuel					
Fuel load (Mg/ha)					
Fenced	6.4	5.7–7.1	19.2	59.5	<0.0001
Open	3.6	2.3–5.0	−7.7		
ROS low FD					
Fenced	51.4	45.9–56.7	19.2	59.5	<0.0001
Open	29.2	18.1–40.3	−7.7		
ROS high FD					
Fenced	130.4	116.6–144.0	19.2	59.5	<0.0001
Open	74.3	46.1–102.1	−7.7		

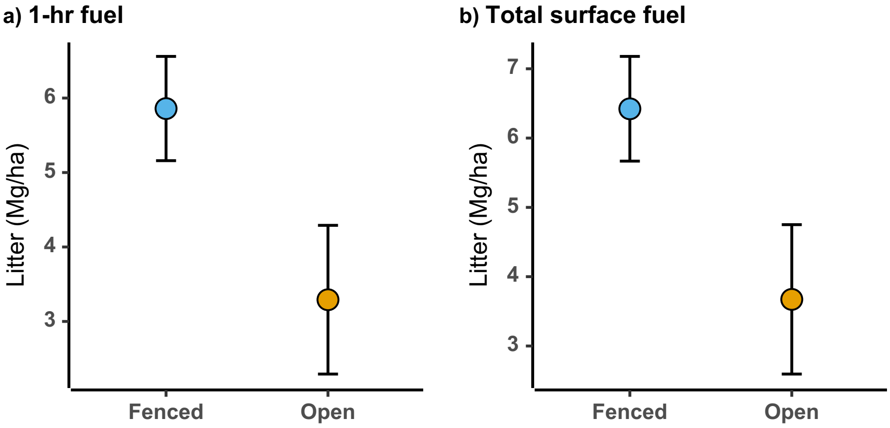

FIG. 2. The amount of estimated litter (mean and 95% CI) in paired fenced (quenda excluded) and open (quenda accessible) treatments for (a) 1-h fuel and (b) total surface fuels at Craigie Bushland, Western Australia.

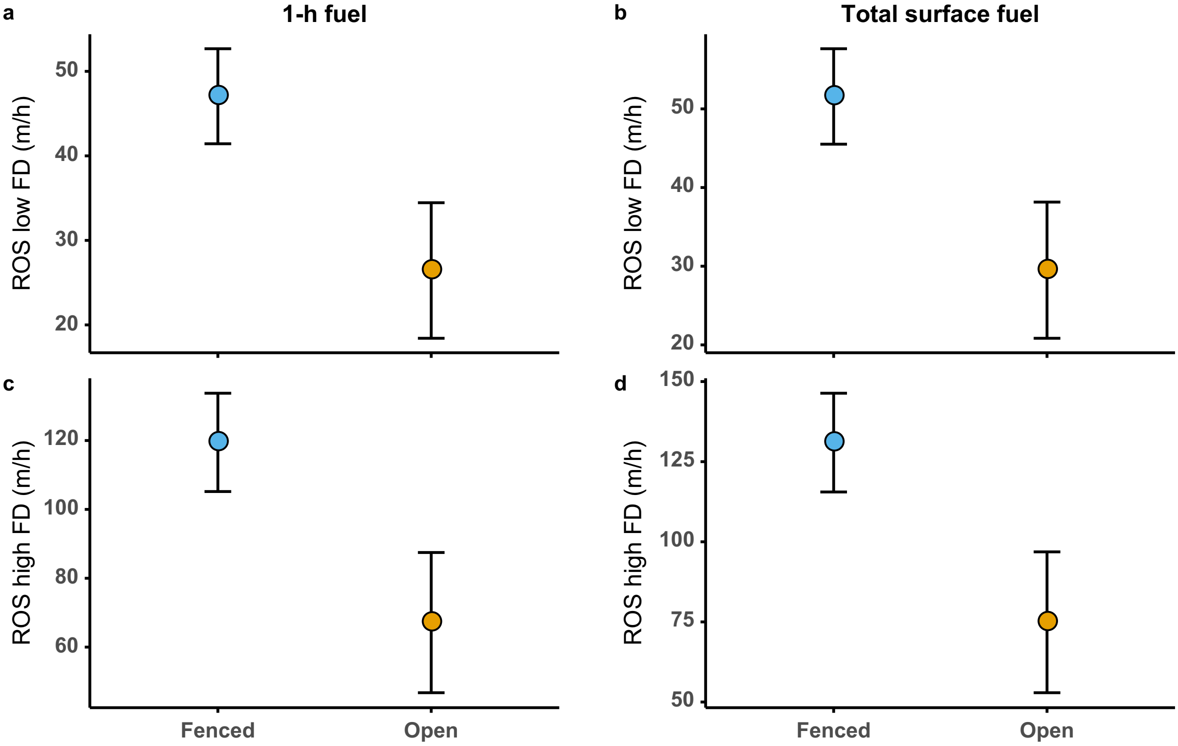

FIG. 3. The estimated rate of spread (ROS; mean and 95% CI) of fire in paired fenced (quenda excluded) and open (quenda accessible) treatments for 1-h fuels (left side of panel) and total surface fuels (right side of panel) fuels under (a and b) low fire danger and (c and d) high fire danger (FD) conditions at Craigie Bushland, Western Australia.

A key finding of this study was that litter depth, litter cover, and estimated litter mass were all significantly higher in the fenced plots, while bare ground cover was higher in the open plots as a consequence of quenda digging. Foraging by the superb lyrebird (*Menura novaholandiae*), using its large legs and feet to rake through surface litter layers for invertebrates in eucalypt woodlands of southern Australia, resulted in similar changes in microhabitat, with litter loads reduced by 25% compared to areas where they couldn't forage (Nugent et al. 2014). Hayward et al. (2016) also found reduced litter mass and litter cover inside large reserves where multiple digging mammal species had been reintroduced. Our results indicate that, within a short time frame (<4 yr since reintroduction, 3 yr since fence construction), the successful translocation of a single digging mammal species can alter surface fuel load characteristics in an urban area.

Accumulation of surface fine fuels results from the difference between litter accession rates and decomposition rates (Gould et al. 2011). The amount of expected fuel loads with time since last fire has been modeled for various Australian habitats, including banksia woodlands (Burrows and McCaw 1990). These relationships typically reach an asymptote when fuel load stabilizes (depending on fuel type, decomposition rate, and time since fire). In banksia woodlands, surface fuel accumulates rapidly, stabilizing at 6–8 Mg/ha about 6 yr since fire, and is capable of supporting a rapidly moving fire under extreme weather conditions (Burrows and McCaw 1990). Given that Craigie Bushland has not been burned for at least 20 yr, it would be expected that surface fuel loads resemble this prediction; and within the fenced plots (where quenda are excluded) the surface fuel loads are as expected (7–8 Mg/ha). However, in the open plots (where quenda are actively digging), the surface fuel loads are substantially less (~3.5 Mg/ha). As quenda were already uncommon north of Perth (Abbott 2008), the patterns observed by Burrows and McCaw (1990) are likely to be indicative of fuel accumulation curves in the absence of abundant digging mammals. We suggest that quenda digging in the Craigie Bushland open plots changed the predicted fuel accumulation patterns.

Quenda digging alters predicted fire behavior

The estimated rate of spread of fire, based on the Mk5 Forest Fire Behavior Model, under high fire conditions, was nearly halved in the presence of quenda digging at Craigie Bushland. Using the same model, estimated fire spread at the much larger Scotia reserve (~65,000 ha) was reduced by 33% in the presence of reintroduced digging mammals (Hayward et al. 2016). Other aspects of fire behavior are also likely to be altered by digging activities of animals that disturb surface fuel loads. Foraging by Lyrebirds reduced the predicted flame height of fire by ~50% in southeastern Australia (Nugent et al. 2014), while the nests of Malleefowl were also predicted to reduce flame height under high fire-danger conditions (Smith et al. 2016).

The FFDI used in our study is predominantly derived from eucalyptus woodland with continuous ground leaf litter. Banksia woodlands often have a patchy ground litter distribution (although at our sites it was > 60% on average) and most of the potential fire spread occurs because of the elevated live fuel (Burrows and McCaw 1990), and the density of understorey shrubs in banksia woodlands will play a large role in fire behavior. The FFDI can also under-predict rate of spread and height, particularly at high wind speeds (McCaw et al. 2008), although we used wind speed variables that allowed more robust predictions. A future improvement to assess the influence of digging animals on fuel loads and fire behavior will be to (1) conduct a wider fuel load assessment (to include elevated fuels in the dense understorey) and (2) utilize additional fire behavior models, such as the highly specific forest flammability model that incorporates plant traits (Zylstra et al. 2016).

The role of digging animals in fire management

There is clearly capacity for animals, including reintroduced digging mammals, to alter fuel loads. Although reintroduction programs face many challenges, they are an increasingly utilized management practice, not just for the conservation of species, but also for the ecosystem services a species provides (Seddon et al. 2014). Few reintroduction programs have occurred in urban areas, but there is a growing awareness of the benefits of engaging people with nature (van Heezik and Seddon 2018). In Australia, the threat of predation from introduced cats and foxes (Woinarski et al. 2015) restricts the broad-scale reintroduction of mammals outside of fenced reserves or islands; however, the reintroduction of mammals may still be feasible in some urban areas (e.g., Craigie Bushland [this project] and Mulligan's Flat [Batson et al. 2016]). Encouragingly, quenda (and some other bandicoot species) occur outside of fenced areas. Although quenda are predated upon by introduced foxes and cats, they have persisted in areas where dense vegetation potentially provides refuge from predators (Abbott 2008). In recent years, quenda have been reintroduced into several unfenced urban reserves throughout Perth, and although published population data are lacking, they are persisting (A. Reaveley, *personal communication*).

From a fuel management perspective it will be important to understand how many digging animals are required to create fuel load reductions that significantly alter fire behavior; presumably, this will vary depending upon the animal and habitat in question. Knowledge on pre-European densities of Australian mammals is lacking, but historical accounts indicate many species, including quenda, were abundant (Abbott 2008). Previous research has documented similar quenda densities (~2 quenda/ha) in both fenced and unfenced areas (Ramalho et al. 2018), as our unquantified observations at Craigie Bushland. This indicates that although quenda are absent from many bushlands, they may be able to support populations large enough to significantly reduce fuel loads in urban areas once a population has reestablished. However, reintroducing mammals into small urban reserves will come with many management challenges, including proximity to urban infrastructure and isolation from other habitat patches. Furthermore, most urban bushlands contain alien plant species and it is unclear how the digging actions of native animals will interact with such plants. As alien plants can influence fuel loads and fire regimes (D'Antonio and Vitousek 1992), further research examining the impact of digging animals on alien plants, especially invasive species, is warranted.

The concept of pyrodiversity, encompassing the interaction between fire regimes, trophic levels, ecological processes, and their feedbacks (Bowman et al. 2016), can be extended to the effect of digging animals on fire behavior. Many Australian mammals, including bandicoots, require unburned habitat that act as refuges from invasive predators (Doherty et al. 2015). For example, long-nosed bandicoots (*Perameles nasuta*) visit small patches of open areas to forage while retreating to denser vegetation for refuge (Hughes and Banks 2010). We observed that the digging by quenda at Craigie bushland provided a heterogeneous and patchy distribution of litter cover between dense understorey vegetation patches where quenda shelter. As patchiness of surface fuels changes the way in which fire progresses and forest fire spread can be impeded by bare areas (Gould et al. 2011, Cheney et al. 2012), the patchiness in litter distribution created by quenda digging may play a protective role for denser vegetation. This may provide a positive feedback to the persistence of quenda populations, especially in isolated urban reserves where they are considered highly sensitive to large-scale fires (Ramalho et al. 2018).

The role of digging animals in altering fuel loads and influencing fire has largely been overlooked; but the loss or decline of many native vertebrates may have subsequently altered fire regimes in landscapes (Hayward et al. 2016, Johnson et al. 2018). Many previously common species are thought to have been important in ecosystem function (Davidson et al. 2012, Fleming et al. 2014), and there is mounting evidence to suggest that native digging animals may play an important role in reducing fuel loads (this study; Hayward et al. 2016). In urban bushland reserves, where reducing fuel loads is a challenge for land managers, the reintroduction of previously common digging animals may have potential value as a complimentary fire management tool.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2018/full

DATA ACCESSIBILITY

Raw data used in this research article are accessible via the University of Western Australia's Research Repository at https://doi.org/10.26182/5d77392100f4d