

# Strength of a Trophic Cascade Between an Apex Predator, Mammalian Herbivore and Grasses in a Desert Ecosystem Does Not Vary with Temporal Fluctuations in Primary Productivity

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## ABSTRACT

There has long been debate regarding the primacy of bottom-up and top-down effects as factors shaping ecosystems. The exploitation ecosystems hypothesis (EEH) predicts that predators indirectly benefit plants because their top-down effects limit herbivores' consumption of plants, and that the strength of trophic cascade increases with increasing primary productivity. However, in arid environments, pulses of primary productivity produced by irregular rainfall events could decouple herbivore–plant and predator–prey dynamics if high conversion efficiency from seed biomass to consumers allows the rapid build-up of consumer populations. Here, we test predictions of the EEH in

an arid environment. We measured activity/abundances of dingoes, red kangaroos and grasses, and diet of dingoes, in landscapes where dingoes were culled or not culled over 3 years. Dingo activity was correlated with rainfall, and their tracks were less frequent at culled sites. Kangaroo abundance was greater at sites where dingoes were culled and increased with rainfall in the previous 6 months. Grass cover was greater at sites where dingoes were not culled and increased with rainfall in the previous 3 months. During a period of average rainfall, dingoes primarily consumed rodents and increased their consumption of kangaroos during a period of drier conditions. Our results are consistent with the hypothesis that suppression of an apex predator triggers a trophic cascade, but are at odds with the EEH's prediction that the magnitude of trophic cascades should increase with primary productivity. Our study demonstrates that temporal fluctuations in primary productivity can have effects on biomasses of plants and consumers which are in many ways analogous to those observed along spatial gradients of primary productivity.

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**Key words:** trophic cascade; arid; apex predator; herbivore; vegetation; top down; bottom up.

## INTRODUCTION

There has long been debate about the primacy of bottom-up (primary productivity driven) and top-down (predator driven) effects as drivers of ecosystem structure (Pace and others 1999; Borer and others 2008). Although often treated as mutually exclusive, top-down and bottom-up effects often operate simultaneously; however, their relative importance may scale with spatial and temporal variation in primary productivity (Melis and others 2009; Hopcraft and others 2010; Letnic and Dickman 2010; DaVanon and others 2016). This can occur because animals and plants require nutrients and energy, and the limited availability of these resources may result in bottom-up limitation when population growth is more constrained by resource availability than by predation (Hopcraft and others 2010).

According to trophic cascade theory, predators can indirectly benefit plants because their top-down effects limit consumption of plant tissue by herbivores (Schmitz and others 2000; Ripple and others 2016). Predators can limit herbivores' consumption of plants through the process of predation whereby they suppress herbivore populations by directly killing them (Estes and Duggins 1995). Predators can also benefit plants if the fear that they instil causes herbivores to shift their patterns of habitat use and in so doing reduce herbivores' consumption of plants (Ford and others 2014). Thus, due to the combined effects of predators' lethal and non-lethal effects on herbivores, trophic cascade theory predicts that there should be a greater biomass of the plant species preferred by herbivores in areas where predators are present than absent (Estes and others 2011).

The exploitation ecosystems hypothesis (EEH) was invoked to explain biogeographic patterns in the abundance of plants and consumers in the northern boreal zone, and differs from top-down and bottom-up dichotomy by suggesting that the relative strength of these processes will vary along gradients of primary productivity (Oksanen and others 1981; Oksanen and Oksanen 2000). According to the EEH, the alternative equilibria to which the biomasses of each trophic level will shift in order to balance biomass exchange between them will vary with primary productivity (Choquenot and Forsyth 2013). The EEH predicts that endothermic consumers will be absent in areas of extremely low primary productivity. As primary productivity increases, herbivore biomass is predicted to increase linearly in two-link trophic systems where carnivores are absent; however, in

three-link trophic systems with carnivores present, herbivore biomass will remain constant above this threshold regardless of the primary productivity due to regulation of herbivores by predators (Oksanen and others 1981; Oksanen and Oksanen 2000). The EEH therefore predicts that the strength of trophic cascades will increase with increasing ecosystem productivity (Oksanen and others 1981; Oksanen and Oksanen 2000).

The EEH has been shown to explain well the spatial patterns of carnivore, herbivore and plant biomass in temperate and arctic regions of the northern hemisphere, but has seldom been evaluated in arid and tropical environments (Crête 1999; Elmhagen and others 2010; Ripple and Beschta 2012). Arid ecosystems are characterized by large temporal variation in primary productivity caused by irregular rainfall (Letnic and Dickman 2006). Simulations indicate that these temporal fluctuations in primary productivity can buffet a plant–herbivore system such that the equilibrium states predicted by the EEH are not attained (Choquenot and Forsyth 2013). The relevance of the EEH to arid environments may also be limited because the existence of many plants as dormant seeds and the focus of predators and herbivores around water sources may violate key assumptions of the EEH (Oksanen and Oksanen 2000). The large dormant seed bank in arid environments may contravene assumptions of the EEH because irregular inputs of rainfall that prompt pulses of seed germination can drive abrupt temporal shifts in the conversion of plant biomass to secondary consumers (Meserve and others 2003; Letnic and others 2005), in contrast to the gradual transition along a spatial continuum of primary productivity that is predicted by the EEH (Oksanen and Oksanen 2000). In addition, because predators often focus their search efforts around rare sources of water in desert environments, encounters between them and prey are unlikely to be randomly distributed throughout the landscape, thus violating a key assumption of the EEH (Oksanen and Oksanen 2000).

In arid regions of Australia (that is, <350 mm mean annual rainfall), the dominant herbivores are kangaroos (*Macropus* spp.) and the largest terrestrial carnivore and major predator of kangaroos is the dingo (*Canis dingo*). Comparisons of the abundances of kangaroos and their primary forage, grasses, in areas where dingo populations were culled versus areas where they were not culled are consistent with the notion that dingoes induce trophic cascades (Letnic and others 2012). Kangaroo density

can be up to more than 20 times lower in the presence of dingoes (Caughley and others 1980; Newsome and others 2001), and grass cover tends to be greater in areas where dingoes are not killed by humans (Letnic and others 2012).

Choquenot and Forsyth (2013) adapted the thinking behind the EEH to simulations of the dynamic interactions between dingoes, kangaroos, pasture and fluctuating rainfall in arid Australia (Figure 1). Their simulations accorded well with the EEH's prediction that the strength of trophic cascades and hence magnitude of dingoes' indirect effects on grasses should increase with primary productivity, however, in their simulations productivity fluctuated through time rather than space (Choquenot and Forsyth 2013). This was predicted to occur because during wet periods, when primary productivity is high, the rate of consumption of grasses by kangaroo populations that are not regulated by resources or predators may exceed the rate of grass growth. Conversely, where kangaroo populations are regulated by dingoes, grass growth will not be limited by herbivory and thus should increase with resource availability (Choquenot and Forsyth 2013). However, Choquenot and Forsyth (2013) predicted that trophic cascades should become weaker with increasing stochasticity in primary productivity and that dietary switching by dingoes should weaken trophic cascades because it decouples the dynamics of dingo and kangaroo populations.

Here, we use field measurements of the activity/abundances of dingoes, red kangaroos (*Macropus rufus*) and grasses collected over 3 years in nearby landscapes where dingoes were culled or not culled to test three key predictions generated from trophic cascade theory and Choquenot and Forsyth's (2013) adaptation of the EEH for three-link trophic systems in an arid environment (Choquenot and Forsyth 2013; Figure 1). Our key predictions were (1) that dingo activity should increase with increasing rainfall, a proxy for primary productivity, and that such increases should be greater in areas where dingoes were not subject to population culling; (2) that kangaroo abundance should increase with increasing rainfall in areas where dingoes were culled but show negligible responses to rainfall in areas where dingoes were not culled; and (3) that grass cover should increase with increasing rainfall, a proxy for primary productivity, in areas where dingoes were not culled but show negligible responses to increasing productivity in areas where dingoes were culled. To provide further insight into dingo–kangaroo interactions, we tested two additional predictions. Because previous studies have

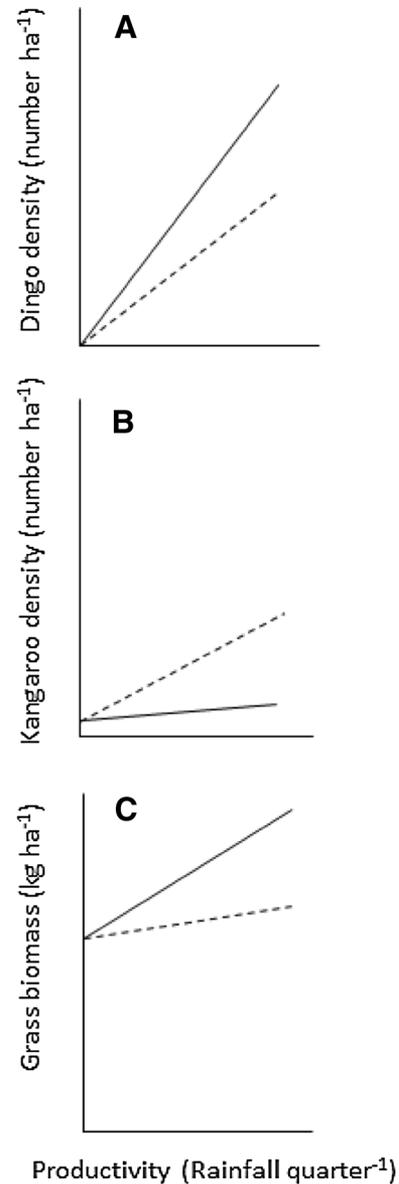


Figure 1. The relationships (*solid line*) predicted by the exploitation ecosystems hypothesis (EEH) between ecosystem productivity indexed as cumulative rainfall in the previous 3 months and (A) dingo density, (B) kangaroo density and (C) grass biomass for a three-link trophic system in arid Australia. The *dashed lines* indicate predictions for systems where dingo populations are culled to 50% below carrying capacity. Adapted from Choquenot and Forsyth (2013).

shown that dingoes preferentially prey on female and juvenile kangaroos (Shepherd 1981) and display prey switching in response to rainfall-driven fluctuations in prey abundance (Corbett and Newsome 1987), we predicted that the proportion of juveniles and females in kangaroo populations should be greater where dingoes are culled and that

dingoes' diet and frequency of consumption of kangaroos should shift in response to climatic conditions.

## METHODS

### Study Areas

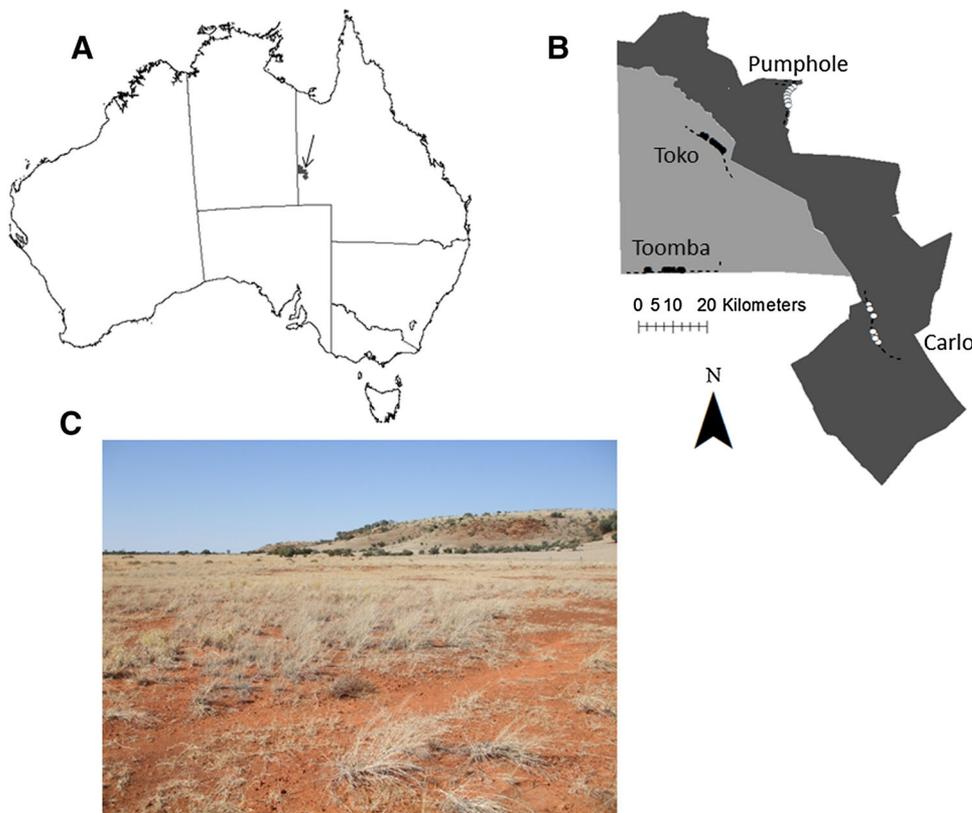
The four study areas were located in private conservation reserves in the Channel Country region of western Queensland (Figure 2A). The two areas where dingoes were not culled (Toko and Toomba) were located on Cravens Peak station (23°16'S, 138°17'E), a conservation reserve operated by Bush Heritage Australia (Figure 2B). The study areas (Pumphole and Carlo) where dingoes were culled were located within the Toko Range Nature Refuge and Mulligan River Nature Refuge (Figure 2B). These conservation reserves operated by North Australian Pastoral Company (NAPCO) are situated within the pastoral properties Glenormiston and Marion Downs, respectively. To protect livestock on neighbouring parts of the properties from attacks by dingoes, dingo populations are culled in the Nature Refuges by distributing fresh meat baits impregnated with 6 mg of the toxin sodium fluoroacetate ('1080') and shooting. Baits are distributed by government agents twice annually, in

the austral autumn and austral spring, in areas that dingoes are known to frequent.

The minimum distance between study areas was approximately 35 km (between Toko and Pumphole and Toko and Toomba), and maximum distance was approximately 65 km (between Carlo and Toomba and between Carlo and Pumphole). Home-range sizes (95% maximum convex polygons) for dingoes in arid Australia have been reported to range from 79 to 999 km<sup>2</sup> (Newsome and others 2013), so it is possible that individual dingoes may have made movements between the study areas. In comparison with dingoes, home-range sizes (95% maximum convex polygons) for red kangaroos are much smaller and are typically less than 10 km<sup>2</sup> (Priddel and others 1988). Thus, we consider it unlikely that many kangaroos undertook movements between the study areas.

The dominant landform within the study areas is stony (gibber) plain on clay soil (Figure 2C). The gibber plains understorey vegetation is generally sparse. After large rainfall events, there is dense cover of grasses including *Astrebala* spp., *Dicanthium* spp. and *Aristida* spp. Trees and shrubs occur in scattered copses dominated by *Acacia georginae*.

The climate of the study area is arid. The nearest long-term weather station to the study areas



**Figure 2.** Locations of the four study areas. **A** The study areas (*shaded and arrowed*) within the State of Queensland, Australia. **B** The four study areas within the unbaited Cravens Peak Reserve (*light grey*) and the baited Mulligan River and Toko Ranges Reserves (*dark grey*). Study areas are indicated by *circles* (culled = *unshaded*, not culled = *shaded*). Transects along which dingo activity and kangaroo abundance were assessed are indicated by *dashed lines*. **C** Landscape and vegetation typical of the study areas.

(Glenormiston; 22°55'S, 138°49'E) has a median annual rainfall of 186 mm and mean annual rainfall of 218 mm ( $n = 105$  years, SD 144.3 mm) with a peak in summer. The annual occurrence and intensity of rainfall in the region is highly variable (Letnic and Dickman 2006). Just prior to the study, in the period encompassing 2010–2011, there was a prolonged period of wet conditions when annual rainfall exceeded the 85th percentile of historical distribution of rainfall for Glenormiston. The mean annual temperature is 21–23°C with maxima of 46–49°C in summer and minima of –6°C in winter.

## Rainfall

Previous studies concluded that vegetation and kangaroo abundance in desert ecosystems are correlated with cumulative rainfall in the previous 3 months and previous 6 months, respectively (Caughley and Shepherd 1987; Letnic and others 2005). We therefore used the cumulative rainfall 3 months prior to each sampling session (Rain 3) and 6 months prior to each sampling session (Rain 6) as indicators of primary productivity at each study area. Total monthly rainfall totals were obtained from automated weather stations located near each study area. Weather stations for the Carlo, Toko and Toomba study areas were operated by the Desert Ecology group, University of Sydney. The weather station at Pumphole was operated by the Australian Bureau of Meteorology.

To make comparisons with the historical rainfall data set, we used medians and percentiles because the annual and monthly rainfall totals were not normally distributed. Thus, median rainfall totals give a better indication of “normal rainfall” conditions than mean rainfall totals (Letnic and others 2005). We defined dry conditions as periods when rainfall was less than the 33rd percentile of the historical record for that same period and wet conditions when rainfall was greater than the 67th percentile for the period. Normal conditions were defined as periods when rainfall was between the 33rd and 67th percentiles.

## Dingo Activity

Estimating the population density of dingoes using non-lethal methods in arid regions is problematic due to low population densities, the low probability of recapturing individuals and the difficulty of identifying individuals by their coat patterns (Edwards and others 2000). Previous studies that used measurements of activity derived from track counts

and camera traps as indices of dingo abundance have found these methods to corroborate predicted declines in dingo abundance following poison baiting campaigns and predicted increases in dingo abundance following resource pulses (Allen and others 1996; Edwards and others 2000; Greenville and others 2014). We calculated indices of dingo activity as proxies for dingo abundance in each study area using two methods, track surveys and infrared game cameras.

To quantify dingo activity using track counts, we established monitoring transects, each with 25 track detection stations at 1-km intervals along low-use, single-lane dirt roads on eight sampling occasions between July 2011 and October 2014 (Allen and others 1996). The tracking stations (2 m long) were raked to produce a consistent tracking surface that spanned the road width (3 m). The tracking stations were monitored and swept daily for three consecutive nights. Each morning, a unique mark was made in the corner of each tracking station. This mark was used to determine whether wind, rain or vehicles would affect the observer's ability to interpret the plot the following morning. If the mark could not be clearly detected the next morning, then the previous night's record from the station was considered invalid. An index of activity for each predator species on each transect on each sampling occasion was calculated as the number of plots crossed per one hundred plot nights. Sampling was conducted on six occasions between March 2012 and October 2014 during the austral autumn and austral spring.

A photographic index of dingo activity was calculated from cameras deployed in each study area in two periods commencing in spring 2012 and spring 2013. Within each study area, we established three or four infrared game cameras (Scout Guard DTC-530V, Shenzhen Siyuan Digital Technology Co. Ltd, Shenzhen, Guangdong, China). Cameras were positioned 1 km apart so that they photographed animals moving along single-lane dirt roads. The cameras were deployed for 6 months at each area. Observations of dingoes were considered independent if the time elapsed between photographs exceeded 30 min. Because the number of operational cameras varied monthly due to disturbance by animals, battery failure and theft, an index of dingo activity at each area for each month was calculated as the number of dingoes observed divided by the sum of the number of nights that each camera was in operation. For analyses, the photographic index of dingo activity at each area for each month was expressed as the number of dingoes observed per hundred camera nights.

## Kangaroo Abundance and Demography

Sampling for kangaroo abundance and demography was conducted on six occasions between March 2012 and October 2014 during the austral autumn and austral spring. We calculated indices of kangaroo abundance using nocturnal spotlight surveys. Spotlight indices of kangaroo abundance were assessed by conducting 2–3 nocturnal spotlight transects (7–20 km long) at each area (Letnic and others 2009). During each survey, kangaroos were counted by an observer using a 50-W spotlight from the roof of a four-wheel-drive vehicle moving at 15 km/h. Indices of kangaroo abundance at each sub-area were expressed as number of animals sighted per 100 km of spotlight survey.

Accurate determination of the sex of kangaroos was not possible during nocturnal spotlight surveys due to poor visibility. To quantify the proportion of female and juvenile kangaroos within the kangaroo population, we conducted afternoon surveys in the hour before sunset on the same roads used to conduct spotlight surveys. We conducted 2–3 afternoon surveys (7–20 km long) at each area on each sampling occasion. Kangaroos were recorded by an observer from the roof of a four-wheel-drive vehicle moving at 15 km/h and the sex and age (adult, juvenile) of the individuals ascertained based on conformation and size (kangaroos are sexually dimorphic). For analyses, the proportion of females and juveniles in the population was expressed as the sum of the number of females and juveniles sighted at each area divided by the total number of kangaroos sighted.

## Grass Cover

Grasses are the primary food resources for red kangaroos, but they also consume other forage such as shrubs and forbs (Caughley and Shepherd 1987). We sampled grass, forb and litter cover using a step-point method (Landsberg and others 2003) on six occasions between March 2012 and October 2014 during the austral autumn and austral spring. On each 1-ha plot on each sampling occasion, three 80-m transects were sampled at 1-m intervals giving 240 points per grid. At each point, ground cover was classified as: bare, grass, forb or litter. For analyses, the cover of grasses was calculated as the percentage of points where grass was recorded.

## Dingo Diet

Searches for dingo scats were undertaken along the same vehicle tracks as the track surveys and at watering points located on these roads. Scats were

placed into paper bags and air-dried until they were sorted. In the laboratory, scats were oven-dried overnight at 100°C, then placed individually in nylon bags and washed in a washing machine. Following washing, items present in the scats were identified to the lowest possible taxonomic level using microscopic analysis of diagnostic residues (that is, hair cross sections, teeth, claws) and comparison against reference specimens. The frequency of occurrence of items in the scats collected in 2012 and 2013 was calculated as the number of scats in which the dietary item was identified divided by the total number of scats sorted. Too few scats were collected in 2014 to make reliable inferences about dingo diet in that year.

## Statistical Analyses

Generalized estimating equations (Zuur and others 2009) with a negative binomial distribution were used to investigate the effects that dingo culling and rainfall had on the track index of dingo activity, spotlight index of kangaroo abundance and photographic index of dingo activity. Culling (culled/not culled) and the cumulative rainfall in the previous 3 months and previous 6 months were fixed factors in the analyses. Generalized estimating equations with a Gaussian distribution were used to analyse the proportion of females and juveniles in kangaroo populations with culling and sampling occasion as fixed factors. Because each area was subject to repeated measures, sampling occasion was specified as a repeated measure in models using a first-order autoregressive (AR1) error structure (Zuur and others 2009). Candidate models for each response variable were ranked using the Quasi-AIC (QAIC) (Grueber and others 2011) corrected for small sample size (QAIC<sub>c</sub>) because  $n/K$  was  $<40$  ( $n$  = sample size,  $K$  = number of estimated parameters in the global model). We selected the best models by comparing QAIC<sub>c</sub> differences ( $\Delta_i$ QAIC<sub>c</sub>). Models with an QAIC<sub>c</sub> difference ( $\Delta_i$ )  $< 2$  units relative to the model with the lowest QAIC<sub>c</sub> (QAIC<sub>min</sub>) have substantial support, whilst those with QAIC<sub>c</sub> $\Delta_i > 10$  are not supported (Burnham and Anderson 2002). We then calculated the QAIC weights ( $w_i$ ) to determine the relative likelihood of each candidate model, given the data (Burnham and Anderson 2002).

Linear mixed-effects models (Zuur and others 2009) with a Poisson distribution were used to investigate the effects of culling (culled/not culled), rainfall in the previous 3 months, rainfall in the previous 6 months and the interaction terms culling  $\times$  rainfall 3 and culling  $\times$  rainfall 6 on grass

cover. Because each plot was subject to repeated measures through time, sampling time was specified as a repeated measure using an ARI error structure (Zuur and others 2009). Due to the nested design, whereby there were multiple plots within each area, we specified area as a random factor with a random intercept. Candidate models for each response variable were ranked using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) (Burnham and Anderson 2002). We selected the best models by comparing  $AIC_c$  differences ( $\Delta_i$ ). Models with an  $AIC_c$  difference ( $\Delta_i$ )  $< 2$  units relative to the model with the lowest  $AIC_c$  ( $AIC_{\min}$ ) have substantial support, whilst those with  $\Delta_i > 10$  are not supported (Burnham and Anderson 2002). We then calculated the Akaike weights ( $w_i$ ) to determine the relative likelihood of each candidate model, given the data (Burnham and Anderson 2002).

To determine whether the diets of dingoes differed between a period of normal climatic conditions (the 2012 calendar year) and a period of dry climatic conditions (the 2013 calendar year), we compared presence-absence data for each prey category in scats using the analysis of similarities (ANOSIM) test based on Bray-Curtis similarity matrices for each year using the software Primer version 6 (Clarke and Gorley 2006). ANOSIM is a nonparametric test that uses permutations to calculate the significance of the difference in the similarity of assemblages between groups. The test statistic was global  $R$ , which can range from  $-1$  to  $+1$ , with a value close to  $-1$  indicating that the variation within groups is higher than the variation between groups and a value close to  $+1$  indicating that the variation between groups is higher than the variation within groups. If a significant result ( $P < 0.05$ ) was obtained using ANOSIM, we used the procedure SIMPER (Clarke and Gorley 2006) to determine which prey categories contributed to differences in dingoes' diets between 2012 and 2013, expressed as the contributions made by each prey category to the overall dissimilarity between years. Dissimilarity contributions were only reported for prey categories that contributed more than 10% to the overall dissimilarity between years.

## RESULTS

### Rainfall

The timing of rainfall events was similar across the four study areas, but rainfalls at Carlo tended to be lower than at the other three study areas (Figure 3).

2012 had normal rainfall, with mean cumulative rainfall of the four study areas from January to December being 194.3 mm (SD 29.7,  $n = 4$  years). This amount was equivalent to the 51st percentile of the distribution of annual rainfall at Glenormiston. 2013 was dry, with mean cumulative rainfall of the four study areas from January to December being 94.5 mm which is between the 16th and 17th percentiles of the distribution of annual rainfall of the Glenormiston weather station (SD 30.0,  $n = 4$  years). 2014 was normal, with a mean of 134.3 mm at the four study areas between January and September, equivalent to the 49th percentile of the distribution of cumulative rainfall for the same period of year for the Glenormiston weather station (median = 143 mm,  $n = 113$  years)

### Dingo Activity

The most parsimonious model explaining the track index of dingo activity was rainfall in the previous 6 months ( $w_i(QAIC_c) = 0.36$ ; Table S1). The 95% confidence intervals for the parameters in the best model excluded zero (Table 1). A plot of the fitted values for this model indicated that dingo activity was correlated positively with rainfall in the previous 6 months (Figure 4A). The second- ( $\Delta_i QAIC_c = 1.37$ ,  $w_i(QAIC_c) = 0.18$ ) and third-ranked models ( $\Delta_i QAIC_c = 1.44$ ,  $w_i(QAIC_c) = 0.18$ ) were also well supported ( $2.00 < \Delta_i QAIC_c$ ) and contained the terms rainfall 6  $\times$  culling and culling + rain 6, respectively. The model containing only the term baiting ( $\Delta_i QAIC_c = 5.63$ ,  $w_i(QAIC_c) = 0.02$ ) was not well supported ( $\Delta_i QAIC_c < 10$ ; Table S1). The parameter estimate for this model was negative and the 95% parameter intervals excluded zero, indicating that the track index was significantly lower where dingo populations were culled (Table S2).

The most parsimonious model explaining the photographic index of dingo activity was rainfall in the previous 3 months ( $w_i(QAIC_c) = 0.49$ , Table S3). Within the best model, the 95% confidence intervals for the parameter rainfall 3 excluded zero (Table 1). A plot of the fitted values for this model indicated that dingo activity was correlated positively with rainfall in the previous 3 months (Figure 4B). The second-ranked model ( $\Delta_i QAIC_c = 2.02$ ,  $w_i(QAIC_c) = 0.18$ ) was the model culling + rainfall 3. This model was closely followed ( $\Delta_i QAIC_c = 2.07$ ,  $w_i(QAIC_c) = 0.17$ ) by the model incorporating the interaction between culling and rainfall in the previous 3 months. The model containing only culling ( $\Delta_i QAIC_c = 7.08$ ,  $w_i(QAIC_c) = 0.01$ ) was not well supported ( $\Delta_i$

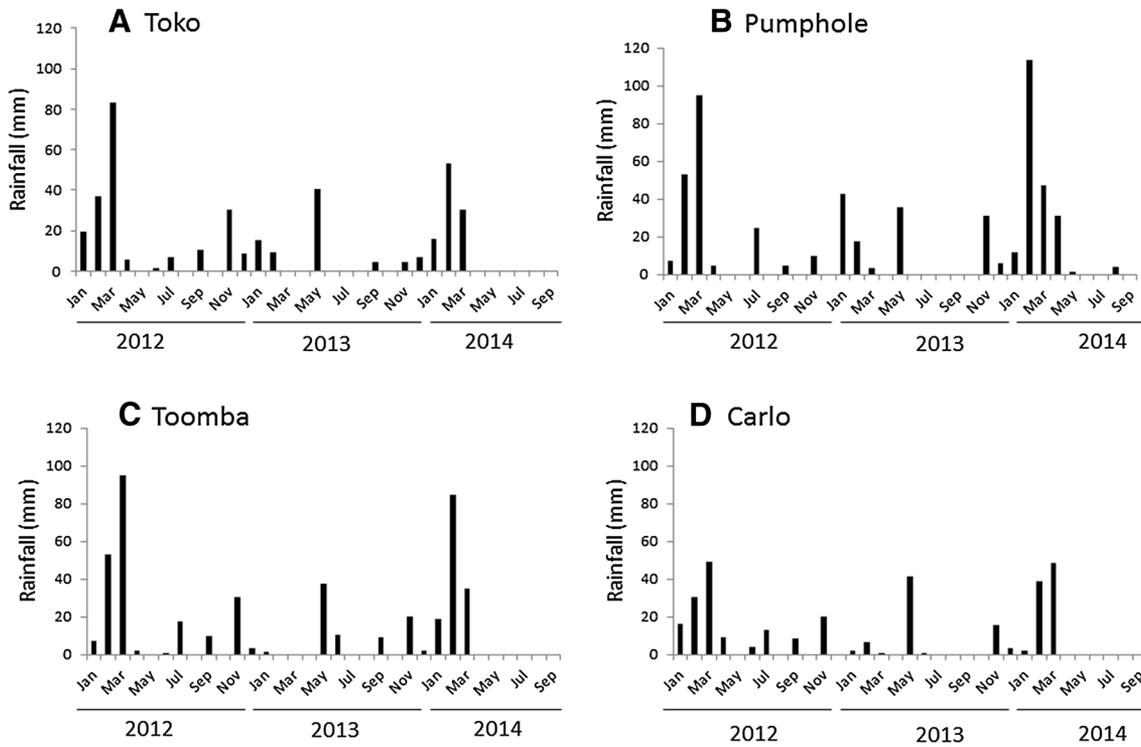


Figure 3. Monthly rainfall at the four study areas between January 2012 and September 2014.

**Table 1.** Parameter Estimates and 95% Confidence Intervals (CI) for the Best ( $\Delta_i\text{QAIC}_c = 0$  and  $\Delta_i\text{AIC}_c = 0$ ) Generalized Estimating Equations (GEE) and Linear Mixed-Effects (LME) Models for Each Response Variable (Dingo Track, Dingo Photographic, Kangaroo Abundance and Grass Cover)

Model	Model type	Intercept ( $\pm 95\%$ CI)	Parameter 1 ( $\pm 95\%$ CI)	Parameter 2 ( $\pm 95\%$ CI)
Dingo track = Rain 6	GEE	1.12 (0.55, 1.68)	Rain 6 0.008 (0.005–0.011)	–
Dingo photographic = Rain 3	GEE	0.86 (0.65, 1.07)	Rain 3 0.019 (0.011–0.028)	–
Kangaroo = Rain 6 + culling	GEE	2.41 (1.41, 3.41)	Rain 6 0.003 (0.001–0.006)	Culling 2.05 (0.98, 3.13)
Grass = Rain 3 + culling	LME	2.78 (2.52, 3.05)	Rain 3 0.006 (0.004–0.008)	Culling –0.37 (–0.73, –0.01)

Mean values (95% CIs) are shown for all parameters.

$\text{QAIC}_c < 10$ ; Table S3) and the 95% confidence intervals for the parameter included zero indicating that there was no significant difference in the photographic index between study areas that were and were not culled (Table S2).

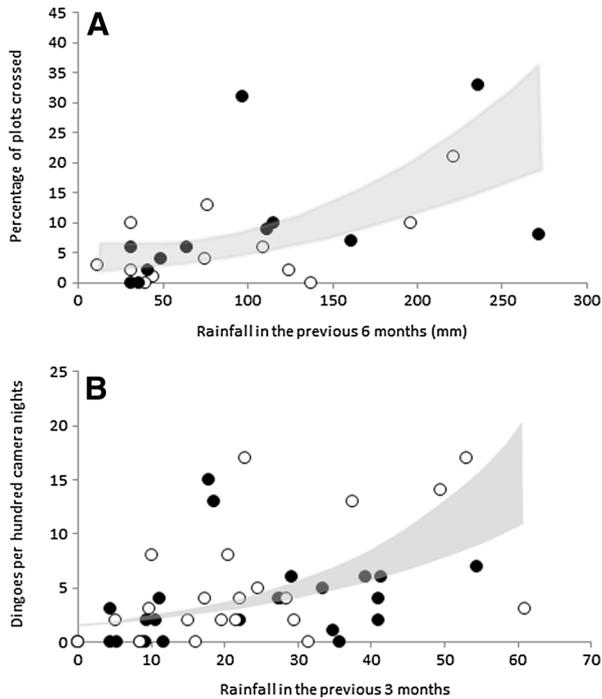
### Kangaroo Abundance

The best model explaining the abundance of kangaroos included the terms culling and rainfall in the previous 6 months ( $w_i(\text{QAIC}_c) = 0.31$ , Table S4). Other models within the best model set ( $< 2.00 \Delta_i\text{QAIC}_c$ ) were the univariate models with the terms culling ( $\Delta_i\text{QAIC}_c = 0.47$ ,  $w_i(\text{QAIC}_c) = 0.25$ ) and rainfall in the previous 6 months ( $\Delta_i$

$\text{QAIC}_c = 0.47$ ,  $w_i(\text{QAIC}_c) = 0.25$ ), respectively. The 95% confidence intervals for the parameters in the best model all excluded zero (Table 1). A plot of the fitted values of the top-ranked model showed that kangaroo abundance was greater at areas where dingoes were culled than areas where dingoes were not culled and that their abundance increased with rainfall in the previous 6 months at both culled and not culled areas (Figure 5A).

### Kangaroo Demography

The most parsimonious model explaining the demography of kangaroo populations (Table 2) contained the term culling. No other models were

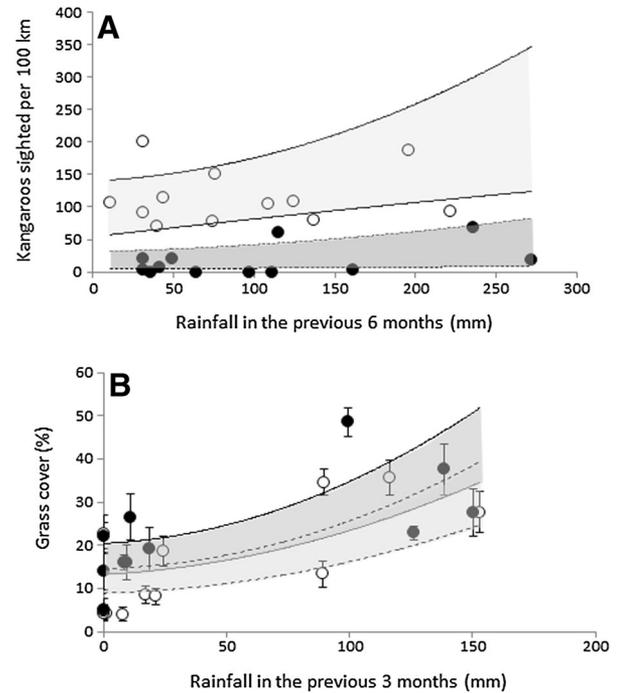


**Figure 4.** **A** Dingo activity and rainfall in the previous 6 months. The shaded area indicates the 95% confidence region for predicted values of the generalized estimating equation dingo track = Rain 6 + intercept. **B** Photographic index of dingo activity and rainfall in the previous 3 months. The shaded area indicates the 95% confidence region for predicted values from the top-ranked generalized estimating equation (dingo = Rain 3 + intercept). In both figures, open and closed circles represent culled and not culled study areas, respectively.

within 2  $\Delta_i\text{QAIC}_c$  units. The 95% confidence interval for the parameter culling ( $\beta = 0.18$ ; CI 0.13–0.24) excluded zero, and the fitted values (culled mean = 0.74 SE  $\pm$  0.021; not culled mean = 0.56 SE  $\pm$  0.018) indicated that the proportion of females and juveniles in kangaroo populations was greater in study areas where dingoes were culled than at those that were not culled.

### Grass Cover

The most parsimonious model explaining variation in grass cover was the additive model including the terms culling and rainfall in the previous 3 months ( $w_i(\text{AIC}_c) = 0.63$ , Table S5). The second-ranked model ( $\Delta_i\text{AIC}_c = 1.15$ ,  $w_i(\text{AIC}_c) = 0.37$ ) included one term, rainfall in the previous 3 months. The 95% confidence intervals for the parameters in the best model, culling and rainfall 3, excluded zero (Table 1). The plot of the fitted values of the top-ranked model (Figure 5B) revealed that grass cover at both culled and not culled areas increased with



**Figure 5.** **A** Relationship between kangaroo abundance at culled (open symbols) and not culled study areas (closed symbols) and rainfall in the previous 6 months. The shaded area indicates the 95% confidence regions for predicted values for culled (light grey, dashed margins) and not culled (dark grey, solid margins) study areas from the top-ranked generalized estimating equation (kangaroo = Rain 6 + culling + intercept). **B** Relationship between grass cover at culled (open symbols) and not culled study areas (closed symbols) and rainfall in the previous 6 months. The shaded area indicates the 95% confidence regions for predicted values from culled (light grey, dashed margins) and not culled (dark grey, solid margins) study areas generated by the top-ranked generalized estimating equation (grass cover = Rain 3 + culling).

increasing rainfall in the previous 3 months. When rainfall in the previous 3 months was held constant, grass cover was significantly greater at not culled than culled areas.

### Dingo Diet

The diet of dingoes changed temporally (ANOSIM Global  $R = 0.267$ ,  $P = 0.001$ ). The SIMPER procedure showed that the occurrence of rodents, macropods and lizards contributed 36, 30 and 11% to the dissimilarity in the diet of dingoes between years of normal and dry climatic conditions, respectively. In 2012, a period of normal rainfall, remains of rodents, primarily *Rattus villosissimus*, were present in 96% of dingo scats, but were only present in 61% of scats in 2013, a period of dry climatic conditions (Table 3). Conversely, kangaroo

**Table 2.** Mean Proportions ( $\pm$ SE) of Female and Juvenile Kangaroos Sighted in Afternoon Surveys at Areas Where Dingoes Were or Were Not Culled on Six Sampling Occasions

Sampling occasion	Culled	(SE)	Not culled	(SE)
May 2012	0.79	(0.02)	0.67	(0.00)
October 2012	0.59	(0.09)	0.25	(0.25)
May 2013	0.77	(0.01)	0.50	*
September 2013	0.76	(0.07)	0.67	*
April 2014	0.81	(0.01)	**	
October 2014	0.71	(0.01)	1	*

\*Kangaroos were only observed at one of the not culled areas on this sampling occasion. \*\*No kangaroos were sighted during surveys at not culled areas on this sampling occasion

**Table 3.** Proportions of Dingo Scats Containing the Listed Dietary Items During 2012 ( $n = 78$ ) and 2013 ( $n = 28$ )

Taxon	Year	
	2012	2013
Rodent	0.96	0.61
Kangaroo	0.03	0.36
Lizard	0.05	0.11
Invertebrate	0.14	0.04
Bird	0.03	0.00
Frog	0.01	0.00
Vegetation	0.01	0.07
Cat	0.03	0.00
Rabbit	0.00	0.04

Some scats contained multiple items.

remains were present in 3% of scats in 2012 but increased to 36% of scats in 2013. Lizard remains were present in 5% of scats in 2012 and increased to 11% of scats in 2013.

## DISCUSSION

Our results are consistent with the prediction of the EEH and trophic cascade theory that predators benefit plants by reducing herbivory. However, although primary productivity was an influential driver of predator, herbivore and plant activity/abundances, the responses of these three variables to temporal changes in primary productivity at areas where dingoes were culled or not culled were not in strict accordance with the predictions of the EEH. The EEH predicts that the strength of trophic cascades should increase along spatial gradients of primary productivity, but in our 3-year study the strength of trophic cascades triggered by the lethal culling of dingoes remained constant despite con-

siderable temporal fluctuations in primary productivity. This result is consistent with the prediction that large temporal fluctuations in primary productivity can buffet a plant–herbivore–carnivore system such that the equilibrium states predicted by the EEH are not attained (Choquenot and Forsyth 2013).

A criticism of many studies reporting trophic cascades is that they are correlative investigations rather than manipulative experiments (Ford and Goheen 2015). We used a pre-existing dingo population culling program as our experimental framework but acknowledge that confounding factors could have influenced our findings. We designed our study to match the four study areas as closely as possible for vegetation type, underlying geology and land use and used independent measures of rainfall recorded in the vicinity of each area as a covariate in analyses. Thus, we suggest that it is unlikely that a result corroborating our a priori predictions regarding the effect of dingo culling on the abundances of kangaroos and grasses could emerge as a consequence of any underlying variation in the physical and biological attributes of the areas or contemporary land use. Nonetheless, we add the caveat that this study provides correlative evidence for a trophic cascade and highlight the need for studies that provide experimental or mechanistic evidence for effects predicted to occur within trophic cascades at each trophic level (Ford and Goheen 2015).

The positive relationship observed between indices of dingo activity and rainfall is consistent with previous studies from arid Australia (Letnic and others 2005; Greenville and others 2014) and is likely to have resulted from both successful recruitment of pups in the austral spring and immigration (Thomson and others 1992). The best predictors of track- and camera-derived indices of dingo activity were rainfall in the previous 6 months and previous 3 months, respectively.

These findings suggest that rainfall had a greater effect on dingo activity than culling. The significantly lower dingo track index in the culled compared to not culled areas suggests that dingo population management effectively reduced dingo activity. However, the photographic index of dingo activity did not differ between culled and not culled areas. One explanation for the relatively small differences in the dingo activity indices between the culled and not culled areas when compared to previous studies that have compared dingo activity in culled/not culled areas (Letnic and others 2009) may be that we were sampling the same population due to their relatively close proximity and the absence of any barrier between them. It is also conceivable that disruption to dingoes' social networks caused by culling may have created a population sink where a breakdown in territorial defences facilitated immigration of dingoes from nearby areas where dingoes were not culled into areas where they were subject to culling (Thomson and others 1992).

The diets of dingoes in our study area changed considerably between a year of normal rainfall (2012) and a dry year (2013). During 2012, which was a year of normal rainfall preceded by two wet years, dingoes preyed primarily upon rodents which were abundant (Letnic and others 2013). However, during the dry conditions of 2013, both the abundance of rodents (ML unpublished data) and dingoes' consumption of rodents decreased. Correspondingly, dingoes increased their consumption of kangaroos and reptiles during 2013. These findings are consistent with previous studies from arid regions that have found dingoes to be dietary generalists that switch their diets depending on the availability of prey (Corbett and Newsome 1987; Cupples and others 2011).

The EEH predicts that the magnitude of the suppressive effect of dingoes on kangaroos should increase with primary productivity and decrease with rainfall stochasticity (Choquenot and Forsyth 2013). This prediction is predicated on the assumption that kangaroos are the primary prey of dingoes regardless of primary productivity. Thus, during periods of high primary productivity numerical increases in dingo population should result in stronger population-level effects on kangaroos (Choquenot and Forsyth 2013). In accord with the EEH and previous studies, our results showed that kangaroo activity increased with rainfall and was considerably greater where dingo populations were subject to culling (Caughley and others 1980; Pople and others 2000). Increases in kangaroo populations in areas where dingo popu-

lations are culled have previously been attributed to lower rates of predation (Caughley and others 1980; Pople and others 2000). Our results suggest that even modest reductions in dingo activity can translate to increased kangaroo abundance. However, at odds with the predictions of the EEH (Figure 1B; Choquenot and Forsyth 2013), kangaroo abundances at culled and not culled areas did not display divergent responses to increasing primary productivity, but instead remained relatively constant. That the strength of dingoes' suppressive effects on kangaroos remained similar irrespective of changes in primary productivity was indicated by the parallel slopes of the fitted values for kangaroo abundance at culled/not culled areas generated by the top-ranked model explaining kangaroo abundance.

Although our results are mostly consistent with the predictions of the EEH and trophic cascade theory, we cannot be certain whether the differences in kangaroo abundance between culled/not culled areas were due to dingoes' lethal or non-lethal effects or another unmeasured factor (Ford and Goh- een 2015). Although fear of dingoes almost certainly causes kangaroos to change their behaviour, we contend that the difference in kangaroo abundance between culled/not culled was likely due to dingoes' lethal effects on kangaroos rather than kangaroos congregating at areas where dingoes were culled. This conclusion is supported by the difference in kangaroo demography between areas where dingoes were culled/not culled. As predicted, females and juveniles that are more susceptible to predation by dingoes (Shepherd 1981) made up a greater proportion of the kangaroo population at areas where dingoes were culled. Future studies should investigate the non-lethal effects of dingoes on kangaroos and whether these effects trigger behaviourally mediated trophic cascades.

Prey switching by dingoes in response to climate-driven shifts in prey abundance may explain why our results show a different pattern to that predicted by the EEH. In 2012, dingoes' consumption of rodents (which were abundant in that year) may have decoupled dingo-kangaroo interactions. However, as dingoes decreased their consumption of rodents during the drier conditions that prevailed in 2013 they increased their consumption of kangaroos. Thus, even though indices of dingo activity/populations were greater during the higher productivity period (2012), their net predatory effect on kangaroo populations may have been similar to that during the lower productivity period (2013) when dingo numbers were lower but they consumed kangaroos more frequently.

As predicted by the EEH, grass cover increased with rainfall and tended to be greater at the study areas where dingoes were not subject to culling than culled. This pattern likely occurred because rainfall is a major driver of grass growth in desert ecosystems (Caughley and Shepherd 1987) and because kangaroo abundance and hence herbivory by kangaroos was lower in areas where dingoes were not culled. However, contrary to the EEH, grass cover did not display divergent responses to rainfall at culled and not culled areas. This result mirrored that observed for kangaroos, except in the case of kangaroos, culled areas had higher abundances than not culled areas. Although we did not quantify the composition of kangaroos' diets or composition of plant assemblages, rainfall events in arid regions typically increase both the abundance of plants and richness of plant communities (Caughley and Shepherd 1987; Letnic and others 2005). A positive correlation between rainfall in the previous 3 months and cover of grasses suggests that this occurred during our study. Previous studies show that kangaroos tend to consume a broader range of plant species during periods of wetter climatic conditions (Caughley and Shepherd 1987). Thus, it is possible that the impacts of kangaroo herbivory on grasses were diluted during periods of wet conditions because they were spread across both a greater number of individual plants and a greater number of plant species.

In their simulation models of dingo–kangaroo interactions, Choquenot and Forsyth (2013) found that dingo consumption of alternative prey (reptiles) increased dingo abundance, but reduced predation pressure on kangaroos which in turn led to divergent responses to rainfall by kangaroos and vegetation at areas where dingoes were culled or not culled. Our results suggest a slightly different dynamic between primary productivity, alternative prey, dingo culling, kangaroos and vegetation, whereby the strength of dingoes' effects on kangaroos and grasses remains relatively constant regardless of primary productivity. A plausible explanation for this pattern is that increased abundance and diversity of alternative prey species consumed by dingoes and probably kangaroos during periods of higher primary productivity may dilute the per capita effects of these consumers by diffusing their inter-specific interactions across a greater number of interaction pathways (Letnic and others 2012; Ripple and others 2014). Another explanation for the failure of grass cover and kangaroo abundance at culled and not culled areas to display the divergent responses to primary productivity predicted by the

EEH is that the extreme variability in rainfall and in turn primary productivity could prevent the system from reaching equilibrium conditions by decoupling the transfer of primary productivity to higher trophic levels (Choquenot and Forsyth 2013).

The EEH was originally invoked to explain spatial trends in the biomass of plants, herbivores and predators in the boreal and arctic regions of the northern hemisphere (Oksanen and others 1981; Oksanen and Oksanen 2000). Subsequent applications of the EEH have shown that it has broad application to explain spatial trends in plant and consumer biomasses in northern hemisphere temperate environments (Crête 1999; Oksanen and Oksanen 2000; Ripple and Beschta 2012). Although not in strict accord with the EEH, our study demonstrates that large temporal fluctuations in primary productivity driven by irregular rainfall can have effects on the biomasses of plants and consumers which are in many ways analogous to those observed along spatial gradients of primary productivity.

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