



Fighting like cats and dogs? Dingoes do not constrain spatial and temporal movements of feral cats

T.L. Kreplins^{a,b,*}, M.S. Kennedy^{c,d}, R.A. O'Leary^c, P.J. Adams^c, S.J. Dundas^e, P.A. Fleming^b

^a Department of Primary Industries and Regional Development, 75 York Rd, Northam, WA 6401, Australia

^b Climate-Impacted Terrestrial Ecosystems, Harry Butler Institute, Murdoch University, 90 South St, Murdoch, WA 6150, Australia

^c Department of Primary Industries and Regional Development, 3 Baron-Hay Court, South Perth, WA 6151, Australia

^d Department of Agriculture and Fisheries, 203 Tor St, Toowoomba, Queensland 4350, Australia

^e NSW Department of Primary Industries, 1447 Forest Rd, Orange, NSW 2800, Australia

ARTICLE INFO

Article history:

Received 27 November 2019

Received in revised form 24 September 2020

Accepted 28 September 2020

Keywords:

Baiting

Dingo

Feral cat

Invasive species

Mesopredator release

Camera traps

ABSTRACT

The mesopredator release hypothesis proposes that when top-down suppression by a larger predator (e.g. dingoes, *Canis familiaris*) is removed, smaller mesopredators (e.g. feral cats, *Felis catus*) increase in abundance. Lethal control of dingoes could therefore potentially exacerbate predation pressure by feral cats on smaller prey species. We monitored the activity of dingoes and feral cats (in the absence of red foxes) in two dingo-baited areas over 16 months using 182 camera traps. First, we estimated population densities across each property and found that dingo and feral cat density were unrelated. Second, we compared daily capture rate of dingo and feral cats and found that both predators' capture rates were weakly related to environmental factors and the baiting program. Third, we analysed temporal overlap in activity of these two predators. Although both predators were nocturnal and showed 78.7% overlap in temporal activity patterns, there was a significant difference in activity peaks. Finally, while both predators were distributed across the whole study site, there was strong temporal separation within 1, 12 and 24 h periods at each individual camera. In conclusion, there was no indication of suppression of feral cat population by dingoes. The large and growing body of similar evidence suggests that calls to restrict dingo control on grounds that it will cause mesopredator releases are unsupported and highly unlikely to yield the biodiversity benefits often hoped for by proponents.

© 2020 Elsevier Inc. All rights reserved.

1. Introduction

Within most ecosystems, opposing forces maintain ecosystem dynamics by top-down and bottom-up processes. In ecosystems dominated by top-down processes, apex predators can be critical in determining ecosystem structure (e.g. Estes et al., 2011; Knight et al., 2005). In addition to influencing prey species, apex predators can also influence the abundance, dispersion and distribution of other smaller (meso-)predators (Newsome and Ripple, 2014). Consequently, under the mesopredator release hypothesis, it is postulated that removal or loss of apex predators can facilitate increases in mesopredator abundance, which in turn can negatively affect the behaviour and population size of prey species (Soule et al., 1988). For example, population control of the wolf (*Canis lupus*; an apex predator) is reported to have led to an

increase in abundance of coyote (*Canis latrans*; a mesopredator) throughout Yellowstone National Park in the USA (e.g. Ripple et al., 2013) (but see Wilmers et al., 2003 for an alternative view). This is reported to have had follow-on effects for native herbivores and grazing of native pastures (Berger and Conner, 2008).

Mesopredator suppression by apex predators can occur by direct or indirect mechanisms. Direct suppression can occur as interference competition (interspecific competitive killing or intra-guild predation). Observations of direct predation of mesopredators by top-predators are common outside Australia (Palomares and Caro, 1999; Smith et al., 2003), and occasionally documented in Australian ecosystems (Moseby et al., 2012). Indirect control of smaller predators can take the form of behavioural suppression, where mesopredators change their activity patterns in response to the presence of apex predators (Brown et al., 1999). For example, mesopredators may avoid apex predators by avoiding areas used by apex predators, or by using the same resources (i.e. prey, water points, or tracks) at different times (Gordon et al., 2015). Spatial and temporal behavioural avoidance (or separation) may limit a mesopredator's ability to survive and reproduce, which could then cause population declines over time (Lima and Dill, 1990).

* Corresponding author at: Department of Primary Industries and Regional Development, 75 York Rd, Northam, WA 6401, Australia.

E-mail addresses: tracey.kreplins@dpird.wa.gov.au (T.L. Kreplins), Malcolm.Kennedy@daf.qld.gov.au (M.S. Kennedy), rebecca.o'leary@dpird.wa.gov.au (R.A. O'Leary), peter.adams@dpird.wa.gov.au (P.J. Adams), shannon.dundas@dpi.nsw.gov.au (S.J. Dundas), t.fleming@murdoch.edu.au (P.A. Fleming).

In Australia, dingoes are perceived to have a role in conservation through suppression of mesopredators, in particular the feral cat (Ritchie and Johnson, 2009). The mesopredator release hypothesis has become popular in applied ecology (Bradshaw et al., 2011), with a 2018 review (Kreplins et al., 2018a) identifying over 130 peer-reviewed papers discussing the topic in respect to dingoes since the term first appeared in the Australian literature in the 1990s. Support for the mesopredator release hypothesis requires evidence that dingoes suppress the abundance of feral cats through direct predation or altering their behaviour and therefore compromising survival and reproduction (Allen et al., 2015; Fancourt et al., 2019).

Conversely, dingoes are also a key threatening process for some endangered fauna (Allen and Leung, 2012), and a source of conflict with livestock production (Fleming et al., 2014). Dingoes are predators of small livestock, costing Australia's livestock production industries \$89.33 million per year in damage and control efforts (McLeod, 2016). Australia produces approximately 14.2 million sheep and 27.4 million cattle per year, and is the third largest exporter of commercial livestock after Brazil and India (Cattle Council of Australia, 2016; Meat and Livestock Australia, 2016). Population control of dingoes is therefore carried out in many livestock production areas to reduce their impacts on stock.

Dingo control in Australia can result in reductions in dingo populations of 22–100%, depending on a range of factors, including the history of baiting program, density of baiting, season and location (Ballard et al., 2020; Fleming, 1996; Thomson, 1986). Where dingo control programs cause significant population reductions (e.g. Ballard et al., 2020; Thomson, 1986), this could potentially affect trophic interactions with feral cats (hypothesized with correlative data in Brook et al., 2012), foxes (hypothesized with correlative data in Colman et al., 2014) and their prey. We took advantage of a dingo control program carried out across two large pastoral properties in WA, where ongoing control has occurred at varying intensity for the last ~40 years, to investigate whether the density of feral cats and their temporal activity changed in response to dingo control (red foxes are absent at these study sites). We monitored numbers of dingoes and feral cats over a period of 16 months, during which time there were three separate baiting events targeting dingo population control on each property. We aimed to assess changes in the dingo population over time that in turn could influence density and temporal activity patterns of feral cats. We analysed the data in the following ways:

- (1) We compared population densities of feral cats and dingoes;
- (2) We compared daily capture rate of dingoes and feral cats, controlling for environmental factors as well as relative prey abundance;
- (3) We compared temporal activity patterns of feral cats and dingoes to determine whether feral cats avoided times that dingoes were active; and
- (4) We compared capture rates within 1, 12 and 24 h periods for each individual camera to determine feral cat activity was temporally separated from dingo activity.

2. Materials and methods

2.1. Site description

This study was conducted on two pastoral properties (Property 'A' and Property 'B') in the southern rangelands, Murchison region, Western Australia. The southern rangelands are typified by an arid environment with annual rainfall of 239 mm and mean maximum temperature in January of 38.2 °C (Mount Magnet Station, 007057; Bureau of Meteorology, 2017). The vegetation is composed of *Acacia* spp. woodlands. The two properties measure 231 km² and 757 km² and were separated by approximately 70 km. Both have a history of sheep farming;

however, during the study, only unmanaged cattle and goats grazed the properties. Dingo control (with 1080) has occurred at varying intensities on the properties for approximately 40 years.

2.2. Control events

From March 2016 to July 2017, three baiting events occurred on each property (Kreplins et al., 2018b) as part of a large landscape-scale coordinated baiting program across adjacent properties within the management region. Dried meat baits for dingo control were manufactured by air drying ~100 g of fresh meat injected with 6 mg of 1080 to a weight of ~40 g (Thomson and Rose, 2006). These baits were deployed twice annually. One of the properties was baited during the coordinated baiting program and bait deployment was delayed by 6 weeks for the other property for comparison with the first property. The order of ground baiting alternated between the two properties (Table 1). This schedule of baiting allowed for a test of the short term variation in feral cat numbers in response to changes in dingo population due to baiting.

2.3. Monitoring predator and prey activity

Camera traps were spaced 1 km apart along station tracks throughout both properties, mounted 0.3–0.5 m above the ground, and directed at an angle of 22° facing along the track (Meek et al., 2012). Tracks were chosen for monitoring, as previous studies in this area showed off-track camera traps were not optimum for predator detections (Kennedy and Kreplins, unpub data). Station tracks were graded, well-travelled pathways, generally wide enough for at least one vehicle to travel along. Two camera models were used: 92 camera traps were deployed at Property A on 3 March 2016 (77 Reconyx hyperfire H500, 15 Scoutguard SG560), and 90 camera traps at Property B on 5 March 2016 (79 Reconyx hyperfire H500, 11 Scoutguard SG560). Scoutguard cameras were interspersed evenly between the Reconyx cameras. Camera traps were serviced every 2 months on average (Table 1). Camera traps were removed on 9 June 2017 (Property A) and 22 July 2017 (Property B). Baits were deployed across each property, as per regular practice (ground baiting of 1 bait/100 m), and a bait was laid on vehicle access tracks in front of each camera.

Camera trap images were viewed as jpeg files in an image viewer program (Windows Live Photo Gallery, Windows 7 Edition, Microsoft Corporation, Redmond, WA, USA). We recorded bait presence in each image and used these data to calculate the number of baits remaining on the ground each day of the study. Images of each predator species at greater than 10 min intervals were recorded as separate capture events, as per previous studies (Fancourt, 2016; Fancourt et al., 2019). Of the 2324 feral cat detections and 1968 dingo detections, on only 20 occasions were both feral cats and dingoes seen on the same camera within a 24 h period. Unique identification is required to obtain density estimates and we therefore identified individual dingoes and feral cats from unique colouration and markings; two researchers (TK and MK) carried out individual identification, as recommended by Kelly et al. (2008). The presence of common prey were also recorded: small mammals (*Notomys alexis*, *Dasyercus* spp.) and macropods (*Osphranter robustus* and *Macropus fuliginosus*). Dingo, feral cat and common prey photo capture numbers were standardised per camera trap per day (to account for variations in camera set-up across the study, accounting for lost data due to flat batteries or filled SD cards, and to deal with varying number of monitoring days per baiting event); these capture rate data were then Log₁₀-transformed to remove the influence of outliers.

We also collected environmental data for each day of monitoring. Daily minimum and maximum temperature (°C) and rainfall (mm) were retrieved from the Bureau of Meteorology records (Station: 007600, ~60 km away; Bureau of Meteorology, 2017). The lunar phase (categorised as 0 = new, 0.5 = half, 1 = full) was retrieved from the United States Naval Meteorology and Oceanography Command

Table 1

Year, month and days when the camera traps were serviced at both properties throughout the trial, as well as, the dates baits were laid. Camera traps were removed on 9 June 2017 (Property A) and 22 July 2017 (Property B).

Year	Month	Days	Baits laid
2016	March	3rd–5th	
2016	April	7th–9th	Property A
2016	June	8th–10th	Property B
2016	August	5th–7th	
2016	September	16th–18th	Property B
2016	November	2nd–4th	Property A
2017	February	20th–22nd	
2017	April	3rd–5th	Property A
2017	June	20th–22nd	Property B

(NMO) records (Naval Meteorology and Oceanography Command, 2017).

2.4. Statistical analyses

2.4.1. Population densities during baiting events

We calculated the densities of feral cats during the 16 months of monitoring for each property using spatially-explicit capture-recapture analyses using the *secrlinear* package (Efford, 2017, 2020) in R (R Core Team, 2019). Using the R package *secrlinear* (Efford, 2017), a combination of the state (animal home range) and observations (probability of detecting an individual at a detector, i.e. camera, in relation to the individual's home range) are used to construct models, with the assumption that the feral cat population was closed for each month period. *Secrlinear* was used rather than simply *secr* given the camera trap deployment along roads only; therefore the estimation of feral cat density along a linear habitat is expressed per km instead of the number of individuals per unit area. All models were derived from the Cormack-Jolly-Seber or Jolly-Seber models with refinements.

The detection function used was hazard rate and the detector type was identified as count. Models were fitted numerically, maximising the log likelihood over the capture histories with spatial information to determine animal density (D ; animals per km). Each model included the parameters:

g_0 – detectability or the probability of capture when the distance between the animal's activity centre and the camera trap is zero. In a null model, g_0 is constant across animals, occasions and detectors;

σ – the spatial scale of detection. More specifically defined as the spatial scale parameter of detection function or an index of home range. σ and g_0 jointly define the detection probability as a function of location and interpreting their meaning alone should be done with caution (Efford, 2017); and.

D_j – density at a flat scale taking into account the spatial distance between traps but ignoring any intervening topography.

A linear mask was constructed with a buffer of 1 km from each camera using poly line shape files of the track transects as camera detections would be well inside a 1 km buffer. Models were run assuming a linear habitat map and the default Euclidean distance model, indicating that feral cats use the tracks for moving around but their movement is not solely restricted to the tracks. Akaike Information Criterion adjusted for small sample size (AICc) was used to rank models. Only models with $\Delta AICc < 2$ are shown and dealt with

further (these models have the greatest likelihood of all the model-set to be the best model fit to the data) (Burnham and Anderson, 2002). AICc weights (w_i) were calculated for these top models as a proportion of all models tested.

Generalised additive mixed models (GAMMs via REML-restricted maximum likelihood) were used to determine if feral cat density (dependent variable) changed over the monitoring period. Predictor variables included (1) month of trial (1–16), (2) number of baits on the ground during the month, and (3) dingo density (MK, unpublished data). Property (A or B) was included as a random factor. The GAMMs were fitted using the *mgcv* package (Wood, 2017; Wood, 2011) in R (R Core Team, 2019). An adjusted R^2 -value was calculated for each model as well as standardised β and P -values. A total of seven models predicting feral cat density were compared. GAMMs were fitted using the *gam* function of the *mgcv* package in R (Wood, 2017, 2019; Wood, 2011).

2.4.2. Daily capture rate, controlling for environmental factors and relative prey abundance

Generalised additive mixed models (GAMMs via REML-restricted maximum likelihood) were used to compare dingo and feral cat capture rates (as dependent variables in two separate analyses). We controlled for environmental variables: (1) maximum temperature ($^{\circ}\text{C}$), (2) daily minimum temperature ($^{\circ}\text{C}$), (3) daily rainfall ($-\text{mm}$), (4) moon phase (percentage of moon visible, %), (5) month (1–16), (6) small mammal capture rate (log-number of individual captures per day), (7) macropod capture rate (log-number of individual captures per day), and (8) the number of baits remaining on the ground as monitored by the camera traps. (9) Property (A or B) was included as a random factor. The analysis of feral cat capture rate also included (10) dingo capture rate (log-number of individual captures per day) as a variable.

To determine the independence of factors, a correlation matrix of all parameters was performed (Appendix 2). The number of independent factors varied between one and five in each model; however, a maximum of five independent variables was used in each model so as not to exceed the ratio of independent factors to replicates to avoid overfitting, and to strive for parsimony in terms of numbers of parameters (Burnham and Anderson, 2002). Dingo capture rate was analysed for 88 models and feral cat capture rate for 138 models. GAMMs were fitted using methodology as per the feral cat density data.

2.4.3. Temporal activity patterns

We used the timestamp recorded on camera trap images to create 'diel' temporal activity profiles for both feral cats and dingoes, as well as small mammals and macropods (Meredith and Ridout, 2017; Ridout and Linkie, 2009). We fitted non-parametric kernel density curves using default smoothing parameters to characterise the probability density distribution of each species' activity pattern. Identical timestamps were altered by 0.00001 degrees (0.06 s) in the raw data. We calculated the coefficient of temporal overlap, where the area under the curve measure ranges from 0 (no overlap) to 1 (complete overlap) and is determined as the minimum of the two density functions for each time point. For each species, we used the non-parametric Watson-Wheeler test in the *circular* package version 0.4–7 (Meredith and Ridout, 2017) to test for homogeneity in species' temporal activity profiles. We analysed temporal data for two wet (winter season) and one dry season (summer season) over the 16 months of monitoring, although because there were no differences in results between seasons (Appendix 3), the data were also analysed together across all 16 months of monitoring. As the properties were only 70 km apart, which is small in terms of dingo movements (Thomson, 1992; Thomson et al., 1992), we also analysed the data for both properties together.

2.4.4. Temporal separation

As a fine-scale measure of temporal separation, we compared how close in time captures of dingoes and feral cats were. For dingo and feral cat photo captures, we recorded the number of photo events of either predator on the same camera within 1 h, 12 h, and 24 h of each other. These were tallied for feral cats following a cat or following a dingo, and dingoes following a feral cat or following a dingo. The number of photo captures were compared using Fisher's exact test (as some of the frequencies were small), where the expected values were calculated as a proportion of the independent camera trap events (3844 camera trap events where the same species was captured at least 10 min apart) that were feral cats (59.7% of the total) or dingoes (40.3% of the total). These analyses were conducted in R using the 'fisher.test' function in the *stats* package in R (R Core Team, 2019).

3. Results

Over the 16 months of monitoring (93,002 camera trap nights for the 182 camera traps), we recorded a total 1968 independent capture

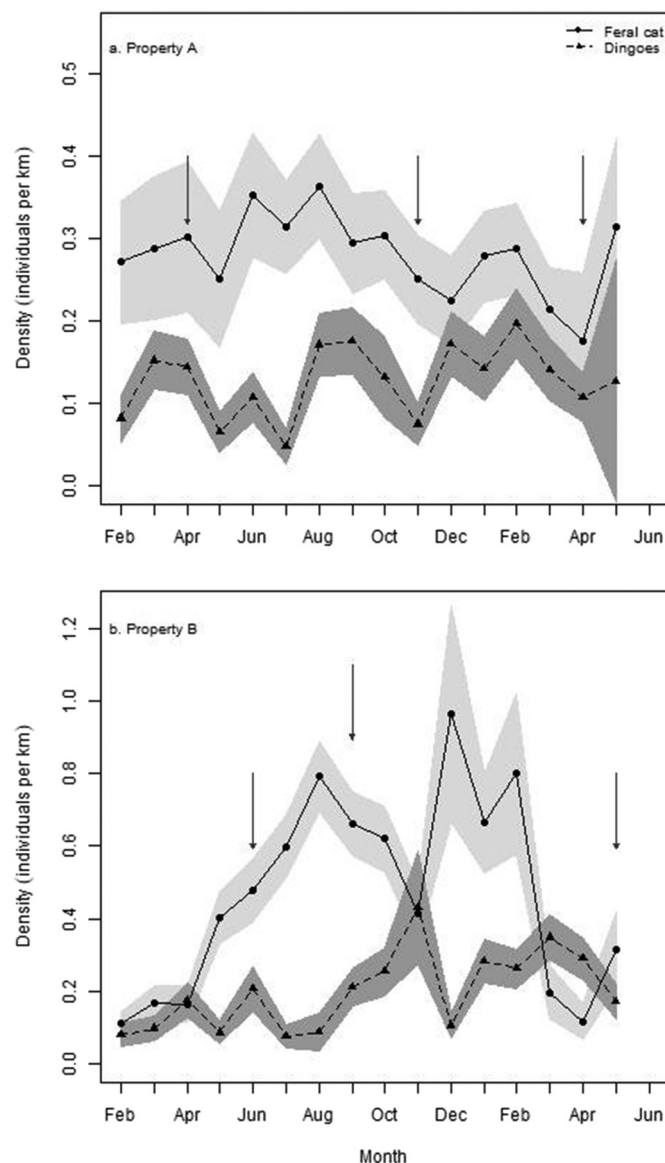


Fig. 1. Density of dingoes and feral cats on two properties (property A and property B) in the southern rangelands, Murchison region, Western Australia during 16-months of monitoring. Dingo density estimates are taken from unpublished data (M. Kennedy). The arrows indicate the baiting event at each property.

events of dingoes and 2324 independent capture events of feral cats. This translated to an average camera trap capture rate of 2.13 dingo capture events per 100 trap nights and 2.49 feral cat capture events per 100 trap nights.

3.1. Population densities

Dingo density varied from 0.05–0.20 per linear km at Property A and 0.08–0.43 per linear km at Property B over the study period, and averaged 0.16 ± 0.04 SE individuals per km of linear habitat (monthly density estimates averaged over 16 months and the two properties; Fig. 1; Unpublished data, M. Kennedy). A total of 80 and 81 individually-identifiable dingoes were observed on Property A and B respectively.

Feral cat density varied from 0.18–0.31 per linear km at Property A and 0.11–0.96 per linear km at Property B over the study period, and averaged 0.37 ± 0.08 SE individuals per km of linear habitat (monthly density estimates averaged over 16 months and the two properties). A total of 90 and 156 individually-identifiable feral cats were observed on Property A and B respectively. During November at Property A, and September at Property B, the sigma values were very high in comparison to other months as the number of feral cat detections rose. Individuals were repetitively seen on more than one camera along a track (on average individual feral cats were seen on cameras: Property A 8 ± 10.45 times, range 1–72; Property B 7 ± 7.61 times, range: 1–37).

The top model for predicting feral cat density had a weak coefficient of determination (adjusted $R^2 = -0.05$, $w_i = 0.87$; Fig. 2) and included no relationship with dingo density ($\beta = 0.27$, $p = 0.775$).

3.2. Daily capture rate, controlling for environmental factors and relative prey abundance

A single best model was identified for dingo capture rate (adjusted $R^2 = 0.10$, $w_i = 0.70$, Table 2; Fig. 3). Dingo capture rate was positively correlated with the moon phase (i.e. moon visibility and dingo capture rates were positively related; Fig. 4a) and the standardised capture rate of macropods (Fig. 4c). Dingo capture rates per day were negatively

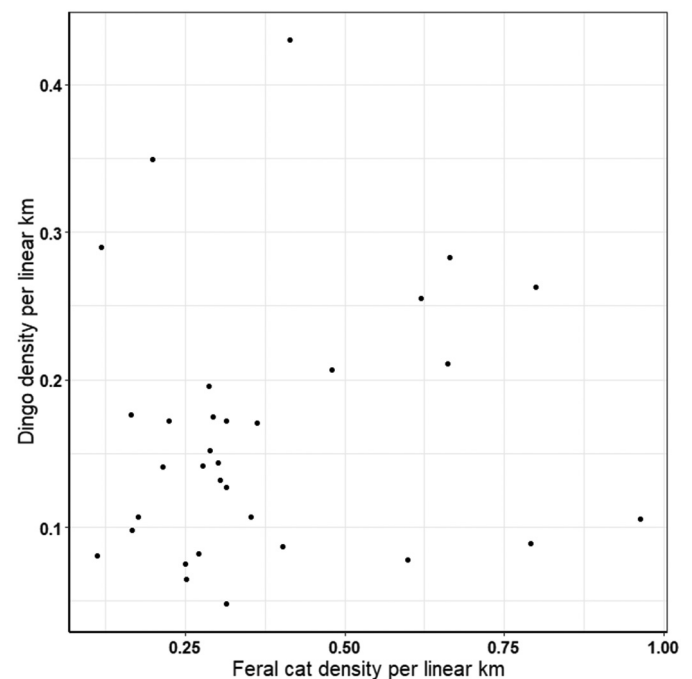


Fig. 2. The relationship between feral cat and dingo density per linear km (where the blue line is the fitted model from the GAMM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

GAMMs results investigating factors associated with feral cat and dingo capture rate per camera trap night (number of individual captures per day). Factors included in the modelling were daily maximum temperature ($^{\circ}\text{C}$), daily minimum temperature ($^{\circ}\text{C}$), daily rainfall (mm), moon phase (% visible), month, small mammal capture rate (number of individual captures per day), macropod capture rate (number of individual captures per day), number of baits on the ground and dingo capture rate (feral cat models only).

Dependant parameter	Model (β and P values)	Adjusted R^2	AICc	w_i
Feral cat capture rate	Maximum temperature (0.004, <0.010), month (0.0, <0.010), and small mammal capture rate (0.009, <0.010)	0.03	203.47	0.87
Dingo capture rate	Moon phase (0.001, 0.002), month (-0.008, <0.010), number of baits on the ground (-0.002, <0.010), and kangaroo capture rate (0.09, 0.060)	0.10	644.5	0.70

related to the month of the study, and the number of baits on the ground (i.e. when baits were present less dingoes were observed on camera; Fig. 4b).

A single best model with poor explanatory power described the feral cat capture rates per day (adjusted $R^2 = 0.03$, $w_i = 0.87$). Feral cat capture rate had a weak positive correlation with maximum temperature (Fig. 4d), month of the study, and standardised small mammal capture rate (Fig. 4e). Although dingo capture rate was included in analysis of feral cat density, dingo density estimates were not included the top model.

3.3. Temporal activity patterns

There were no major changes in temporal activity of the two predators during the different seasons of the study period (two wet and one dry season values; Watson Wheeler value range = 51.9, 52.1, 58.1, $p = 0.010$, and overlap value range = 83.5%, 72.9%, 80.2%). Temporal activity patterns across each month was therefore used for further analyses. Although their activity patterns overlapped by 78.7%, dingo and feral cat temporal activity peaks were significantly different (Watson-Wheeler value = 235.01, $p < 0.001$; Fig. 5a). Both predators were primarily nocturnal at the study sites, but dingoes had a peak of activity at 06:00 h whereas feral cats were active over much of the night with a slight peak at 01:00 h (Fig. 5a).

Temporal activity of dingoes and macropods overlapped by 87.9% but their peak activity was statistically different (Watson-Wheeler value = 67.71, $p < 0.001$; Fig. 5c). Similarly, dingoes and small mammals overlapped by 62.38% but their peak activity was statistically different (Watson-Wheeler value = 21.02, $p < 0.001$). Overall, dingoes were most active at dawn, while macropods and small mammals were mostly active overnight.

Temporal activity of feral cats and small mammals overlapped by 77.6% with the majority of activity overnight for both taxa (Watson-Wheeler value = 5.48, $p = 0.065$; Fig. 5b). Feral cats and macropods overlapped by 84.2% but their peak activity was significantly different (Watson-Wheeler value = 182.14, $p = 0.010$): both macropods and feral cats were primarily nocturnal, but macropods were more active around dusk and feral cats were more active in the early hours of the morning.

3.4. Temporal separation

All 182 camera traps captured an image of at least one predator over the 16-month study, with 87% of cameras capturing images of both dingoes and feral cats, indicating that spatial overlap was the rule rather than the exception (Appendix 4). However, simultaneous dingo and

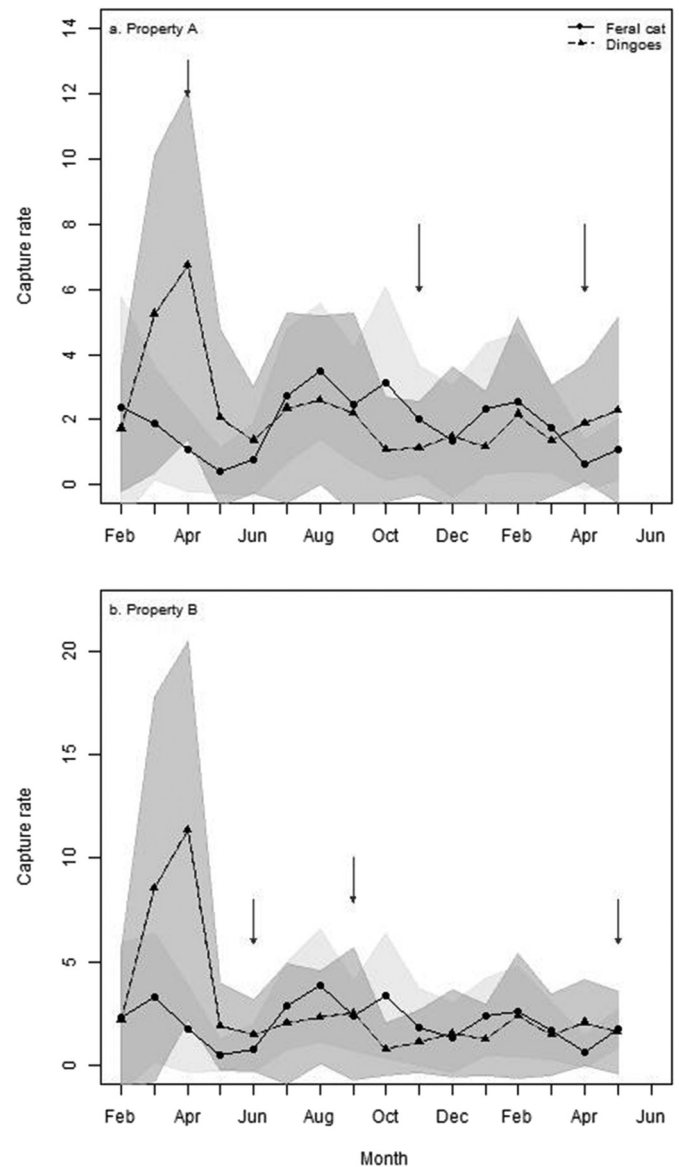


Fig. 3. Capture rate (number of captures per trap night) of dingoes and feral cats on two properties (property A and property B) in the southern rangelands, Murchison region, Western Australia during 16-months of monitoring. Dingo density estimates are taken from unpublished data (M. Kennedy). The arrows indicate the baiting event at each property.

feral cat activity on the same cameras within 1, 12 and 24 h of each other was less common than would be predicted as a function of their activity at these sites ($p < 0.001$ for each analysis). If a dingo was recorded on camera, then it was significantly unlikely that a feral cat would be captured on the same camera over the preceding or subsequent 1, 12 or 24 h.

4. Discussion

Dingoes have been hypothesized by some authors to suppress feral cats, either directly or indirectly, leading some to conclude that lethal dingo control will free feral cats from suppression and result in increased densities of feral cats (Brook et al., 2012). In our study, densities of dingoes and feral cats fluctuated independently over time and there was no evidence that dingoes had any direct effect on feral cat densities. It is likely that both predators were responding to environmental factors and prey availability, rather than suppressing the activity of one another. Contrary to our expectations, baiting did not affect the density of dingoes (M. Kennedy, unpub data). These results are similar to those

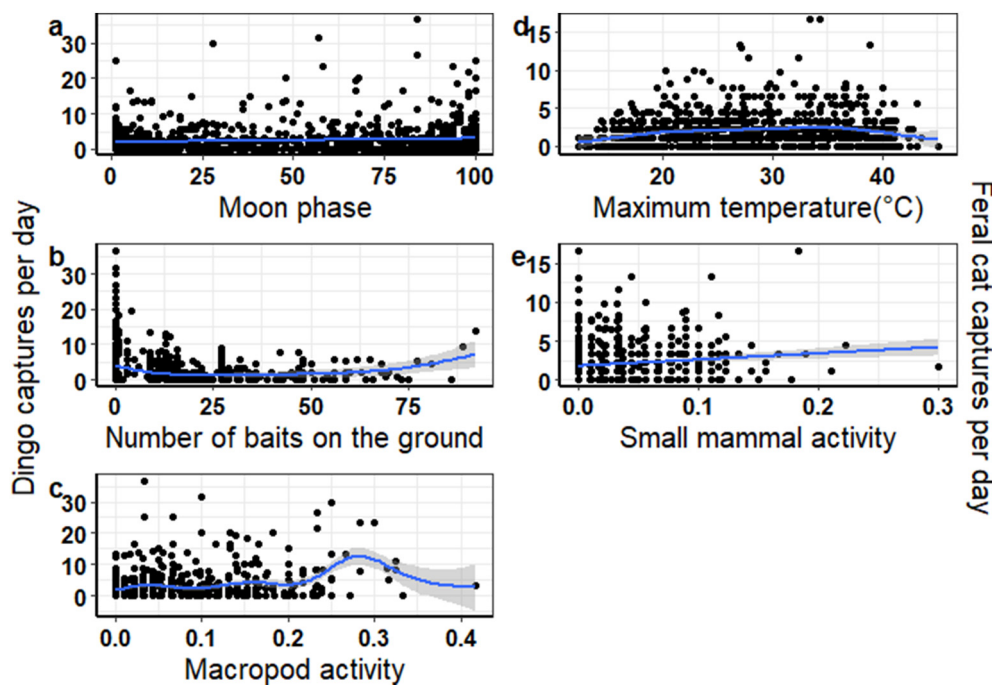


Fig. 4. The relationship of the dingo capture rate per camera trap month with (a) moon phase (percentage visible), (b) the number of baits on the ground and (c) standardised activity of macropods. The relationship of the feral cat activity per camera trap night with (d) maximum temperature ($^{\circ}\text{C}$), and (e) the standardised activity of small mammals at two properties in the southern rangelands, Western Australia. Data represent records for 513 days of monitoring at Property A and 464 days at Property B (16 months of monitoring 2016–2017). The blue line is the fitted model from the GAMM, and the grey shading indicates the 95% confidence bounds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of Allen et al. (2013) who showed that changes in dingo relative abundance indices in response to baiting did not influence feral cat indices at nine sites across Australia from monsoonal north Queensland to arid South Australia. Allen et al. (2014) also found no evidence of a cat increase following dingo control at several other sites, and Arthur et al. (2012) also showed no sign of mesopredator release in an analysis of a 30-year natural experiment in south-eastern New South Wales. Indeed, very few studies have reported a negative relationship between dingoes and cats, let alone a relationship where dingoes suppress cats (Allen et al., 2015).

In addition to direct population suppression of mesopredators, various authors have tested for evidence of indirect mesopredator suppression, through changes in activity patterns (spatial and temporal), diet shifts, and/or reproductive effort (Cupples et al., 2011; Gordon et al., 2017; Letnic and Koch, 2010). Peaks in temporal activity patterns of the predators did differ. Although, both species were more active at night, feral cats were most active around midnight and dingoes were most active around dawn (06:00–07:00 h). On a fine spatial scale, we recorded feral cats and dingoes on the same camera within 1, 12 and 24 h of each other significantly less often than would be predicted if their activity had been randomly distributed across time. Other studies of dingoes and feral cats in Western Australia similarly noted separation of dingo and feral cat activity at a fine scale (Hernandez-Satin et al., 2016). It has been hypothesized that, over the long term, even such fine-scale temporal separation could lead to reduced feral cat fitness, if there was a reduction in hunting success and/or reproduction rate (i.e. higher mortality of offspring) leading to long-term population effects (Kennedy et al., 2012; Lima and Dill, 1990). In the presence of dingoes, feral cats could potentially experience these impacts, but to date this has not yet been found in any study (Allen et al., 2015).

Differences in temporal activity patterns can be influenced by prey activity (Hayward and Slotow, 2009; Wysong, 2016). Here we observed correlations between activity of both predator species and their primary

prey. Feral cats are likely responding to small mammal activity overnight (Paltridge et al., 1997), and we observed 77.6% overlap in temporal activity of feral cats and small mammals on our cameras. Although dingoes also depredate small native species (Brook and Kutt, 2011; Davis et al., 2015; Newsome et al., 1983; Newsome et al., 2014) and livestock (Allen and Fleming, 2004; Allen et al., 2012), the temporal activity overlap of dingoes and macropods (87.9%) is likely a reflection of macropods being common prey of dingoes, as recorded in Caughley et al. (1980). Overall, feral cat density is more likely to be related to the prey available in the landscape rather than dingo density.

Predator capture rates on camera were not only related to prey capture rates but environmental variables in the arid rangelands of Western Australia. However, the strength of these relationships are weak as predators move over large landscapes, and respond to stochastic changes in their surroundings which, in turn, influences their detections on camera traps (Broadley et al., 2019). Dingo capture rate was positively related to moon phase and macropod captures, and negatively related to the number of baits on the ground. Macropods are a known food source for dingoes (Caughley et al., 1980) but the abundance of macropods will fluctuate with a range of environmental variables such as rainfall and grazing availability (Choquenot and Forsyth, 2013). Moon phase has been little studied in relation to dingoes but anecdotally the full moon may alter dingo hunting abilities and rates (Shepherd, 1981).

Season and climate are also likely to alter interactions between trophic levels in an ecosystem, particularly in the arid regions of Australia (Morgan et al., 2016). A lack of support for interactions between the two predators could be a consequence of semi-arid environments that are dominated by bottom-up ecosystem effects (Choquenot and Forsyth, 2013; Greenville et al., 2014; Pople et al., 2000), rather than top-down trophic processes. Prey availability for both the feral cat and dingo varies with seasonal and climatic changes. For example, high feral cat density in Australia is driven by higher rainfall, most likely a result of greater prey availability (Legge et al., 2017) and we have

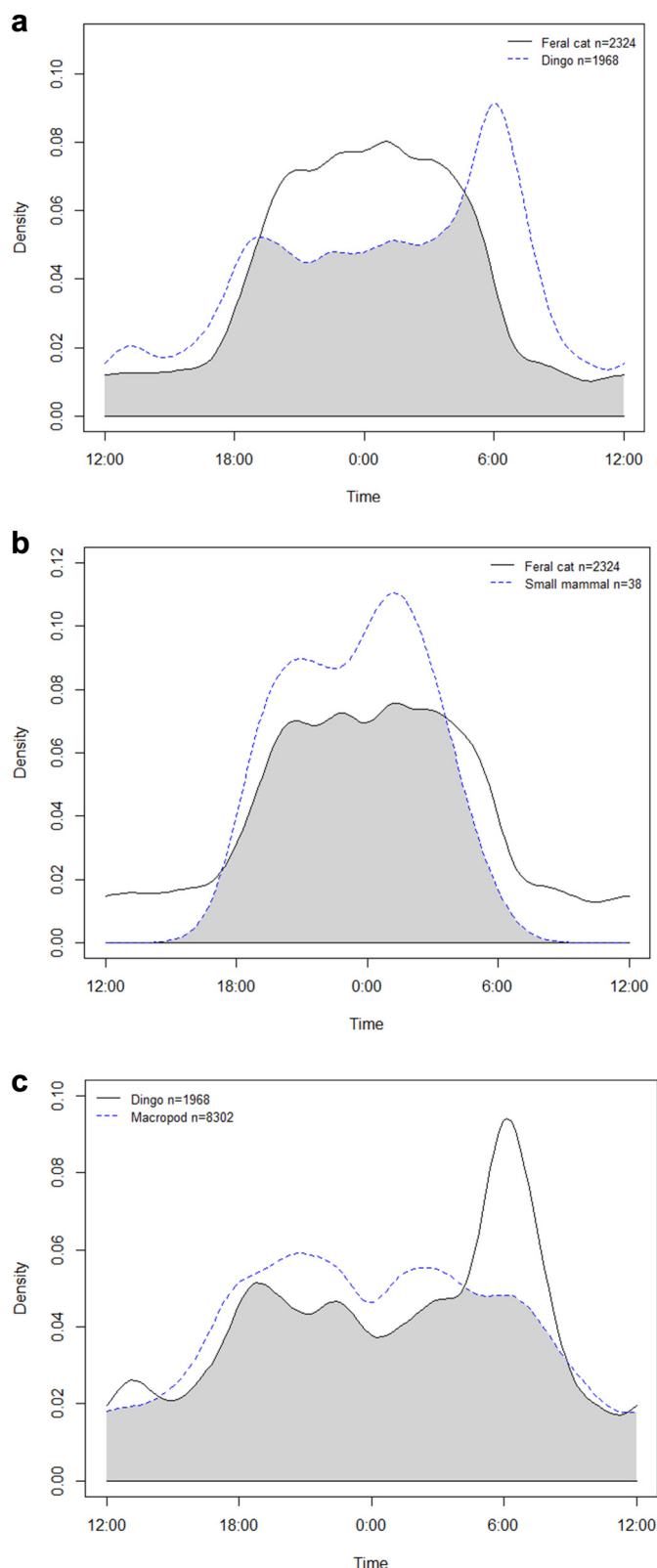


Fig. 5. Temporal activity of (a) dingoes and feral, (b) feral cats and small mammals and (c) dingoes and macropod on roads over 16 months monitoring at two properties.

demonstrated relationships between both predators and their primary prey, albeit weak relationships for the reasons described above. In arid regions like this study area, resources are more limited than other areas in Australian with a higher rainfall. As such, competition between

the two predators should have been heightened (Greenville et al., 2014). However, responses to reduced competition may be muted by low resource availability. Elmhagen and Rushton (2007) note that in 'low productivity' systems, even if mesopredator releases were to occur, the mesopredators may not have the available resources for population growth in the absence of the top-predators. Resource availability is a function of the seasonal variables (White, 2004; White, 2008), therefore in arid areas like this study it is more likely that the resources available to feral cats are limiting their population size rather than top-down suppression by dingoes.

Density estimates of feral cats in this study were high and varied markedly between the two properties. The densities recorded in this study are substantially higher than might be expected given published literature. However, we used *secrlinear*, which provides a measure of density per linear km, and therefore differs from most measures of predator density presented per km². On average, the estimates from the present study at 0.37 cats per linear km and peaking at 0.96 cats per linear km in December 2016 (Figure 6) are higher than those recorded feral cat averages for Australia (Legge et al., 2017). Legge et al. (2017) reports a mean density of feral cats of 0.27 cats per km² (95% CI: 0.18–0.45 cats per km²) across the Australian continent with estimates at the lower end of this range (95% CI: 0.13–0.28 cats per km²) in arid or low rainfall areas (such as our study site). Although there were substantial numbers of feral cats at our study sites, there are challenges in attempting direct comparison between studies that use the different methods.

There is some debate over camera placement to estimate feral cat abundance, density or activity rates (Hayward and Marlow, 2014). Camera traps were positioned on tracks in this study. Feral cat activity is more common off-track than on-track in some studies (Algar et al., 2011; Mahon et al., 1998; Raiter et al., 2018; Read and Eldridge, 2010). However, other studies have detected no difference in on- or off-track use by feral cats (Algar et al., 2001; Wysong, 2016). Feral cat movements and use of tracks is likely to be related to variables including vegetation, habitat and landscape productivity (Bengsen et al., 2016; Wysong, 2016). On this site, we have tested off-track and on-track cameras (Kennedy and Kreplins unpub data) and found off-track cameras did not improve detections, thus we consider monitoring on track provides a realistic reflection of cat and dingo activity.

Dingoes are a charismatic Australian species, and calls to protect dingoes based on conservation outcomes (see Allen et al., 2017) are attractive to a wide portion of society (Hyttén, 2009). However, dingoes also pose a threat to livestock production and threatened native wildlife and hence are subject to a range of control measures. In rangeland systems, it is a challenging task to balance potential biodiversity benefits with control for protection of livestock. Studies (including this one) identify that interactions between dingoes and cats are not straightforward, and assuming that dingo conservation will protect biodiversity by reducing feral cat impacts is too simplistic (Allen et al., 2013; Claridge, 2013; Claridge et al., 2010). We believe that generalisation of the mesopredator release hypothesis to dingo and feral cat management requires a much greater body of evidence than is presently available. Direct application of this hypothesis to management is also very limited.

Here we have demonstrated that both dingoes and feral cats coexist across the Western Australian rangelands, with no evidence that there is an increase in feral cat density in response to a changes in dingo density, and no evidence of a spatial pattern of separation. At best, night time peaks in dingo and cat activity are separated by a few hours. In semi-arid environments that are predominately driven by bottom-up processes, control of a top-order predator is likely to have less effect than that observed in mesic environments where the mesopredator release hypothesis originated. It is likely that predator relationships are flexible across Australia's variable landscapes, habitats and seasons. Interpreting interactions between dingoes and feral cats will require robust data to inform management in relation to the prevailing landscape.

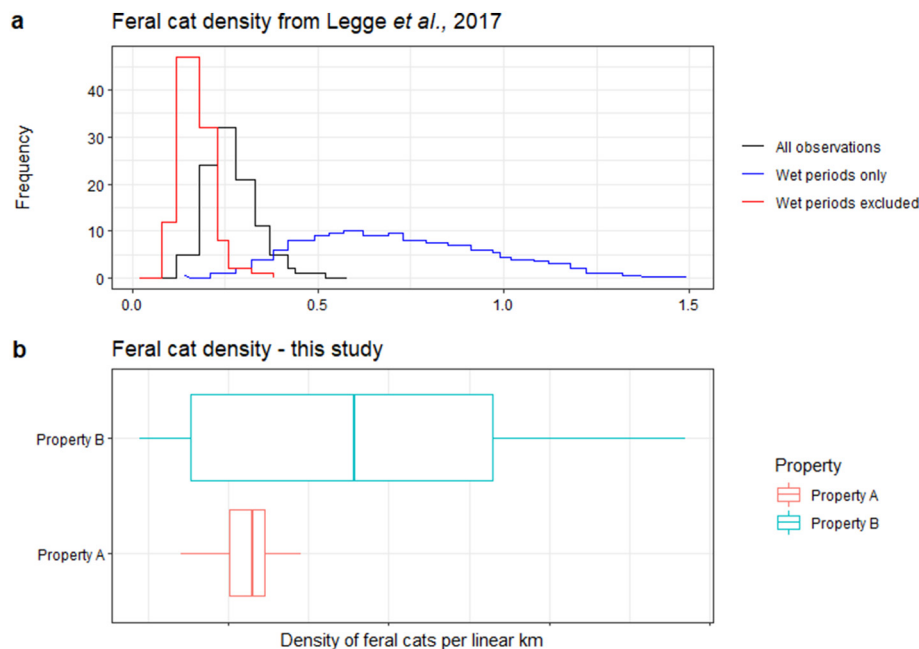


Fig. 6. (a) Feral cat density estimates (number of individuals per km²) across Australia (all observations, wet periods only, wet periods excluded) as taken from Legge et al., (2017) (95%CI) and (b) box and whisker plot of the density of feral cats (number of individuals per km along linear habitat) in this study at property A and B (upper and lower boundaries of the boxes are the 25th and 75th percentiles, the whiskers of the boxes are the minimum and maximum values).

Funding sources

This project was funded by the Royalties for Regions Boosting Biosecurity Fund.

Declaration of competing interest

There are no conflicts of interest concerning our article.

Acknowledgements

Thanks to Jim Miller and Glen Coupar from the Western Australian Department of Primary Industries and Regional Development for their hard work in the field, and to the Meekatharra Recognised Biosecurity Group for their cooperation. Thanks to Peter Fleming, Ben Allen and two anonymous reviewers for their constructive review of the manuscript. This project was carried out under the approval of the Murdoch University Animal Ethics Committee- O2775/15 and RW2788/15.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2020.e00173>.

References

- Algar, D., Hamilton, N., Onus, M., Hilmer, S., Comer, S., Tiller, C., Bell, L., Pinder, J., Adams, E., Butler, S., 2011. Field Trial to Compare Baiting Efficacy of Eradicator and Curiosity Baits. Department of Environment and Conservation, Western Australia.
- Algar, D.A., Burbidge, A.A., Angus, G.J., 2001. Cat eradication on Hermite Island, Montebello Islands, Western Australia. In: Veitch, C.R., Clout, M.N. (Eds.), *Proceedings of the International Conference on Eradication of Island Invasives*. IUCN The World Conservation Union, University of Auckland.
- Allen, B.L., Leung, L.K.-P., 2012. Assessing predation risk to threatened fauna from their prevalence in predator scats: dingoes and rodents in arid Australia. *PLoS One* 7, e36426 (doi:10.1371/journal.pone.0036426).
- Allen, B.L., Allen, L.R., Engeman, R.M., Leung, L.K.-P., 2013. Intraguild relationships between sympatric predators exposed to lethal control: predator manipulation experiments. *Front. Zool.* 10.
- Allen, B.L., Lundie-Jenkins, G., Burrows, N.D., Engeman, R.M., Fleming, P.J., Leung, L.K.P., 2014. Does lethal control of top-predators release mesopredators? A re-evaluation of three Australian case studies. *Ecol. Manag. Restor.* 15 (3), 191–195.
- Allen, B.L., Allen, L.R., Leung, L.K.P., 2015. Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? *Biol. Invasions* 17, 761–776.
- Allen, B.L., Allen, L.R., Ballard, G., Jackson, S.M., Fleming, P.J.S., 2017. A roadmap to meaningful dingo conservation. *Canid Biology and Conservation* 20, 45–56.
- Allen, L.R., Fleming, P.J.S., 2004. Review of canid management in Australia for the protection of livestock and wildlife - potential application to coyote management. *Sheep and Goat Research Journal* 19, 97–104.
- Allen, L.R., Goullet, M., Palmer, R., 2012. The diet of the dingo (*Canis lupus dingo* and hybrids) in north-eastern Australia: a supplement to Brook and Kutt. *The Rangeland Journal* 34, 211–217.
- Arthur, A.D., Catling, P.C., Reid, A., 2012. Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral Ecology* 37, 958–970.
- Ballard, G., Fleming, P.J.S., Meek, P.D., Doak, S., 2020. Aerial baiting and wild dog mortality in south-eastern Australia. *Wildl. Res.* 47, 99–105.
- Bengsen, A.J., Algar, D., Ballard, G., Buckmaster, T., Comer, C., Fleming, P.J., S., Friend, J.A., Johnston, M., McGregor, H., Moseby, K., Zewe, F., 2016. Feral cat home-range size varies predictably with landscape productivity and population density. *J. Zool.* 298, 112–120.
- Berger, K.M., Conner, M.M., 2008. Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. *Ecol. Appl.* 18, 599–612.
- Bradshaw, C.J.A., Sodhi, N.S., Laurance, W.F., Brook, B.W., 2011. Twenty landmark papers in biodiversity conservation. In: Pavlinov, I.Y. (Ed.), *Research in Biodiversity - Models and Applications*. InTech, Rijeka, Croatia, pp. 97–112.
- Broadley, K., Burton, A.C., Avgar, T., Boutin, S., 2019. Density-dependent space use affects interpretation of camera trap detection rates. *Ecology and evolution* 9, 14031–14041.
- Brook, L.A., Kutt, A.S., 2011. The diet of the dingo (*Canis lupus dingo*) in North-Eastern Australia with comments on its conservation implications. *The Rangeland Journal* 33, 79–85.
- Brook, L.A., Johnson, C.N., Ritchie, E.G., 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J. Appl. Ecol.* 49, 1278–1286.
- Brown, J.S., Laundre, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399.
- Bureau of Meteorology, 2017. Climate data online, Bureau of Meteorology. <http://www.bom.gov.au/climate/data/>. (Accessed 21 August 2017).
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*. 2nd edition. Springer-Verlag, New York.
- Cattle Council of Australia, 2016. *Beef Industry Strategic Plan 2020*. ACT, Barton.
- Caughley, G., Grigg, G., Caughley, J., Hill, G.S.E., 1980. Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7, 1–12.
- Choquenot, D., Forsyth, D.M., 2013. Exploitation ecosystems and trophic cascades in non-equilibrium systems: pasture – red kangaroo – dingo interactions in arid Australia. *Oikos* 12 (9), 0–15.

- Claridge, A.W., 2013. Examining interactions between dingoes (wild dogs) and mesopredators: the need for caution when interpreting summary data from previously published work. *Australian Mammalogy* 35, 248–250.
- Claridge, A.W., Cunningham, R.B., Catling, P.C., Reid, A.M., 2010. Trends in the activity levels of forest-dwelling vertebrate fauna against a background of intensive baiting for foxes. *For. Ecol. Manag.* 260, 822–832.
- Colman, N.J., Gordon, C.E., Crowther, M.S., Letnic, M., 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proc. R. Soc. B Biol. Sci.* 281.
- Cupples, J.B., Crowther, M.S., Story, G., Letnic, M., 2011. Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *J. Mammal.* 92, 590–600.
- Davis, N.E., Forsyth, D.M., Triggs, B., Pascoe, C., Benshemesh, J., Robley, A., Lawrence, J., Ritchie, E.G., Nimmo, D.G., Lumsden, L.F., 2015. Interspecific and geographic variation in the diets of sympatric carnivores: dingoes/wild dogs and red foxes in south-eastern Australia. *PLoS One* 10, e0120975.
- Efford, M., 2017. Secrlinear: spatially explicit capture–recapture for linear habitats. R package version 1.1.1. <https://CRAN.R-project.org/package=secrlinear>.
- Efford, M., 2020. secr: spatially explicit capture–recapture models, R package version 4.2.0. <https://CRAN.R-project.org/package=secr>.
- Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecol. Lett.* 10, 197–206.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* 333.
- Fancourt, B., 2016. Avoiding the subject: the implications of avoidance behaviour for detecting predators. *Behav. Ecol. Sociobiol.* 70, 1535–1546. <https://doi.org/10.1007/s00265-00016-02162-00267>.
- Fancourt, B.A., Cremasco, P., Wilson, C., Gentle, M.N., 2019. Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in Australia suggests not. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2666.13514>.
- Fleming, P.J.S., 1996. Ground-placed baits for the control of wild dogs evaluation of a replacement-baiting strategy in North-Eastern New South Wales. *Wildl. Res.* 23, 729–740.
- Fleming, P.J.S., Allen, B.L., Allen, L.R., Ballard, G., Bengsen, A.J., Gentle, M.N., McLeod, L.J., Meek, P.D., Saunders, G.R., 2014. Management of wild canids in Australia: free-ranging dogs and red foxes. In: Glen, A.S., Dickman, C.R. (Eds.), *Carnivores of Australia: Past, Present and Future*. CSIRO Publishing, Collingwood, pp. 105–149.
- Gordon, C.E., Feit, A., Gruber, J., Letnic, M., 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proc. R. Soc. B* 282. <https://doi.org/10.1098/rspb.2014.2870>.
- Gordon, C.E., Moore, B.D., Letnic, M., 2017. Temporal and spatial trends in the abundances of an apex predator, introduced mesopredator and ground-nesting bird are consistent with the mesopredator release hypothesis. *Biodivers. Conserv.* <https://doi.org/10.1007/s10531-01017-11309-10539>.
- Greenville, A.C., Wardle, G.M., Tamayo, B., Dickman, C.R., 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia* 17, 1349–1358.
- Hayward, M.W., Marlow, N., 2014. Can dingoes really conserve wildlife and can our methods tell? *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2666.12250>.
- Hayward, M.W., Slotow, R., 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *S. Afr. J. Wildl. Res.* 39, 109–125.
- Hernandez-Satin, L., Goldizen, A.W., Fisher, D.O., 2016. Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biol. Conserv.* 203, 160–167.
- Hytten, K.F., 2009. Dingo dualisms: exploring the ambiguous identity of Australian dingoes. *Australian Ecologist* 35, 18–27.
- Kelly, M.J., Noss, A.J., Di Bitetti, M.S., Maffei, L., Arispe, R.L., Paviolo, A., De Angelo, C.D., Di Blanco, Y.E., 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *J. Mammal.* 89 (2), 408–418.
- Kennedy and Kreplins, unpub data, Camera trapping on grids, roads and water points in the Southern Rangelands.
- Kennedy, M., Phillips, B.L., Legge, S., Murphy, S.A., Faunlkner, R.A., 2012. Do dingoes suppress the activity of feral cats in northern Australia? *Austral ecology* 37, 134–139.
- Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., Holt, R.D., 2005. Trophic cascades across ecosystems. *Nature* 437, 880.
- Kreplins, T.L., Gaynor, A., Kennedy, M.S., Baudains, C., Adams, P., Bateman, P.W., Fleming, P.A., 2018a. What to call a dog? A review of the common names for Australian free-ranging dogs. *Pac. Conserv. Biol.* 25 <https://doi.org/10.1071/PC18018>.
- Kreplins, T.L., Kennedy, M.S., Adams, P.J., Bateman, P.W., Dundas, S.D., Fleming, P.A., 2018b. Fate of dried meat baits aimed at wild dog (*Canis familiaris*) control. *Wildl. Res.* 45, 528–538.
- Legge, S., Murphy, B.P., McGregor, H., Woinarski, J.C.Z., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C.R., Doherty, T., Edwards, G., Eyre, T., Fancourt, B.A., Ferguson, D., Forsyth, D.M., Geary, W.L., Gentle, M., Gillespie, G., Greenwood, L., Hohnen, R., Hume, S., Johnson, C.N., Ramsey, D., Read, J., Rendell, A., Rich, M., Ritchie, E.G., Rowland, J., Short, J., Stokeld, D., Sutherland, D.R., Wayne, A.F., Woodford, L., Zewe, F., 2017. Enumerating a continental-scale threat: how many feral cats are in Australia? *Biol. Conserv.* 206, 293–303.
- Letnic, M., Koch, F., 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* 35, 167–175.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 38.
- Mahon, P.S., Banks, P.B., Dickman, C.R., 1998. Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildl. Res.* 25, 11–22.
- McLeod, R., 2016. Cost of pest animals in NSW and Australia, 2013–14. eSYS Development Pty Ltd. Report Prepared for the NSW Natural Resources Commission.
- Meat & Livestock Australia, 2016. Meat Industry Strategic Plan (MISP 2020), Including the Outlook to 2030. The Australian Red Meat and Livestock Industry.
- Meek, P.D., Ballard, G., Fleming, P., 2012. An Introduction to Camera Trapping for Wildlife Surveys in Australia. PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.
- Meredith, M., Ridout, M., 2017. Overlap: estimates of coefficient of overlapping for animal activity patterns. <https://CRAN.R-project.org/package=overlap>.
- Morgan, H.R., Hunter, J.T., Ballard, G., Reid, N.C.H., Fleming, P.J.S., 2016. Trophic cascades and dingoes in Australia: does the Yellowstone wolf-elk-willow model apply? *Food Webs* <https://doi.org/10.1016/j.fooweb.2016.1009.1003>.
- Moseby, K.E., Neilly, H., Read, J.L., Crisp, H.A., 2012. Interactions between a top order predator and exotic mesopredators in the Australian rangelands. *International Journal of Ecology* 2012.
- Naval Meteorology and Oceanography Command, 2017. Phases of the moon, United States naval meteorology and oceanography command (NMOOC). <http://aa.usno.navy.mil/data/docs/MoonPhase.php>. (Accessed 21 August 2017).
- Newsome, A.E., Catling, P.C., Corbett, L.K., 1983. The feeding ecology of the dingo .2. Dietary and numerical relationships with fluctuating prey populations in southeastern Australia. *Aust. J. Ecol.* 8, 345–366.
- Newsome, T.M., Ripple, W.J., 2014. A continental scale trophic cascade from wolves through coyotes to foxes. *J. Anim. Ecol.* 84, 49–59.
- Newsome, T.M., Ballard, G.-A., Fleming, P.J.S., van de Ven, R., Story, G.L., Dickman, C.R., 2014. Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* 175, 139–150.
- Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. *Am. Nat.* 153, 492–508.
- Paltridge, R., Gibson, D., Edwards, G., 1997. Diet of the feral cat (*Felis catus*) in Central Australia. *Wildl. Res.* 21, 67–76.
- Pople, A.R., Grigg, G.C., Cairns, S.C., Beard, L.A., Alexander, P., 2000. Trends in the numbers of red kangaroos and emus on either side of the south Australian dingo fence: evidence for predator regulation? *Wildl. Res.* 27, 269–276.
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL <https://www.R-project.org/>.
- Raiter, K.G., Hobbs, R.J., Possingham, H.P., Valentine, L.E., Prober, S.M., 2018. Vehicle tracks are predator highways in intact landscapes. *Biol. Conserv.* 228, 281–290.
- Read, J., Eldridge, S., 2010. An optimised rapid detection technique for simultaneously monitoring activity of rabbits, cats, foxes and dingoes in the rangelands. *The Rangeland Journal* 32, 389–394.
- Ridout, M., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14, 322–337.
- Ripple, W.J., Wirsing, A.J., Wilmsers, C.C., Letnic, M., 2013. Widespread mesopredator effects after wolf extirpation. *Biol. Conserv.* 160, 70–79.
- Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12, 982–998.
- Shepherd, N.C., 1981. Predation of red kangaroos, *Macropus rufus*, by the dingo, *Canis familiaris dingo* (Blumenbach), in north-West New South Wales. *Australian Wildlife Research* 8, 255–262.
- Smith, D.W., Peterson, R.O., Houston, D.B., 2003. Yellowstone after wolves. *Bioscience* 53, 330–340.
- Soule, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Soric, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, 75–92.
- Thomson, P.C., 1986. The effectiveness of aerial baiting for the control of dingoes in north-western Australia. *Australian Wildlife Research* 13, 165–176.
- Thomson, P.C., 1992. The behavioural ecology of dingoes in North-Western Australia. IV. Social and spatial organisation, and movements. *Wildl. Res.* 19, 543–563.
- Thomson, P.C., Rose, K., 2006. Wild Dog Management. Best Practice Manual. Department of Agriculture and Food, Western Australia. State Wild Dog Management Advisory Committee.
- Thomson, P.C., Rose, K., Kok, N.E., 1992. The behavioural ecology of dingoes in North-Western Australia. VI. Temporary extraterritorial movements and dispersal. *Wildl. Res.* 19, 585–595.
- White, T.C.R., 2004. Limitation of populations by weather-driven changes in food: a challenge to density dependent regulation. *Oikos* 105, 664–666.
- White, T.C.R., 2008. The role of food, weather and climate in limiting the abundance of animals. *Biol. Rev.* 83, 227–248.
- Wilmsers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *J. Anim. Ecol.* 72, 909–916.
- Wood, S., 2017. Generalized Additive Models: An Introduction with R 2 edition. Chapman and Hall, CRC.
- Wood, S., 2019. Package 'mgcv'. R package version 3.4.3 <http://www.R-project.org/>.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series C-Applied Statistics* (B) 73, 3–36.
- Wysong, M.L., 2016. Predator Ecology in the Arid Rangelands of Western Australia: Spatial Interactions and Resource Competition between an Apex Predator, the Dingo *Canis dingo* and an Introduced Mesopredator, the Feral Cat *Felis catus*. School of Plant Biology. University of Western Australia, Perth.