Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression

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Summary

1. Apex predators can benefit ecosystems through top–down control of mesopredators and herbivores. However, apex predators are often subject to lethal control aimed at minimizing attacks on livestock. Lethal control can affect both the abundance and behaviour of apex predators. These changes could in turn influence the abundance and behaviour of mesopredators.

2. We used remote camera surveys at nine pairs of large Australian rangeland properties, comparing properties that controlled dingoes *Canis lupus dingo* with properties that did not, to test the effects of predator control on dingo activity and to evaluate the responses of a mesopredator, the feral cat *Felis catus*.

3. Indices of dingo abundance were generally reduced on properties that practiced dingo control, in comparison with paired properties that did not, although the effect size of control was variable. Dingoes in uncontrolled populations were crepuscular, similar to major prey. In populations subject to control, dingoes became less active around dusk, and activity was concentrated in the period shortly before dawn.

4. Shifts in feral cat abundance indices between properties with and without dingo control were inversely related to corresponding shifts in indices of dingo abundance. There was also a negative relationship between predator visitation rates at individual camera stations, suggesting cats avoided areas where dingoes were locally common. Reduced activity by dingoes at dusk was associated with higher activity of cats at dusk.

5. Our results suggest that effective dingo control not only leads to higher abundance of feral cats, but allows them to optimize hunting behaviour when dingoes are less active. This double effect could amplify the impacts of dingo control on prey species selected by cats. In areas managed for conservation, stable dingo populations may thus contribute to management objectives by restricting feral cat access to prey populations.

6. *Synthesis and applications.* Predator control not only reduces indices of apex predator abundance but can also modify their behaviour. Hence, indicators other than abundance, such as behavioural patterns, should be considered when estimating a predator's capacity to effectively interact with lower trophic guilds. Changes to apex predator behaviour may relax limitations on the behaviour of mesopredators, providing enhanced access to resources and prey.

Key-words: carnivore, interference competition, intraguild interactions, invasive species, landscape of fear, pest management, risk effects

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Introduction

When predators occur in sympatry, smaller mesopredators may face a reduction in fitness due to competition from larger apex predators (Creel & Creel 1996). This can take the form of exploitation competition among species that consume the same prey species or interference competition via harassment, killing and (sometimes) consumption of smaller mesopredators by apex predators (Polis, Myers & Holt 1989; Polis & Holt 1992). These two forms of competition can directly affect mesopredators by reducing their abundance and causing modifications of behaviour that allow them to avoid encounters with their larger enemies (Durant 2000; Hunter & Caro 2008; Salo et al. 2008; Ritchie & Johnson 2009; Elmhagen et al. 2010).

Mesopredator avoidance of apex predators can occur in both space and time, but most research has focussed on spatial shifts (Kronfeld-Schor et al. 2001). Although some studies have recorded temporal partitioning between sympatric, similar-sized felids (Di Bitetti et al. 2010; Romero-Muñoz et al. 2010), few have directly explored temporal shifts involving apex- and mesopredators (but see Hayward & Slotow 2009). Patterns of temporal activity are driven primarily by circadian stimuli such as light, but animals may shift activity in response to other factors such as predation risk (Rasmussen & Macdonald 2011) or competition (Kronfeld-Schor et al. 2001). These shifts may incur costs such as reduced foraging opportunities (Rasmussen & Macdonald 2011). Larger predators are not immune: their activity patterns can be influenced by the risk of encounter with humans (Theuerkauf 2009), particularly when facing persecution (Ordiz et al. 2012). Rasmussen & Macdonald (2011) found that African wild dogs *Lycaon pictus* shifted hunting activity to moonlit periods, which would probably reduce the success rate of hunting, to avoid encounters with humans.

Persecution by humans contributes to the decline of apex predator populations (Treves & Karanth 2003) and consequent ecological disruptions via trophic cascades (Estes et al. 2011). Removal of apex predators can 'release' mesopredators from top–down pressure (Soulé et al. 1988; Ritchie & Johnson 2009), lifting previous constraints on abundance and behaviour and allowing their populations to expand. As a consequence, abundance and diversity of prey may decline (Crooks & Soulé 1999; Berger, Gese & Berger 2008). Maintaining apex predators may indirectly protect vulnerable prey and sustain biodiversity (Sergio et al. 2006).

Since its arrival in Australia 3500–5000 years ago (Savolainen et al. 2004), the dingo *Canis lupus dingo* (L.) has been the largest mammalian predator on the continent. Widespread control programmes, using poison baiting, trapping and shooting, aim to reduce the dingo's impacts on livestock (Fleming et al. 2001). There is evidence that dingoes can suppress abundance of the invasive red fox *Vulpes vulpes* and thereby have positive effects on species preyed upon by foxes (Johnson, Isaac & Fisher 2007; Johnson & VanDerWal 2009; Letnic et al. 2009; Wallach et al.

2010). Dingoes may also suppress a smaller mesopredator, the feral cat *Felis catus* (L.), but there is less evidence for this (Letnic, Ritchie & Dickman 2012; but see Moseby et al. 2012). Feral cats arrived with European settlers in the 1800s (Abbott 2002) and now occur across the entire continent (Denny 2008). They have contributed to the decline and extinction of native mammals, reptiles and birds (Johnson 2006), thwarted reintroduction programmes for threatened species (Gibson et al. 1994; Priddel & Wheeler 2004) and may be partly responsible for current mammal declines across Northern Australia (Woinarski et al. 2011). Unfortunately, feral cats are difficult to control or monitor. Control efforts aimed at dingoes, and foxes usually involve distribution of baits laced with the poison sodium fluoroacetate (known as 1080), but these are ineffective against cats because cats are disinclined to take baits.

Both dingoes and feral cats are mostly active during crepuscular and nocturnal periods in warm climates (Jones & Coman 1982; Thomson 1992). They have physiological adaptations for crepuscular and nocturnal activity, such as optimal vision in low-light conditions and highly developed olfactory (dingo) and auditory (cat) capabilities (Kavanau & Ramos 1975; Kitchener, Van Valkenburgh & Yamaguchi 2010). In addition, predators may adjust their activity schedules to match periods when their prey are most active or vulnerable (Ferguson, Galpin & de Wet 1988). We would expect crepuscular periods, particularly dusk and early evening, to provide optimal foraging conditions for both predators, because they coincide with activity of preferred prey: nocturnal reptiles such as geckoes are most active in the hours following dusk (Bustard 1967), while diurnal reptiles are retreating, and mammals such as kangaroos and small marsupials (Coulson 1996), rodents (Breed & Ford 2007) and rabbits (Williams et al. 1995) tend to be crepuscular or nocturnal. However, we might expect feral cats to underutilize these time periods if they trade-off foraging benefits against the higher risk of encountering dingoes.

In this study, we explored the effects of predator control on interactions between dingoes and feral cats. We worked on nine pairs of large properties across Australia, where each pair consisted of a site that controlled dingoes (mainly by 1080 baiting, but also by opportunistic shooting) and a similar site in the same environment that did not. We examine (i) how predator control affected indices of abundance and activity schedules of dingoes, (ii) whether predator control resulted in shifts in spatio-temporal activity by feral cats and (iii) whether predator control and/or dingo removal led to increased abundance of feral cats.

Materials and methods

STUDY AREA AND DATA COLLECTION

We surveyed dingoes and feral cats on eighteen properties spread across North and Central Australia, spanning tropical to arid climates, in habitats varying from open forest and woodlands to native grasslands (Fig. 1). The properties were arranged in pairs,

each consisting of one property on which dingoes were controlled and a matched property with no dingo control. Properties varied in size from 7850 to 705 496 ha and ranged from being adjacent to up to 153 km apart. Paired properties were selected to minimize differences in habitat, climate and management. Most properties were working cattle stations, with three exceptions: the Townsville Field Training Area (TFTA), owned by the Department of Defence, and Mt Zero-Taravale, owned by the Australian Wildlife Conservancy (AWC) and managed for conservation, both in the Einasleigh Uplands, and Piccaninny Plains on the Cape York Peninsula (CYP), jointly owned by the AWC and WildlifeLink. The TFTA was paired with Mt Zero-Taravale. Neither property controls dingoes, but we selectively surveyed sections of the TFTA along the property boundary with cattle stations that do control dingoes to measure the effect of that baiting and obtain a contrast with Mt Zero-Taravale. Piccaninny Plains, which has a herd contained behind wire and is grazed at low levels by feral cattle and horses outside these paddocks, was paired with a cattle station with patchy grazing pressure and broad areas of ungrazed woodland.

We surveyed dingoes and feral cats (and other wildlife) using infrared remote movement-triggered cameras. We used either I-60 Game Spy (Moultrie; EBSCO Industries, Birmingham, AL, USA) or DLC Covert II (DLC Trading Co., Lewisburg, KY, USA) cameras. Cameras were distributed in pairs along transects, with a spacing of 2–5 km to avoid correlation between pairs (Sargeant, Johnson & Berg 1998). We used minor, unsealed vehicle tracks as transects, and each camera pair consisted of one camera placed 1–5 m from the track and the other 50–200 m away, to allow for fine-scale differences in predator activity due to the presence of the track. Cameras were baited with different combinations of attractants such as chicken, the synthetic fermented egg spray FeralMone™ (Animal Control Technologies, Somerton, VIC, Australia), Felid Attracting Phonics (Westcare Industries, Bassendean, WA, Australia), bird seed or wild cat urine (Outfoxed Pest Control, Ivanhoe, VIC, Australia). In some paired areas, we surveyed for prey prior to predator surveys, using small mammal bait (rolled oats, vanilla and peanut butter) and positioning cameras 100 m off the road midway between camera pairs. We used 20–40 cameras on each property depending on property size and available tracks and operated the cameras for 5–8 days. Surveys

were generally run consecutively or concurrently on the properties within each pair, except on two occasions where surveys were up to 2 months apart but still within the same season. Camera type, number and spacing, survey duration and lure combinations were consistent within paired study areas. In the three most northern areas (areas 7, 8 and 9; Fig. 1), surveys were repeated in the early and late dry season, with a maximum of three surveys on CYP over 3 years. For this analysis, repeat surveys in the same area were pooled. Other pairs of properties were surveyed once, between March and November. Cameras were programmed to record 5-s videos at night and 20- or 5-s videos during the day. Time and date were recorded with each video.

ANALYSIS

Abundance indices

To distinguish repeat 'captures' of the same individual on the same camera at night, we plotted histograms of times elapsed between consecutive nightly records for each predator species. These showed a distinct peak for elapsed times of <10 min, which we assumed were repeats. To avoid these, we considered records as being independent only when separated by 30 min or more, unless individuals were distinguishable. We then calculated an abundance index (AI) for each species at each property (individuals individuals per trap night) (Rovero & Marshall 2009), which accounted for the number of cameras, survey length and camera failure in each survey. Abundance indices derived from camera trap rates have successfully detected reductions in feral cat abundance (Bengsen, Butler & Masters 2011). Cumulative indices (such as our AI) are better than proportional indices at detecting changes in density, and the relationship between AI and true abundance is likely to be linear (MacFarland & Van Deelen 2011).

Contrasts in abundance indices

To contrast differences in dingo and feral cat AI within paired areas, we calculated ratios of the AI on properties without predator control over properties with control. The ratios were then converted to natural logs so that their values were centred on
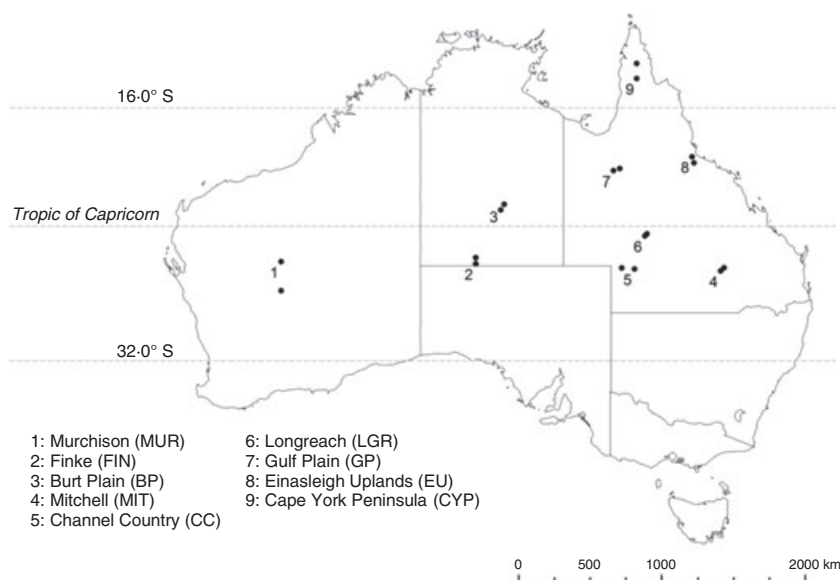

1: Murchison (MUR)
2: Finke (FIN)
3: Burt Plain (BP)
4: Mitchell (MIT)
5: Channel Country (CC)

6: Longreach (LGR)
7: Gulf Plain (GP)
8: Einasleigh Uplands (EU)
9: Cape York Peninsula (CYP)

Fig. 1. Paired survey areas across Australia. Each pair consists of one site that controls dingoes and one without dingo control.

zero and symmetrical about zero. To allow use of zero measures of the raw AI scores in the ratio calculation, we added 0·003 to each index record, a value smaller than the minimum nonzero recorded index (0·004).

Station-level activity rates

We examined the potential for local separation by comparing dingo and feral cat trap rates at camera stations, using quantile regression implemented in the QUANTREG package version 4.76 (Koenker 2011) in R version 2.14.1 (R Development Core Team 2011). We calculated regressions for the 50th, 75th, 95th and 99th quantiles. Least squares regression was unsuitable for several reasons: the data distributions were triangular and not normally distributed, and we were interested in a limiting effect of dingoes on feral cat activity rather than the average correlation (Cade, Terrell & Schroeder 1999). Standard errors were estimated using bootstrapping. Camera stations with no predators recorded were excluded.

Temporal data

We surveyed over a wide longitudinal range and at different times of year, introducing variation to the relationship between clock time, day and night length and the timing of sunrise and sunset. We therefore rescaled clock time for each survey to a standard unit range (from 0 to 1) with equal spacing between sunset (at 0·5) and sunrise (at 0 and 1). Temporal distributions were analysed in the program ORIANA 4 (Kovach Computing Services, Wales, UK), using the nonparametric Mardia–Watson–Wheeler test to detect differences in the mean angle or angular variance of circular data (Batschelet 1981). This test assumes no repeat data, so identical records were altered by 1-s in the raw data. Each independent (>30 min interval) capture of a species was considered one time record, regardless of the number of individuals detected.

Prey activity

We analysed the temporal patterns of mammal prey recorded incidentally in the camera surveys. Species were categorized depending on the prey preferences of the two predators. The large macropod category included wallabies (>7 kg) and kangaroos hunted only by dingoes. The small mammal category (≤ 6.65 kg) included species such as rodents, possums and small wallabies, which are known to be preyed upon by cats and also potentially by dingoes.

Results

We recorded 398 independent dingo records (334 time records) and 211 independent cat records (210 time records) over 5308 trap nights.

EFFECT OF CONTROL ON INDICES OF DINGO ABUNDANCE

Dingo abundance index (AI) varied widely between different properties, ranging from zero at MIT to a maximum of 0·27 at Piccaninny Plains on CYP (Fig. 2). Abundance indices were generally lower on properties where dingoes were controlled than on matched properties without control: the natural log of the ratio of dingo AIs in unbaited vs. baited areas was larger than zero (one-sided one-sample *t*-test: $t = 1.94$, d.f. = 8, $P = 0.044$), demonstrating a significant reduction attributable to control. However, the effectiveness of control was variable (Fig. 2), and in one case, dingo AI was actually higher on the property with dingo control.

RELATIONSHIPS BETWEEN INDICES OF DINGO AND FERAL CAT ABUNDANCE

We detected a shift in abundance indices of feral cats inverse to dingoes within paired sites ($R^2 = 0.70$, $F_{1,7} = 16.25$, $P = 0.005$, Fig. 3). As the ratio of dingo AI in the unbaited to baited sites increased, cats were more likely to show the inverse trend, that is, to occur at a higher rate on the baited site than on the unbaited site. The x-intercept at 0·75, indicating a dingo AI ratio of 2·12, suggests that once dingo indices were reduced by more than half, feral cat indices tended to be higher on the baited property. Feral cat abundance indices did not increase consistently with dingo control when tested across all areas; the natural log of the ratio of AIs in unbaited vs. baited areas was not <0 (one-sided one-sample *t*-test: $t = 0.03$, d.f. = 8, $P = 0.51$).

Trap rates at individual camera stations also suggested a limiting effect of dingoes on feral cats. We found a threshold relationship between the trap rates of dingoes and feral cats (Fig. 4). Where dingoes were rare or not
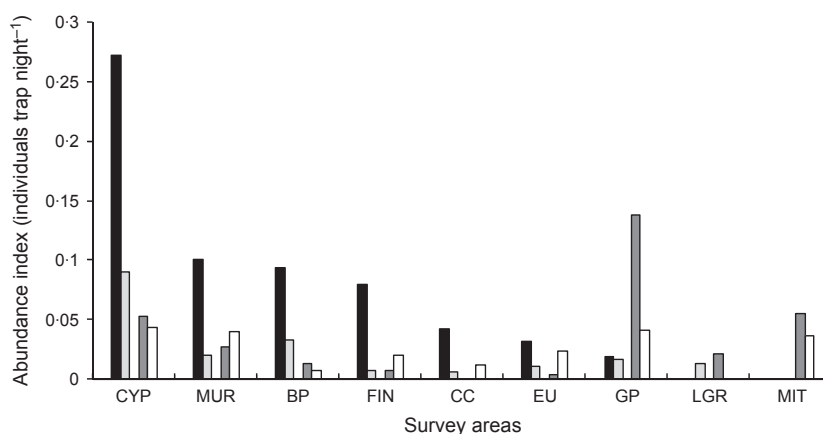

Fig. 2. Abundance indices of dingoes and feral cats derived from camera records in each paired survey area. Black and light grey bars represent dingoes in sites without and with predator control, and dark grey and white bars represent feral cats in sites without and with predator control, respectively.
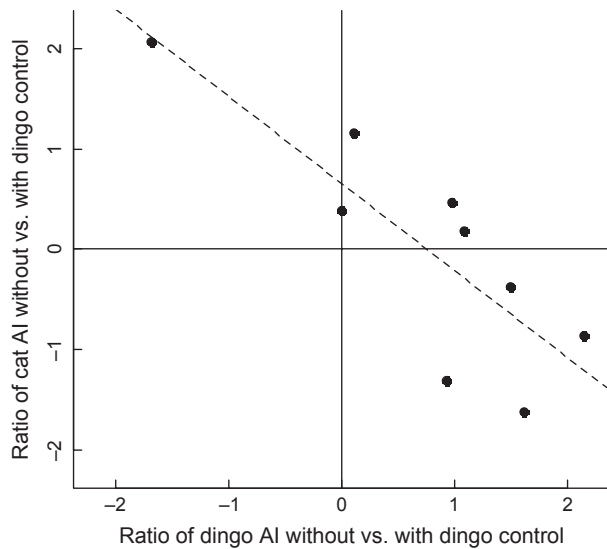
Fig. 3. Contrast in predator abundance indices (AI) in paired survey areas differing in dingo control ($n = 9$). Positive values represent higher abundance indices in the site without dingo control, and negative values represent higher abundance indices in site with control. Hence, the bottom right quadrant represents survey areas with more dingoes in the site without control and more cats in the site with control.
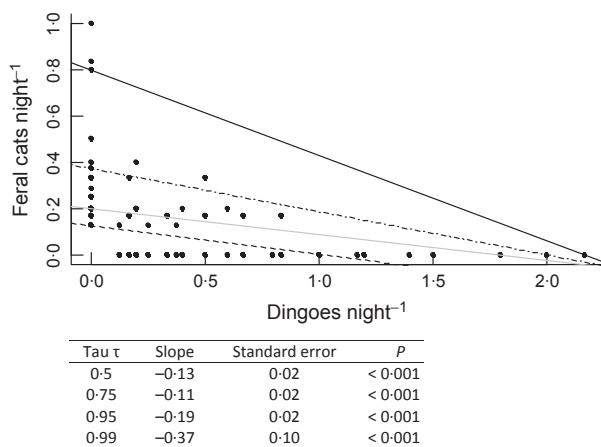

Tau τ	Slope	Standard error	P
0·5	−0·13	0·02	< 0·001
0·75	−0·11	0·02	< 0·001
0·95	−0·19	0·02	< 0·001
0·99	−0·37	0·10	< 0·001

Fig. 4. Predator trap rates at individual camera stations ($n = 279$ stations with at least one predator recorded). Regression lines, slope coefficients and significance values for quantiles are shown (50th quantile: dashed; 75th: grey; 95th: dot-dashed; 99th: solid).

recorded, feral cat trap rates ranged from 0·125 to 1 cats per night. As dingo trap rates increased, feral cat records declined. No feral cats were recorded at stations where dingoes were recorded at least once per night. All quantile regression slopes were significant.

DINGO BEHAVIOUR

Activity patterns of dingoes were significantly different on properties with and without dingo control (Mardia–

Watson–Wheeler test: $W = 22·95$, $P < 0·001$; Fig. 5a,b). Crepuscular activity in the early evening was reduced in areas with predator control, and the activity pattern shifted towards a single peak before sunrise.

FERAL CAT BEHAVIOUR

Feral cat activity patterns differed on properties with and without predator control ($W = 5·87$, $P = 0·053$), and were significantly different from dingoes in areas both with ($W = 23·78$, $P < 0·001$; Fig. 5a) and without predator control ($W = 25·50$, $P < 0·001$; Fig. 5b). In areas where dingoes were baited, feral cat activity peaked in the early evening, when nocturnal dingo activity was lowest.

There was a negative relationship in the proportion of activity concentrated around dusk (that is, during the hour before and 3 h after sunset) between the two species across survey areas: feral cats were more likely to be active at dusk when dingoes were less active at dusk ($R^2 = 0·39$, $F_{1,11} = 6·94$, $P = 0·023$; Fig. 6).

The shift in predator activity patterns under dingo control was most evident in areas where baiting was more effective in reducing dingo AI. In BP, EU, GP, LGR and MIT, where the difference in dingo AI with control was weaker, the contrasting activity patterns between dingoes and feral cats disappeared in baited areas ($W = 1·17$, $P = 0·56$, $n = 16$ dingoes, 36 cats), while in CYP, MUR, FIN and CC, sites with a larger contrast in dingo AI, the inverse relationship in crepuscular activity remained strong ($W = 23·78$, $P < 0·001$, $n = 69$ dingoes, 45 cats).

PREY ACTIVITY PATTERNS

Activity patterns of dingoes were not significantly different from those of their large macropod prey (number of prey records $n = 82$) in unbaited areas ($W = 5·03$, $P = 0·081$; Fig. 7a), but the reduction in dusk activity in areas with predator control shifted dingo activity away from the crepuscular peaks of large mammals ($n = 157$) ($W = 13·07$, $P = 0·001$). In contrast, feral cat activity patterns were closer to the nocturnal activity of small mammals ($n = 56$) in areas with dingo control ($W = 3·28$, $P = 0·19$; Fig. 7b) than without ($W = 5·37$, $P = 0·068$, small mammal $n = 196$).

Discussion

Our study confirms that predator control can influence not only abundance but also the behaviour of large predators. The effects of predator control on dingoes and their behaviour may provide opportunities in the spatial and temporal landscape for increased feral cat activity, by reducing the encounter rate between predators and lowering risk for feral cats (Laundré, Hernández & Altendorf 2001).
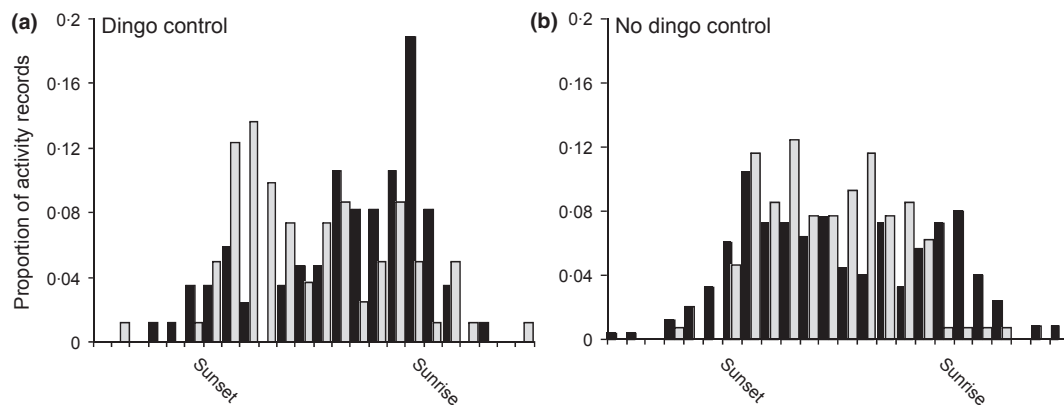
Fig. 5. Proportion of activity records (a) with and (b) without dingo control. Time has been scaled to a circular distribution with equal distance between sunset and sunrise. In 5a and b, black bars represent dingoes with ($n = 85$) and without ($n = 249$) control, and light grey bars represent cats with ($n = 81$) and without ($n = 129$) control.
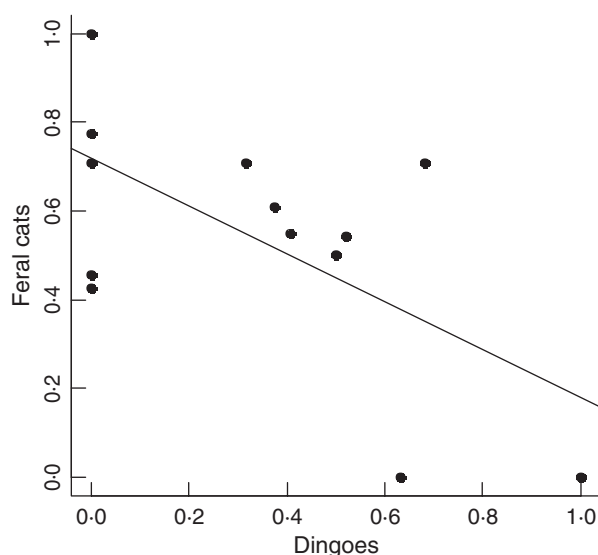

Fig. 6. Proportion of activity records in the dusk/early evening (1 h pre-sunset to 3 h post-sunset) ($n = 13$ sites with at least one dingo and one cat record). Data are square-root-transformed.

PREDATOR CONTROL AND PREDATOR NUMBERS

Sites with dingo control had significantly lower indices of dingo abundance than sites without control, but not in all cases. The exceptions may be due to (i) ineffective control, (ii) control effects flowing into neighbouring properties or (iii) low detection rates. The effectiveness of dingo control is dependent on numerous factors. Dingo density may actually increase following baiting (Wallach *et al.* 2009), as young dingoes can colonize vacant territories at high density if control is not coordinated over sufficiently large areas (Allen & Gonzalez 1998). Poison baits may not be as accessible to dingoes in complex habitats and landscapes, and abundant prey can also reduce bait uptake (Allen & Sparkes 2001). Dingo density on unbaited sites may be reduced if dingoes visit adjacent baited properties and are killed. Dingoes probably traversed property boundaries despite our large survey areas, as dingo home ranges can be extensive (up to 22, 622 ha in south-east Australia), and they can also make long-distance forays up to 60 km (Claridge *et al.* 2009). That detectability was imperfect was evident in one area (MIT), where dingo tracks were observed on roads, but no dingoes were recorded on camera (A. McNab, pers. obs.).

Shifts in indices of dingo abundance due to control were associated with inverse shifts in feral cat abundance, suggesting a negative relationship between abundances of the two species. Although this shift was significant when comparing paired sites, we did not find an overall increase in feral cat indices in direct response to predator control. However, we would not expect feral cats to respond to predator control *per se*, but to consequent changes in the dingo population, which were variable. In some areas, both feral cat and dingo abundance indices were higher on unbaited properties, suggesting competition may have been minimized by prey densities that could sustain both predators or by habitat features. Habitat complexity can mediate interference competition between predators (Janssen *et al.* 2007) by reducing the encounter rate. Additionally, feral cats can climb trees to avoid dingoes. Hence, in areas with considerable tree cover, such as CYP, feral cats may be able to occur at relatively high densities due to the protection provided by complex habitats (Lima & Dill 1990; Ritchie & Johnson 2009).

AVOIDANCE IN TIME

Temporal activity of dingoes in unbaited areas was similar to previous observations, with bimodal crepuscular peaks, frequent activity during the night and sporadic activity during the day (Harden 1985; Thomson 1992; Robley *et al.* 2010). However, in areas where dingoes were controlled, activity at dusk was reduced and shifted to a peak before sunrise. This could allow dingoes to avoid poten-
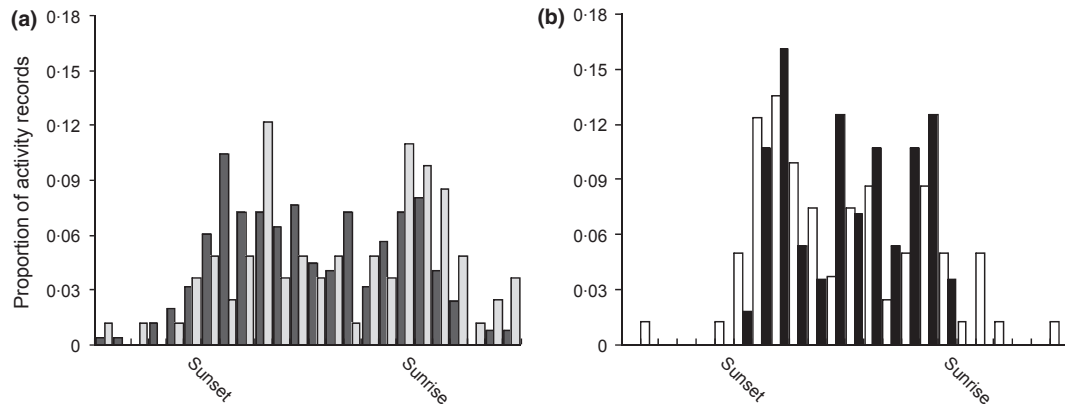
Fig. 7. Proportion of (a) dingo (dark grey) and large macropod (light grey) activity records in areas without predator control and (b) feral cat (white) and small mammal (black) activity records in areas with predator control.

tially lethal encounters with people, given that although poison baiting is the primary method of lethal control, landholders also opportunistically shoot dingoes. Canids may trade-off crepuscular or diurnal hunting activity to minimize the risk of encountering people (Theuerkauf 2009), particularly when faced with persecution (Kitchen, Gese & Schauster 2000).

Feral cat activity was inversely related to differences in dingo activity due to control of dingoes. This relationship was evident in areas where dingo control was more effective, and was not apparent in areas where dingo control had less effect, providing further support for the inference that feral cats were responding to reduced dingo presence. Feral cats may inherently have a bimodal circadian rhythm (Randall *et al.* 1987), but they can exhibit crepuscular and nocturnal patterns (Jones & Coman 1982; Burrows *et al.* 2003) or irregular cathemeral activity (Molsher *et al.* 2005; Moseby, Stott & Crisp 2009), to adapt to different needs such as predator avoidance (Langham 1992).

Temporal partitioning is probably due to interference rather than exploitation competition, as it allows competitors to reduce aggressive encounters (Carothers & Jaksić 1984). Harrington *et al.* (2009) found the invasive American mink *Neovison vison* exhibited a diel shift from nocturnal to diurnal activity, without reducing abundance, following recolonization by native competitors in the UK. Apart from a few such examples, competitors are unlikely to drastically shift activity from their circadian rhythms, which are entrained to environmental cues (Kronfeld-Schor & Dayan 2003; but see Gutman & Dayan 2005). Competitors that evolve under similar ecological conditions may develop similar activity schedules, a further limitation to diel-scale partitioning (Kronfeld-Schor & Dayan 2003). Almost all small mammals in Australia, a substantial prey resource for feral cats, are crepuscular or nocturnal (Van Dyck & Strahan 2008); hence, the activity shifts we observed in feral cats, which still provide some prey overlap, may be a more likely response to interference competition than a complete diel shift.

AVOIDANCE IN SPACE

Species exposed to predation (or interference competition) also avoid high-risk areas in space, forgoing potential foraging gains from using those areas (Brown, Laundré & Gurung 1999; Laundré, Hernández & Altendorf 2001; Wirsing *et al.* 2008). For feral cats, hotspots of dingo activity may carry a greater risk of potentially lethal encounters. Our results suggest that space use by dingoes restricts feral cats at a patch level, although factors such as habitat and prey availability will also influence their abundance. Patterns of mesopredators avoiding dingoes have been observed in other studies. In arid Australia, dingoes are common around water points, and feral cats are rare, in areas without predator control. However, where dingoes are poisoned, feral cats use areas near water more often (Brawata & Neeman 2011). Studies analysing field data (Johnson & VanDerWal 2009) and historical bounty data (Letnic *et al.* 2011) both found significant effects of dingo activity indices on the upper range of fox indices, suggesting dingoes can limit fox activity.

HOW COULD BEHAVIOURAL SHIFTS AFFECT PREY SPECIES?

Predators are expected to optimize their activity by matching it to that of their prey. The reduced activity of dingoes around dusk decoupled their activity patterns from those of macropod prey. An indirect consequence of this behavioural shift may be reduced hunting pressure from dingoes and the demographic release of herbivores such as kangaroos or rabbits. Herbivores trade-off optimal foraging conditions with the perceived threat associated with obtaining those resources (Lima & Dill 1990). Herbivores can more effectively exploit preferred foraging areas if predator presence is reduced, potentially leading to population growth and impacts on vegetation.

Reduced dingo activity at dusk may also provide a window for feral cats to hunt with less interference. Mesopredators released from top–down control can exert more predation pressure on prey than apex predators

(Prugh *et al.* 2009). They tend to be more effective hunters, allowing them to coexist with apex predators (Polis & Holt 1992). Many Australian animals are active at dusk, and some may be particularly vulnerable to predation by feral cats at this time: reptiles become slower as temperature declines (Bennett 1983), and mammals must forage or hunt to satisfy energy demands and are likely to show a surge of activity early in the night. In Northern Australia where native mammals are in rapid decline (Woinarski *et al.* 2011), increased hunting success by feral cats in the absence of dingoes could accelerate the extinction trajectories of these vulnerable species.

Our study shows that mesopredators can coexist with apex predators by concentrating their use of space and time to avoid encounters. Control measures not only reduce the abundance of apex predators, but can lead to behavioural changes that may relax top–down pressure on mesopredators, potentially allowing them to shift to more prey-rich areas or time periods, facilitating an increase in mesopredator abundance and predation pressure on prey. If predator control is used to reduce apex predator abundance, but maintain a population to retain ecological functions such as suppression of herbivores and mesopredators (Soulé *et al.* 2003), it is important to consider the effects of control on behaviour as well as abundance (Ritchie *et al.* 2012). Hence, in areas managed primarily for conservation, predator control should be reconsidered in the light of potential risks to wildlife. The presence of dingoes may restrict feral cats to suboptimal niches and thus provide refuge from cat predation for prey.

Acknowledgements

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