

Do dingoes suppress the activity of feral cats in northern Australia?

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Abstract Large predators can have profound impacts on community composition. Not only do they directly affect prey abundance, they also indirectly affect prey abundance through their direct effects on smaller predators. In Australia, dingoes fill the role of a large predator and, in southern Australia, have clear impacts on introduced foxes. Their effect on introduced cats, however, is less clear. Here we present data from multiple sites across northern Australia (where foxes are absent), which reveal a negative correlation between cat and dingo activity. This relationship could arise because cats avoid areas where dingoes are active, or because cats are less abundant in areas with high dingo densities, or a combination of both. At a subset of our study sites, we experimentally reduced dingo (but not cat) abundance by poison baiting. This resulted in a 55% drop in dingo activity within 4 weeks of baiting, but without a compensatory increase in cat activity. This suggests the negative correlation between cat and dingo activity is not a simple consequence of cats reactively avoiding areas with higher dingo traffic, but rather, that there are fewer cats in areas where dingoes are more active. This study is a rare demonstration of the potential for dingoes to affect the behaviour and potentially the population size of feral cats, and therefore reduce the impact of feral cats on vulnerable native prey species.

Key words: dingo, feral cat, mesopredator release, northern Australia, trophic regulation.

INTRODUCTION

There is an increasing appreciation of the role that large predators can play in ecosystem function (Soule *et al.* 2003, 2005). Large predators can affect several levels of a trophic hierarchy; not only can they directly suppress prey abundance (Pople *et al.* 2000; Terborgh *et al.* 2001; Berger & Gese 2007), but also suppress smaller predators ('mesopredators') through exploitation or interference competition (Soule *et al.* 1988; Berger & Gese 2007; Glen *et al.* 2007). Suppression of prey and mesopredators can, in turn, entrain trophic cascades affecting taxa lower in the trophic hierarchy (Terborgh *et al.* 2001; Berger *et al.* 2008).

By suppressing mesopredators, large predators may facilitate the persistence of taxa that are directly preyed upon by mesopredators. 'Mesopredator release' where smaller predators are released from competition by the removal of a larger predator has been demonstrated to result in dramatic changes in some prey communities

(Soule *et al.* 1988; Litvaitis & Villafuerte 1996; Crooks & Soule 1999). Examples of this phenomenon have been documented in Australia where reduction in abundance of larger predators has been followed by increases in abundance of smaller, introduced predators (e.g. Short *et al.* 2002) and changes in prey communities (Risbey *et al.* 2000; Letnic *et al.* 2009a; Read & Cunningham 2010).

The dingo (*Canis lupus dingo*) is Australia's largest extant predator. It was brought to Australia between 4–5000 years ago (probably by seafaring traders) and has spread to occupy the entire mainland (Corbett 1995; Savolainen *et al.* 2004). It now appears to occupy a stable and significant role in Australian ecosystems (Johnson *et al.* 2007). In contrast, the more recently arrived predators, cats (*Felis catus*) and European foxes (*Vulpes vulpes*) have been heavily implicated in recent massive declines of small–medium sized native mammals, including the extinction of 22 species on mainland Australia in the last 100 years (Dickman 1996; Smith & Quinn 1996; Johnson 2006; Burbidge *et al.* 2008).

Evidence is accumulating that, at least in some circumstances, dingoes may suppress introduced mesopredators, and so act to buffer Australia's prey communities from their impact (Johnson 2006; Glen *et al.* 2007; Johnson *et al.* 2007; Wallach *et al.* 2010).

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Much of the evidence for dingo suppression of introduced predators comes from southern and central Australia, where both cats and foxes are present, and tends to suggest that dingoes are effective at suppressing foxes in particular. Evidence for suppression of cats is however, less clear (see review in Glen & Dickman 2005). Northern Australia presents an opportunity to explore the specific interactions between dingoes and cats, because foxes are absent from the tropics.

Predator interactions have been little studied in northern Australia; for example, to our knowledge there is no information on the relationship between dingoes and feral cats from the north. Similarly, we lack even the most basic information on cat densities, ecology and impacts in north Australia (Denny & Dickman 2010). This knowledge gap is of concern because northern Australia is currently experiencing precipitous declines in its native small mammal community (Woinarski *et al.* 2001, 2010). The causes of these declines are not clear, but probably involve interactions between several threats: changed fire regimes, the introduction of large herbivores, predation by introduced mesopredators (cats), and possibly other factors like cane toads (*Rhinella marina*) and disease (Woinarski *et al.* 2010). There is a pressing need to understand these threats, how they impact small mammal communities, and how they can be managed. If the presence of dingoes effectively suppresses cats and leads to a commensurate reduction in their impact on prey communities, then encouraging dingoes (or at least reducing their persecution by land managers) could be part of a strategy for mitigating one of the threats potentially contributing to the northern mammal declines.

Here, we take a first step in this direction, and ask whether dingo activity is correlated with cat activity across several sites in Top End and Kimberley regions of northern Australia. We also carried out an experimental manipulation of dingo density at a subset of the sites; we predicted that if the observed negative correlation between dingo and cat activity was a simple behavioural avoidance response on the part of cats, then reducing dingo abundance and activity would lead to an immediate compensatory increase in cat activity.

METHODS

Data collection

Cat and dingo activity was assessed using passive activity plots (Allen *et al.* 1996). Between 2007–2009 we set up 10 transects at various sites in the central Kimberley of Western Australia and the Top End of the Northern Territory (Fig. 1). Each transect ran along a dirt track. At 1 km intervals a swathe was raked and sieved across the track to create a sand plot of 3 × 1.5 m. Each transect had between 30–50 sand plots along its length. Sand plots were checked for the pres-

ence of dingo and cat prints each morning and each crossing of the sand plot by a cat or dingo was recorded. Plots were reset by smoothing the sand after daily checking. Samples were taken this way for four consecutive days at each transect and a sample consisted of a count of the number of crossings of both dingoes and cats on each plot. The transects were sampled at the same time of year, between September and October, to circumvent any potential issues because of seasonal differences in activity.

Our transects were located on three adjacent properties in the Kimberley: Glenroy, Marion Downs and Mornington, and on two adjacent properties in the Northern Territory: Wongalara and Mainoru (Fig. 1). Each property ranged in size from 190 000 ha to 325 000 ha and transects were separated by a minimum of 10 km. In some cases transects included disjunct segments. This was due to some lengths of track having higher vehicle traffic. In these instances the disjunct segment is included with the closest transect. The properties spanned a range of different dingo management techniques including no baiting, annual road-based 1080 baiting and annual aerial 1080 baiting. Consequently, we expected to sample a reasonable variation in dingo activity across the transects.

At a subset of transects (four of ten), we were able to collect activity data immediately before and then 2–4 weeks after dingo abundance was reduced by poison baiting. This experiment was incorporated into the scheduled annual baiting programs on these particular properties (Mainoru and Glenroy bait around October most years; Wongalara had been baited regularly around October before its acquisition by Australian Wildlife Conservancy in December 2008; subsequently, AWC ceased baiting on half the property and continued baiting on the other half as part of a landscape-scale experiment investigating the impacts of dingoes on cats and native fauna). Dingo baiting was achieved by injecting 500 gm pieces of raw beef with 1080 (sodium monofluoroacetate) and distributing the baits from a vehicle at 500 m intervals along the transects and other surrounding roads. The baiting program is unlikely to have affected cat numbers because cats tend to specialize on live prey and typically exhibit low uptake of large baits (Risbey *et al.* 1997; Burrows *et al.* 2003; Denny & Dickman 2010). However, if cat activity is affected by that of dingoes, an abrupt reduction in dingo activity, particularly if associated with social disruption (Allen & Gonzalez 1998; Wallach *et al.* 2009) may be associated with a change in cat activity.

Analysis

Our data consisted of counts (summed over 4 days) of tracks at each plot. Preliminary analyses showed that cat activity data were well described by a Poisson error structure (and resulted in models with a dispersion error of less than or close to one), so a Poisson error structure was used for this response variable throughout. Dingo activity, however, exhibited overdispersion with a Poisson error structure (dispersion parameter 1.6), presumably because dingoes sometimes travel in small groups, so we used a negative binomial error structure to fit models using this response variable.

Analyses consisted of generalized mixed models (Poisson or negative binomial errors, with a log link) with the fixed

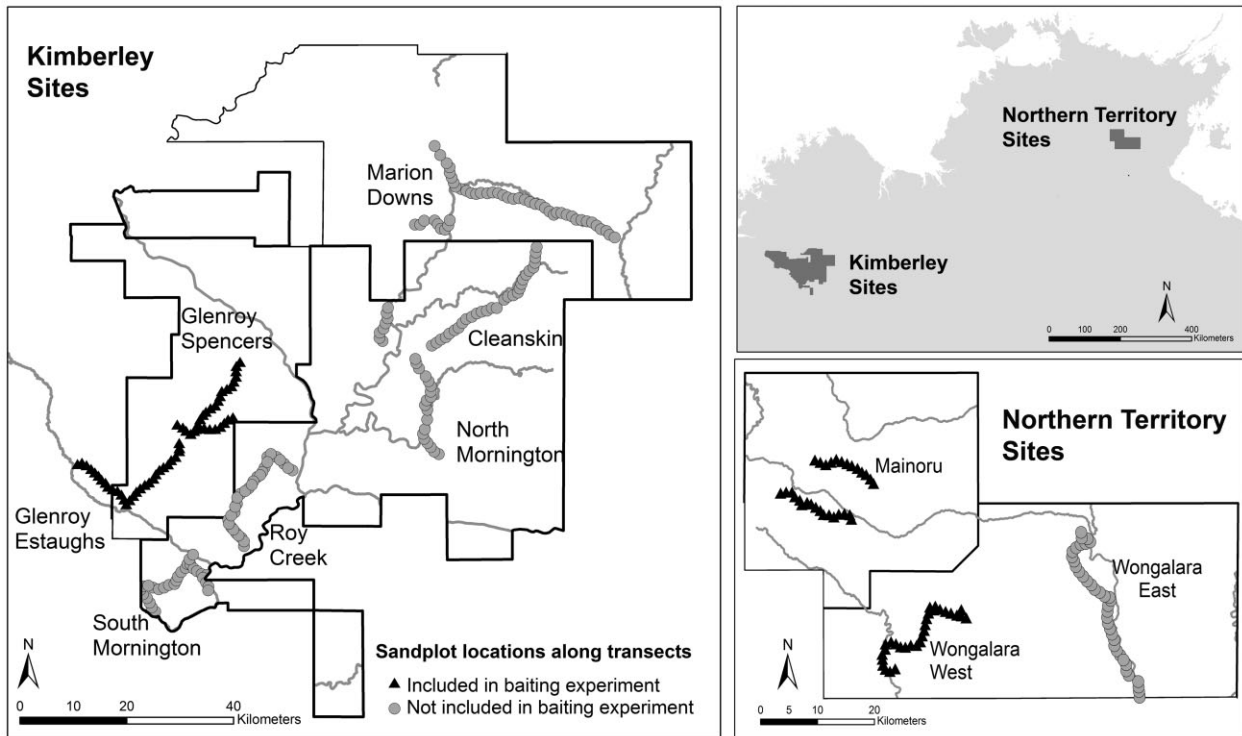


Fig. 1. Map of the study area and transects. Transects marked triangles were those used in the experimental manipulation of dingo numbers in 2008. Cleanskin, North Mornington, Roy Creek and South Mornington transects had not been baited for at least 15 years; Glenroy Estaughs and Glenroy Spencers had been baited irregularly; Mainoru and Wongalara West had been baited annually; Marion Downs was baited until 2007 and Wongalara East was baited until 2008 (when AWC acquired each property, respectively, and ceased baiting).

effect of interest included along with nested random effects accounting for variation due to transect, year, and broad location (Kimberley *vs.* Northern Territory). We nested transect within year within broad location because we considered that the effect of year was more likely to be localized (within broad locations) rather than global (across all locations): exploratory analysis confirmed this approach, as the majority of yearly variance was found at this nesting level. The baiting experiment was conducted only once (in 2008) at each of the transects, so the random effect of year was dropped from this analysis. Given the various complications associated with significance testing in this modelling framework (Pinheiro & Bates 2009), we refrain from making significance tests, and used a Bayesian analysis to generate parameter estimates and 95% credible intervals. Data organization and initial analyses were performed in the R statistical environment (R Development Core Team 2008) before using the OpenBUGS software (Lunn *et al.* 2000) to fit the Bayesian model. We used minimally informative priors throughout, and parameter estimates were derived from 100 000 samples of the posterior distribution (following a burn-in of 10 000 iterations, which reliably resulted in convergence of three randomly initiated chains).

RESULTS

Between 2007 and 2009, we collected data totalling 4504 plot nights across 341 plots within 10 transects.

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Cat activity was relatively low at our plots (grand mean of 0.06 cats per plot night). Dingo activity was over seven times higher (grand mean of 0.46 dingoes per plot night).

Mixed models showed that there was a clear negative correlation between dingo and cat activity (Fig. 2, Table 1: parameter estimates for the coefficient of the effect of dingo activity = -0.076 , 95% CI = -0.16 to -0.001). This negative correlation could be due to behavioural avoidance of dingoes by cats, without reflecting differences in cat density among sites. The baiting experiment indicated a 55% decrease in dingo activity following baiting (Fig. 3, Table 2: Parameter estimate for effect of pre-baiting = 0.53 with 95% CI of 0.31 to 0.80), but there was no corresponding change in cat activity at those sites (Fig. 3, Table 2: Parameter estimate for effect of pre-baiting = -0.08 with 95% CI of -0.63 to 0.46).

DISCUSSION

These data demonstrate a negative correlation between cat and dingo activity in northern Australia. In particular, where dingo activity was very low, cat activity was greatly heightened (Fig. 2). The transects

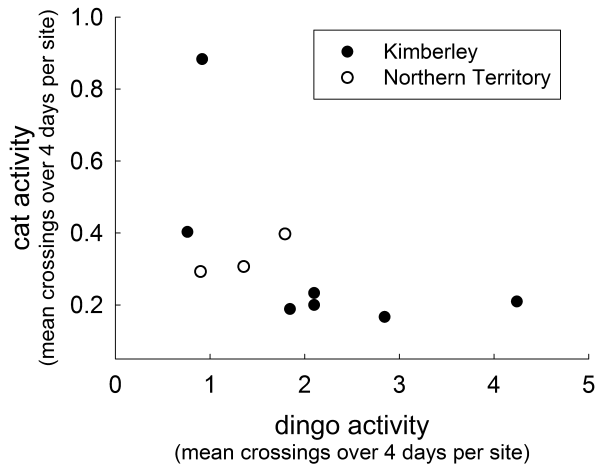


Fig. 2. Cat and dingo activity across 10 sites in northern Australia. Points from the Northern Territory were adjusted (+0.15) to remove locality effect before plotting.

Table 1. Fitted generalized linear mixed model (Poisson errors with log-link) investigating the effect of dingo activity on cat activity in the Kimberley and Northern Territory

Model term	Posterior median (95% credible interval)
Fixed effects	
Intercept	-1.19 (-1.8 to -0.64)
Dingo activity	-0.076 (-0.16 to -0.001)
Locality (Northern Territory)	-0.91 (-1.9 to 0.10)
Random effects	
Variance due to site	0.16
Variance due to year within site	0.38
Sample size	670
Deviance	802

Parameter estimates come from 100 000 samples of the posterior distribution following a burn in of 10 000 iterations.

were located across several properties in the Kimberley and Top End with different histories of dingo management. The Top End properties had a much narrower spread of dingo activity, perhaps reflecting a more consistent history of dingo control at these sites. Across all Top End and Kimberley sites, the variance recorded in dingo activity could reflect the effects of historical dingo control efforts, natural variation across the landscape, or a combination of the two. If natural variation is the primary cause of variance in dingo activity, cats are mostly active where dingoes are naturally scarce. Alternatively, if dingo activity is a function of control effort, then cats are most active where dingoes have been most heavily persecuted. These possibilities are not mutually exclusive.

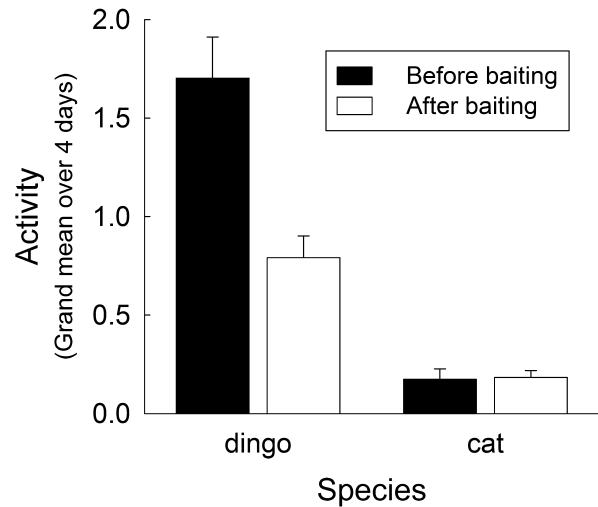


Fig. 3. Change in activity of dingoes and cats following poison baiting at four sites in northern Australia. Bars represent one standard error.

The data presented here consist of track counts on passive activity transects (Allen *et al.* 1996) so are a composite measure of both abundance and activity. For example, if two areas have the same abundance, but individuals differ in their activity levels between the locations, then our plots will pick up a difference that is not related to a difference in abundance. Thus the negative correlation between cat and dingo activity recorded in this study may be a consequence of the following possible scenarios: (i) different habitat use by the two species; (ii) direct population-level suppression, such as predation, agonistic encounters and physical exclusion from resources of cats by dingoes (Glen *et al.* 2007); or (iii) behavioural suppression, whereby cats react flexibly to the presence of dingoes by avoiding areas of high dingo activity (e.g. by driving them off tracks).

To determine if the negative correlation between cats and dingoes was the result of behavioural suppression, we experimentally reduced dingo numbers and measured cat and dingo activity before and then immediately (2–4 weeks) after the laying of poison baits, which would target dingoes but have little impact on cats. If the response of cats to high dingo activity was primarily behavioural we would expect an increase in cat activity within the short term once dingo activity was reduced. This experiment substantially reduced dingo activity on sand plots, by 55% on average (Fig. 3). Two to four weeks following this baiting, we did not observe an increase in cat activity in response to this large reduction in dingo activity. Thus, if behavioural suppression does occur, it either requires only low densities of dingoes to remain effective, or else it takes longer than 2–4 weeks for cat behaviour to adjust to changes in dingo activity. In the extreme case,

Table 2. Fitted generalized linear mixed models investigating the effect of dingo baiting on cat (Poisson errors with log-link) and dingo (Negative binomial errors with log-link) activity in the Kimberley and Northern Territory, Australia

Dingo activity		Cat activity
Model term	Posterior median (95% credible interval)	Posterior median (95% credible interval)
Fixed effects		
Intercept	0.79 (0.13 to 1.68)	-1.40 (-2.27 to -0.71)
Treatment (pre-baiting)	0.53 (0.31 to 0.80)	-0.08 (-0.63 to 0.46)
Locality (Northern Territory)	-0.18 (-1.35 to 1.01)	-0.58 (-1.64 to 0.36)
Random effects		
Variance due to site	0.23	0
Sample size	421	421
Deviance	820	291

Parameter estimates come from 100 000 samples of the posterior distribution following a burn-in of 10 000 iterations.

behavioural suppression may be so systemic as to limit an individual cat's ability to find food, mates, etc., leading ultimately to population-level suppression. We therefore tentatively conclude that the relationship between cat and dingo activity in northern Australia is driven by differential habitat use, and/or some degree of population-level suppression of cats by dingoes. Dingoes are known to prey upon cats elsewhere (Glen & Dickman 2005 and references therein), and we have observed this several times on Mornington, either directly (observation of a dingo carrying a cat kitten) and indirectly (from the presence of cat remains in dingo scats, unpubl. data).

More work is needed to examine the occurrence and nature of dingo suppression of cat populations. This will likely require landscape-scale manipulative experiments (with population estimation and detailed knowledge of habitat use of both species). A major challenge is our ability to accurately measure cat densities. In our study, we invested a large sampling effort (over 4500 plot nights) to detect effects, but these effects were still not measured with precision. The grand mean number of cats per plot night was 0.06, so the vast majority of plot nights revealed zero cats. Yet spotlight searches and GPS radio-collaring suggest that cats are more abundant than dingoes at our study sites (Legge, 2010 unpubl. data). Techniques for more effectively censusing cats in northern Australia are badly needed if our knowledge of the ecology of cats and their impacts is to improve quickly.

The results presented here are consistent with a growing literature on both the ability of dingoes to suppress introduced mesopredators (e.g. Glen & Dickman 2005; Johnson *et al.* 2007; Letnic *et al.* 2009b) and the flow on effects of such suppression to native prey species (Johnson *et al.* 2007; Letnic & Koch 2010; Read & Cunningham 2010; Wallach *et al.* 2010). Much of this work shows a clear impact of dingoes on foxes in particular, with a more equivocal effect on cats (Glen & Dickman 2005). However,

almost all of this work has been carried out in southern and central Australia, where both cats and foxes are present and intra-predator interactions are likely to be complex; when dingoes are controlled cats may simply be trading one form of top-down regulation (dingoes) for another (foxes), with little detectable change. The situation in northern Australia is different because foxes are absent, so the only potential top-down regulation on cats is from dingoes. Given the potential role of feral cats as drivers of native mammal declines in northern Australia, the nature and mechanisms of dingo-cat interactions in this region urgently requires further study.

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