

Dingo interactions with exotic mesopredators: spatiotemporal dynamics in an Australian arid-zone study

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Abstract

Context. Apex predators occupy the top level of the trophic cascade and often perform regulatory functions in many ecosystems. Their removal has been shown to increase herbivore and mesopredator populations, and ultimately reduce species diversity. In Australia, it has been proposed that the apex predator, the dingo (*Canis dingo*), has the potential to act as a biological control agent for two introduced mesopredators, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*). Understanding the mechanisms of interaction among the three species may assist in determining the effectiveness of the dingo as a control agent and the potential benefits to lower-order species.

Aims. To test the hypotheses that feral cats and foxes attempt to both temporally avoid dingoes and spatially avoid areas of high dingo use.

Methods. Static and dynamic interaction methodologies based on global positioning system (GPS) telemetry data were applied to test temporal and spatial interactions between the two mesopredators ($n = 15$) and a dingo pair ($n = 2$). The experimental behavioural study was conducted in a 37-km² fenced enclosure located in arid South Australia.

Key results. The dynamic interaction analysis detected neither attraction nor avoidance between dingoes and cats or foxes at short temporal scales. There was no suggestion of delayed interactions, indicating that dingoes were not actively hunting mesopredators on the basis of olfactory signalling. However, static interaction analysis suggested that, although broad home ranges of cats and foxes overlapped with dingoes, core home ranges were mutually exclusive. This was despite similar habitat preferences among species.

Conclusions. We found that avoidance patterns were not apparent when testing interactions at short temporal intervals, but were manifested at larger spatial scales. Results support previous work that suggested that dingoes kill mesopredators opportunistically rather than through active hunting.

Implications. Core home ranges of dingoes may provide refuge areas for small mammals and reptiles, and ultimately benefit threatened prey species by creating mesopredator-free space. However, the potential high temporal variation in core home-range positioning and small size of mutually exclusive areas suggested that further work is required to determine whether these areas provide meaningful sanctuaries for threatened prey.

Additional keywords: apex predator, European fox, feral cat, dynamic, static.

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Introduction

Globally, ecosystems are connected through interaction webs in which each species has the potential to have an impact on various other species, forming a highly complex network. This complexity is underpinned by ecological processes such as predation and competition (Estes *et al.* 2011). Interactions occur among and within species, at the same and at different trophic levels (Crooks and Soulé 1999). Many ecosystem processes can be shaped by apex predators, providing a regulating function on lower trophic levels through direct and indirect interaction chains (Paine 1966; Estes *et al.* 2011). Hence, apex predators may perform important controlling functions in global ecosystems by regulating community composition and

ecosystem processes such as storage and flux of atmospheric carbon (Sergio *et al.* 2008; Atwood *et al.* 2013).

Removal of apex predators may reduce species diversity because the limiting effects of resource exploitation on species in lower trophic levels are removed (Paine 1966). On a global scale, large apex predators are declining faster than other species, allowing an increase in herbivorous populations, resulting in reduced plant biomass (Estes *et al.* 2011; Wilmer *et al.* 2012; Ripple *et al.* 2014). Decline or removal of apex predators may also increase populations of smaller predators, a concept termed ‘mesopredator release’ (Crooks and Soulé 1999). These smaller predators predominantly prey on small vertebrate species, therefore increasing predation pressure,

which ultimately increases risk of decline and extinction of prey species (Crooks and Soulé 1999).

In Australia, interactions among mammalian apex and mesopredators are particularly interesting because the carnivorous mesopredators are recently introduced predator species (Ritchie and Johnson 2009). The dingo (*Canis dingo*) is the largest mammalian predator in Australia, regulating ecosystem processes as an apex predator, particularly because of its capacity to hunt in packs (Glen and Dickman 2005; Johnson *et al.* 2007; Wallach *et al.* 2009). However, since the arrival of Europeans, the dingo has been heavily persecuted because it preys on livestock. Simultaneous with dingo removal, cats and foxes were introduced to Australia (Woinarski *et al.* 2011). These two events, combined with the introduction of rabbits and habitat alteration by cattle and sheep farming, have had detrimental effects on small mammal populations and might be closely related to the high extinction rate of mammals observed over the past 200 years (Johnson 2006). Small to medium-sized mammals are more likely to co-exist with dingoes than with feral cats and foxes because the ecological and biological traits of dingoes (large ranges, low population densities and reproductive rates) place less predation pressure on prey species than do those of feral cats and foxes (Johnson *et al.* 2007). Additionally, dingo presence may also alter behavioural patterns of mesopredators intending to avoid the apex predator (Ritchie and Johnson 2009).

Direct interactions between the apex predator and introduced mesopredators include interspecific killing of cats (*Felis catus*) and foxes (*Vulpes vulpes*) by dingoes because of intraguild predation (Glen and Dickman 2005) or interspecific interference competition (Glen and Dickman 2005; Ritchie and Johnson 2009; Moseby *et al.* 2012). Fatal encounters are thought to be opportunistic rather than a result of active hunting of cats and foxes by dingoes (Moseby *et al.* 2012). Changes in interaction behaviour may occur during various phases of the reproductive cycle of dingoes because dingo activity patterns vary naturally during the year in response to breeding periods, in particular during pup rearing (Allen *et al.* 2011).

Dingoes use olfactory communication to determine the presence of prey and other predators (Kleiman and Eisenberg 1973). Like other canids, dingoes (and foxes) use scent marking to locate and collect information about other individuals such as members of their pack, con- and heterospecific competitors and prey (Kleiman and Eisenberg 1973; Macdonald 1983; Allen *et al.* 1999). Scent marking is also used for the marking of territory (Ausband *et al.* 2013). In particular, core utilisation areas are repeatedly marked by olfactory signalling to leave long-lasting scent marks and re-establish territory boundaries (Asa *et al.* 1985; Allen *et al.* 1999; Wallach *et al.* 2009). Cats (felids) rarely use olfaction in hunting, but rely on it for interspecific as well as intraspecific communication (Kleiman and Eisenberg 1973).

Studying direct and indirect species interactions has advanced with developments in global positioning systems (GPS) and satellite-tracking technologies. With GPS location data, home ranges of individuals can be estimated, which allows for calculation of the intersecting area of home ranges (Miller 2012). This static approach of interaction analysis provides data on areas shared, which is useful to detect large-scale

range use and interaction patterns. However, despite using spatiotemporal GPS data, this approach fails to provide information about a possible temporal association of two individuals. Even though individuals might share the same area, encounters could be rare if the same place is seldom visited simultaneously (Amlaner and Macdonald 1980). Including the temporal component in analyses of species interactions can provide a better understanding of association rates, including information on possible attraction, or avoidance of individuals (Kenward *et al.* 1993). This type of analysis is termed dynamic interaction (Doncaster 1990) and delivers greater insight about behavioural aspects among and within species.

The present study investigates dynamic and static interactions between dingoes and introduced mesopredators. We hypothesised that cats and foxes attempt to both temporally avoid dingoes and spatially avoid areas of high dingo use. Specifically, we applied dynamic interaction analysis to test whether dingoes and cats, and dingoes and foxes, avoid or attract each other more than expected by chance. This analysis was refined to test whether interaction patterns differ during reproductive cycles of dingoes, and whether olfactory communication signals may delay dynamic interaction patterns. We then calculated intersecting areas of total and core home range, to determine static interactions (home-range overlap) between apex and mesopredators. Furthermore, we modelled whether habitat preferences differed among the three species. Results were used to infer the role dingoes may play in suppressing mesopredators.

Materials and methods

Study area

The study was conducted at the Arid Recovery Reserve, close to the town of Roxby Downs in arid South Australia. The study site is a 37-km² fenced enclosure incorporated into the reserve (Fig. 1). The climate in the region is arid, with an average annual rainfall of 166 mm (Read 1995). During the study period (2008–2009), a lower than average annual rainfall of 100 mm was recorded. Longitudinal sand dunes and interdunal clay swales are the dominant topographic features in the area. The vegetation comprises sand dune canegrass (*Zygochloa paradoxa*), low open chenopod shrubland (*Atriplex* spp., *Maireana* spp.) and Acacia species (*A. ligulata*, *A. aneura*; Moseby *et al.* 2012). Vertebrate species such as red kangaroos (*Osphranter rufus*), rabbits (*Oryctolagus cuniculus*), rodents (e.g. *Notomys alexis*, *Pseudomys bolami*, *Mus musculus*) and reptiles (*Ctenopus* spp., *Ctenophorus* spp.) commonly occur in the region, providing food resources for mammalian predators (Read and Bowen 2001).

The study area is fenced on three sides with a 1.6-m-high netting fence with a 50-cm floppy top that curves inward to contain predators within the enclosure. The fence on the southern boundary of the enclosure is 1.15 m high and of similar design. The fence design allows cats and foxes to climb in, but prevents dingoes, cats and foxes from leaving the enclosure. The area also includes a near-permanent dam, filled with rainwater from three ephemeral creek lines during a significant rainfall event in November 2008, which provided continuous water supply during the study period. To ensure that food was sufficient inside

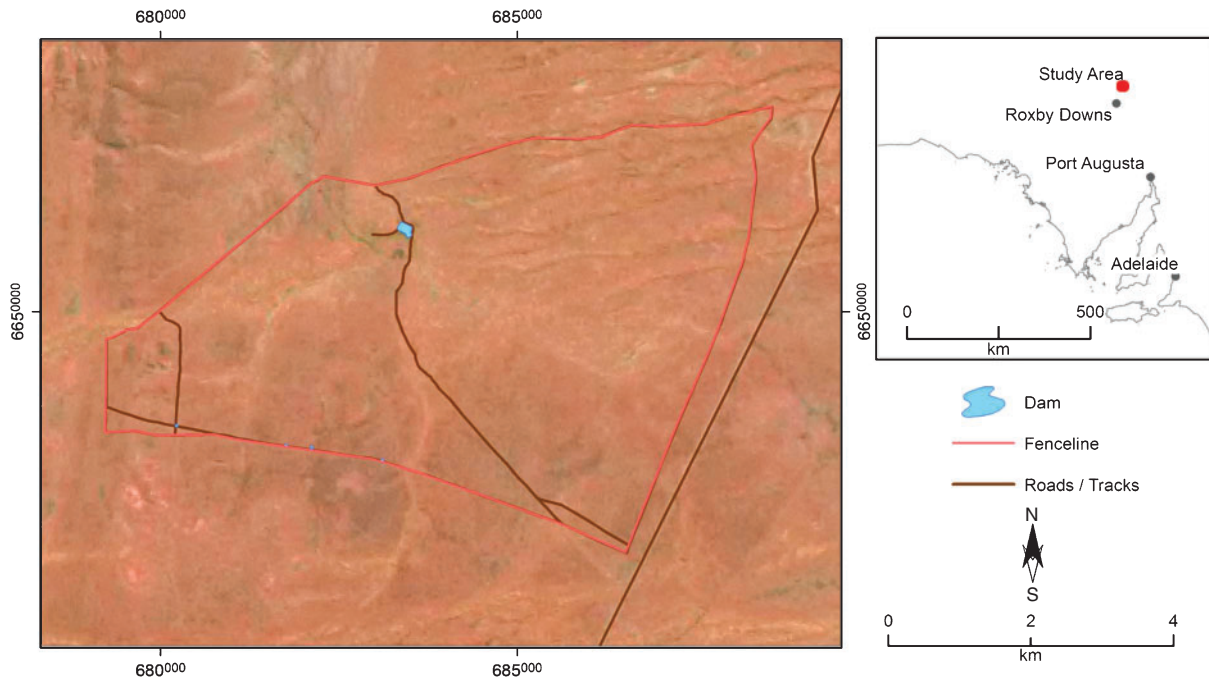


Fig. 1. Map of the study area at the Arid Recovery Conservation Reserve.

the enclosure, kangaroo and rabbit carcasses and meat cut-offs were placed near the dam approximately fortnightly. The frequency of attendance at the carcass dump was measured with motion cameras and provided an indication of food availability in the enclosure (Moseby *et al.* 2012).

Animal capture, handling and radio-telemetry

The principal data for this study originate from a field-based predator-behaviour experiment, as described in detail by Moseby *et al.* (2012). In December 2008, a wild male and female dingo were trapped, lightly anaesthetised and fitted with ARGOS linked GPS datalogger collars (SIRTRACK, Havelock North, New Zealand) set to capture location data every 2 h. Both dingoes were subsequently released into the fenced enclosure. Existing feral cats ($n=4$) within the fenced enclosure were trapped after its construction in August 2008. Additionally, a further six feral cats and seven foxes were captured between April and October 2009 and placed in the enclosure. All trapped cats and foxes were anaesthetised and fitted with GPS datalogger collars that included VHF transmitter (SIRTRACK). Again, collars were set to record GPS fixes every 2 h, being synchronised with the dingo collars. After recovering from reversal of the anaesthetic, the animals were released in the enclosure. In total, GPS data were available for two dingoes (m/f), 10 feral cats (3m/7f) and five foxes (3m/2f). Additional information on the time period of the study and radio-tracking details for each animal are provided in the results section.

Data analysis

Data preparation

All data available from GPS dataloggers and ARGOS were downloaded and pre-processed to correct for location errors and

time-zone adjustments. All locations with a low expected accuracy (horizontal dilution of precision (HDOP) < eight) owing to satellite positioning and obstructions (i.e. vegetation/ or cats, foxes hiding in rabbit warrens) were excluded from the analyses (Graves and Waller 2006; Frair *et al.* 2010; Augustine *et al.* 2011).

Dynamic interaction

Interspecific dynamic interaction analysis (DIA; Doncaster 1990) was applied to determine whether dingoes, cats and foxes interact spatially and temporally or whether their movements are independent of each other. Interactions analysed for the present study are dyadic, involving two animals only. Each dyad referred to a different combination of two animals and involved a dingo and either a cat, a fox or a dingo. Dynamic analysis of location data requires location records to be simultaneous or near simultaneous for each dyad (Kenward 2001; Whitehead 2008). The observed geometric mean distance (O) is compared with the expected geometric mean distance (E) between each dyad at same time locations (STL). Expected distances are based on randomly selected location of dyads from the same sample using chi-square tests.

The Jacobs index (D ; Jacobs 1974) is applied to rank geometric mean distances and is calculated as $D = (\text{expected distance} - \text{observed distance}) / (\text{expected distance} + \text{observed distance})$. Results provide an indication of whether animals ignore ($O = E$), avoid ($O > E$) or attract ($O < E$) each other and are expressed in values ranging from -1 (maximum avoidance), 0 (neutral association) to $+1$ (maximum attraction; Kenward *et al.* 1993; Poole 1995). No consistent value is provided to define the significance of attraction or avoidance, and values are treated differently in the literature (Mattisson *et al.* 2011).

For the present study, a significant attraction or avoidance was defined as $\geq +0.5$ and ≤ -0.5 , respectively (Stakėnas *et al.* 2013).

Dynamic interaction – simultaneous locations

To examine spatial and temporal interactions between dingoes and cats and dingoes and foxes at the same time locations, all dyads (dingo–cat ($n=20$), dingo–fox ($n=10$), male–female dingo ($n=1$)) were calculated using Ranges 8 V2.2 software (Kenward *et al.* 2008). The GPS recording interval in many collars drifted, resulting in non-synchronous recording of fixes. Therefore, pairs of locations were considered to be simultaneous if they occurred within a 1–60 min time frame. Dynamic interaction at same time locations was then calculated for each dyad with 10-, 30- and 60-min thresholds. To allow for a maximum sample size, only the 60-min threshold results were included in the analysis, because these were available for all dyads. A preliminary interaction analysis was run with the limited data available for the 10- and 30-min thresholds; however, Jacobs indices were identical to the 60-min threshold for dingo–cat dyads and increased by +0.02 D for dingo–fox dyads.

Dynamic interaction – olfactory signalling

To account for a temporal delay in interaction because of olfactory communication behaviour among dingoes, cats and foxes, a 4-h, 8-h and 12-h time lag was added to the cat and fox GPS fixes. The increased temporal separation allowed determination of whether temporal-interaction scores with dingoes changed in comparison to real time locations (Doncaster 1992). The assumption was made that by matching dingo locations with cat and fox locations from 4, 8 and 12 h previously, an increased attraction would be noted if the dingo was actively seeking out cats and foxes by following fresh scent marks (Doncaster 1992).

Dynamic interaction – reproductive cycle of dingoes

The dataset allowed for analyses of differences in interactions during breeding (March–May), whelping (June–August) and rearing (September–November) cycles of dingoes. Therefore, the dataset was reduced to monthly timeframes to account for detection of interaction patterns that might become apparent on a shorter temporal scale.

Static interaction

Home-range overlap was determined for dingoes ($n=2$), feral cats ($n=10$) and foxes ($n=5$) on the basis of the time intervals each dyad occupied the enclosure. Home-range sizes were calculated using a nearest-neighbour clustering approach to allow for calculation of multiple cores (Kenward *et al.* 2001; Walls and Kenward 2001). This methodology reduces the influence of outliers on home-range size and provides a more accurate image of area utilisation by the animal, defining areas of high and low usage (Harris *et al.* 1990) and is well suited to define social effects and allow for analysis of microspatial overlap (Kenward *et al.* 2001).

To quantify range overlap of each dyad, core (25% and 50%) and total (95%) home ranges were calculated using convex cluster polygons for the entire period that each dyad shared the enclosure. In line with most home-range studies, 25%

and 50% of the home ranges were classified as core areas (Laver and Kelly 2008). Home-range overlap was then calculated for each dingo–cat and dingo–fox dyad on the basis of the results of the nearest-neighbour home-range calculations for core and total home range. Calculations of home-range overlap are given as the proportion (%) of overlap.

Habitat utilisation

To test whether home-range overlap was influenced by differences in the habitat selection of each species, habitat use was calculated for the 50% core home ranges of each individual animal. The four main habitats of the study area are swale, dune, sandplain and creeks. A GIS layer was created, quantifying the area of all habitats. This file was then clipped to the extent of the 50% core home range of each animal. Total area for each habitat type was then calculated and apportioned to the total area occupied for each animal's core home range. A linear mixed effects (LME) analysis (Pinheiro and Bates 2000) was performed to explore the relationship between species and habitat preference. Models included 'species' and 'habitat type' as fixed effects and controlled for variability and repeated-measures by using the individual animal as the random effect. Visual inspection of residual plots did not reveal any considerable deviation from normality and homoscedasticity. *P*-values were obtained by likelihood ratio tests of the full model with fixed effects 'species' and 'habitat type', against the model without 'species' as a fixed effect. Statistical analyses were conducted using statistical computing software 'R' (R Core Team 2013) with the package 'nlme' (Pinheiro *et al.* 2013).

Results

Dynamic interaction

Dynamic interaction – simultaneous locations

In total, 20 dingo–cat and 10 dingo–fox dyads were analysed, averaging 424 (s.e. = 88) same-time locations for each dingo–cat dyad and 62 (s.e. = 19) same-time locations for each dingo–fox dyad. Simultaneous dingo and cat location data were available for an average of 53 days for each dyad, whereas dingo and fox data averaged only 8 days because of foxes being killed by dingoes. For those periods, GPS fixes averaged 10 (cats), 9 (foxes) and 12 (dingoes) per day (Tables 1, 2).

Dingo–cat and dingo–fox interaction indices were neutral, showing neither attraction nor avoidance towards each other on the basis of analysis of the data for the entire period (mean Jacobs index for dingo–fox: +0.06 (range = -0.15 to +0.30; Table 1, Fig. 2), mean Jacobs index for dingo–cat: +0.01 (range = -0.08 to +0.09; Table 2, Fig. 3). Only one dynamic interaction between a female fox (F35) and the female dingo showed a low positive attraction (Jacobs index +0.30; Table 1). This fox was killed by dingoes within 5 days after release into the enclosure (Moseby *et al.* 2012). Additionally, dynamic interaction results for the male and female dingo dyad were similar (mean Jacobs index for male dingo–fox: +0.04; mean Jacobs index for female dingo–fox: +0.07; mean Jacobs index male dingo–cat: +0.02; mean Jacobs index female dingo–cat: +0.00). Same time locations for the male and female dingo pair were also analysed as a dingo–dingo dyad, showing a very strong attraction, with a Jacobs index of +0.91 (Table 1).

Table 1. Dynamic interaction analysis of dingo pair and fox and dingo dyads at the same time locations (STL) and with a time lag of 4, 8 or 12 h F31 (etc.), unique identifier for foxes; DF, dingo female; DM, dingo male. Jacobs indices highlighted in bold are the lowest and highest attraction/avoidance values

Dyad	Sex	STL	Days	Data for same time locations (STL) at 60 min threshold						Jacobs Index			
				Time period		GPS fixes total		GPS fixes/day		S TL	4h	8h	12h
				from	to	Dingo (M)	Dingo (F)	Dingo (M)	Dingo (F)				
Dingo – Dingo													
DM– DF	M/F	4105	370	21/12/2008	31/12/2009	3553	3465	10	9	+0.91			
Foxes – Dingoes				From	To	Fox	Dingo	Fox	Dingo	S TL			
F31 – DF	M/F	22	4	1/06/2009	4/06/2009	34	33	9	8	+0.00	-0.03	-0.02	-0.02
F31 – DM	M/M	34	4	1/06/2009	4/06/2009	34	48	9	12	+0.13	+0.16	+0.20	+0.17
F32 – DF	M/F	19	3	9/06/2009	12/06/2009	32	29	11	10	-0.15	-0.21	-0.07	-0.09
F32 – DM	M/M	31	3	9/06/2009	12/06/2009	32	36	11	12	-0.09	-0.13	-0.12	-0.10
F34 – DF	M/F	172	16	27/06/2009	13/07/2009	177	203	11	13	+0.15	+0.15	+0.11	+0.08
F34 – DM	M/M	169	16	27/06/2009	13/07/2009	177	201	11	13	+0.13	+0.14	+0.15	+0.11
F35 – DF	F/F	26	6	15/08/2009	20/08/2009	27	69	5	12	+0.30	-0.14	-0.12	+0.07
F35 – DM	F/M	24	6	15/08/2009	20/08/2009	27	70	5	12	+0.10	-0.03	+0.07	+0.02
F36 – DF	F/F	59	10	18/10/2009	28/10/2009	81	125	8	13	+0.05	-0.12	-0.04	-0.10
F36 – DM	F/M	59	10	18/10/2009	28/10/2009	81	126	8	13	-0.07	-0.13	-0.12	-0.07
Mean		62	8			70	94	9	12	+0.06	-0.03	+0.00	+0.01
s.e.		19	2			19	21	1	0	+0.04	+0.04	+0.04	+0.03

Table 2. Dynamic interaction analysis of cat and dingo dyads at same time locations (STL) and with a time lag of 4, 8 or 12 h C21 (etc.), unique identifier for cats; DF, dingo female; DM, dingo male. Jacobs indices highlighted in bold are the lowest and highest avoidance/attraction values

Dyad	Sex	STL	Days	Data for same time locations (STL) at 60 min threshold						Jacobs Index			
				Time period		GPS fixes total		GPS fixes/day		S TL	4h	8h	12h
				From	To	Cat	Dingo	Cat	Dingo				
Cats – Dingoes													
C21 – DF	F/F	1407	180	21/12/2008	21/06/2009	1530	1980	9	11	+0.04	+0.03	+0.03	+0.03
C21 – DM	F/M	1454	180	21/12/2008	21/06/2009	1530	2094	9	12	-0.00	+0.03	+0.02	+0.02
C22b – DF	M/F	123	13	26/04/2009	9/05/2009	133	162	10	12	+0.03	+0.06	+0.14	+0.09
C22b – DM	M/M	132	13	26/04/2009	9/05/2009	133	161	10	12	+0.09	+0.08	+0.06	+0.02
C23 – DF	M/F	697	79	19/01/2009	8/04/2009	789	869	10	11	-0.06	+0.01	-0.04	-0.02
C23 – DM	M/M	704	79	19/01/2009	8/04/2009	789	896	10	11	-0.05	-0.04	-0.09	-0.09
C23b – DF	F/F	27	3	30/10/2009	2/11/2009	39	48	13	16	-0.01	-0.04	-0.02	-0.03
C23b – DM	F/M	25	3	30/10/2009	2/11/2009	39	43	13	14	-0.02	+0.02	-0.02	+0.02
C24 – DF	M/F	312	48	21/12/2008	9/02/2009	339	546	7	11	+0.01	+0.05	+0.08	+0.09
C24 – DM	M/M	313	48	21/12/2008	9/02/2009	339	551	7	11	+0.04	+0.10	+0.09	+0.11
C24b – DF	F/F	593	91	28/08/2009	29/11/2009	605	1101	7	12	-0.08	-0.03	-0.03	-0.03
C24b – DM	F/M	581	91	28/08/2009	29/11/2009	605	1084	7	12	-0.05	-0.11	-0.08	-0.07
C25 – DF	F/F	323	37	21/12/2008	28/01/2009	351	422	9	11	+0.09	+0.06	+0.11	+0.10
C25 – DM	F/M	320	37	21/12/2008	28/01/2009	351	427	9	12	+0.09	+0.07	+0.12	+0.11
C25b – DF	F/F	207	20	16/09/2009	6/10/2009	248	248	12	12	-0.01	+0.09	-0.03	+0.09
C25b – DM	F/M	208	20	16/09/2009	6/10/2009	248	247	12	12	-0.01	+0.02	-0.04	+0.05
C28 – DF	F/F	238	27	3/04/2009	30/04/2009	257	323	10	12	-0.04	+0.00	+0.01	+0.05
C28 – DM	F/M	250	27	3/04/2009	30/04/2009	247	331	9	12	+0.03	+0.06	+0.07	+0.05
C29 – DF	F/F	284	34	26/04/2009	30/05/2009	294	410	9	12	+0.04	+0.05	+0.09	+0.04
C29 – DM	F/M	286	34	26/04/2009	30/05/2009	294	416	9	12	+0.06	+0.08	+0.09	+0.04
Mean		424	53			458	618	10	12	+0.01	+0.03	+0.03	+0.03
s.e.		88	11			95	129	0	0	+0.01	+0.01	+0.02	+0.01

Dynamic interaction – olfactory signalling

The temporally manipulated location data to test for olfactory communication cues provided an average of 410 (s.e.=82) and 61 (s.e.=19) same time locations for the analysis of each dingo–cat and dingo–fox dyad, respectively. Neither avoidance nor attraction among dyads could be inferred, with mean Jacobs indices of -0.01 for dingo–fox dyads (Table 1, Fig. 2) and +0.03 for dingo–cat dyads (Table 2, Fig. 3) for all added time lags. Again, dynamic

interaction results for male and female dingoes were similar (mean Jacobs index for male dingo–fox: +0.02; mean Jacobs index for female dingo–fox: -0.03; mean Jacobs index for male dingo–cat: +0.03, mean Jacobs index for female dingo–cat: +0.03).

Dynamic interaction – reproductive cycle of dingoes

Analysis of the location data for each dyad on a monthly basis showed no avoidance or attraction pattern, with a mean Jacobs

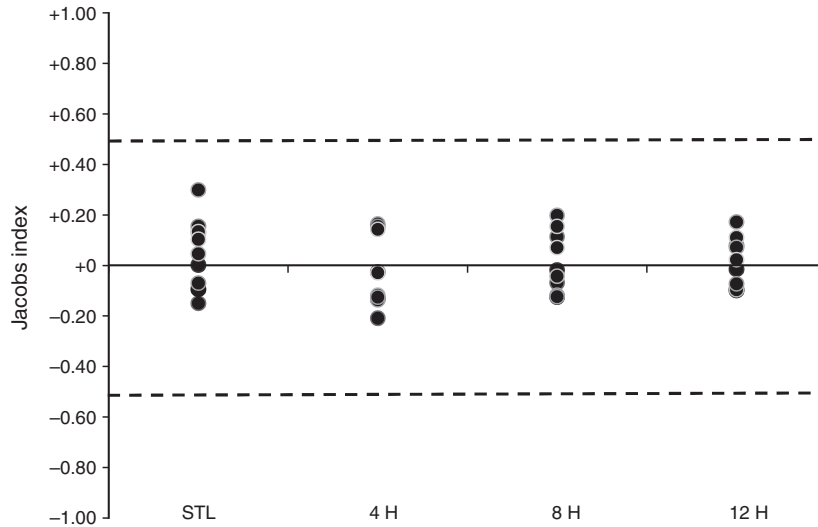


Fig. 2. Jacobs index for all dingo and fox dyads ($n=10$) at same time locations (STL) and time-lagged locations. Dashed line indicates significant Jacobs index.

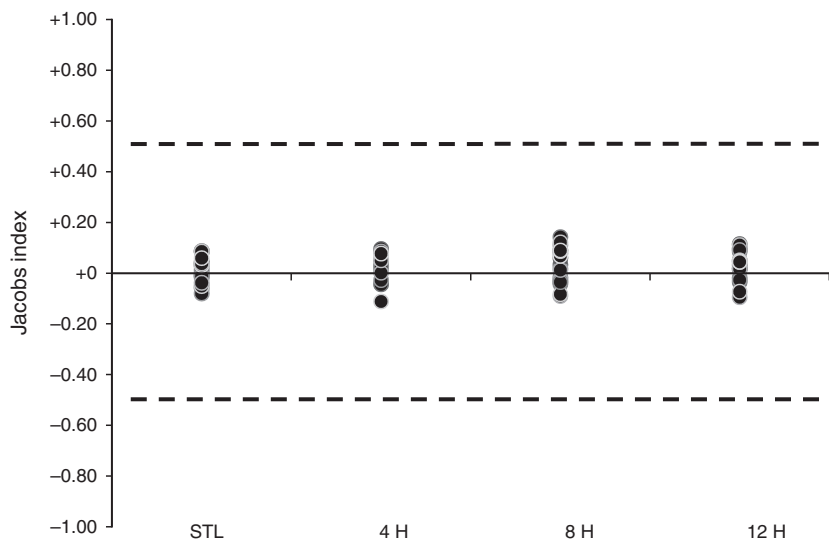


Fig. 3. Jacobs index for all dingo and cat dyads ($n=20$) at same time locations (STL) and time-lagged locations. Dashed line indicates significant Jacobs index.

index of -0.01 for dingo–cat dyads and $+0.03$ for dingo–fox dyads (Table 3). No shift in temporal interactions was detected during the dingo reproductive cycle including the breeding (March 2009 – May 2009), whelping (June 2009 – August 2009) and rearing (September 2009 – November 2009) periods, despite a pup being born in June 2009, with the female dingo using the breeding den from 1 June to 16 July 2009 (Moseby *et al.* 2012). Detailed analysis during the individual reproductive cycles did not show an increase in attraction or avoidance behaviour for any of the cycles between male and female dingoes, and cats and foxes (mean Jacobs index: -0.02 for male dingo–cat, -0.01 for female dingo–cat, 0.03 for male dingo–fox and -0.05 for female dingo–fox).

Static interaction

Analysis of core home-range overlap indicated that cats and foxes did not share core areas of utilisation with dingoes (Fig. 4). Cats shared less than 5% (s.e. = 1.9%) of their core home ranges with dingoes when 25% and 50% of the fixes were used to estimate core home-range overlap. Separation of core distribution areas was more pronounced for foxes. All but one fox (F31) showed no overlap of core areas with dingoes. When total (95%) cat and fox home ranges were considered, the overlap proportion with dingo home range increased to up to 54% for cats (s.e. 6.4) and 18% for foxes (s.e. 9.4). Results indicated strong separation of core fox and cat home ranges from high-occupancy areas of dingoes.

Table 3. Monthly analysis of dynamic interactions among dingoes, cats and foxes

Pup was born in June 2009. It should be noted that foxes were not present during the breeding cycle and were present only for 10 days during the rearing period

Reproductive cycle dingo	Breeding				Whelping				Rearing			
	Dec-08	Jan-09	Feb-09	Mar-09	Apr-09	May-09	Jun-09	Jul-09	Aug-09	Sep-09	Oct-09	Nov-09
Cats / Dingoes												
No. dyads	4	8	6	4	10	6	2	–	2	4	4	4
Mean STL	80	156	177	303	125	210	150	–	17	187	114	102
Mean Jacobs index	–0.05	+0.04	+0.01	+0.02	–0.04	+0.07	+0.01	–	–0.08	–0.10	+0.01	–0.02
Foxes / Dingoes												
No. dyads	–	–	–	–	–	–	6	2	2	–	2	–
Mean STL	–	–	–	–	–	–	28	25	74	–	59	–
Mean Jacobs index	–	–	–	–	–	–	–0.06	–0.20	+0.17	–	–0.01	–

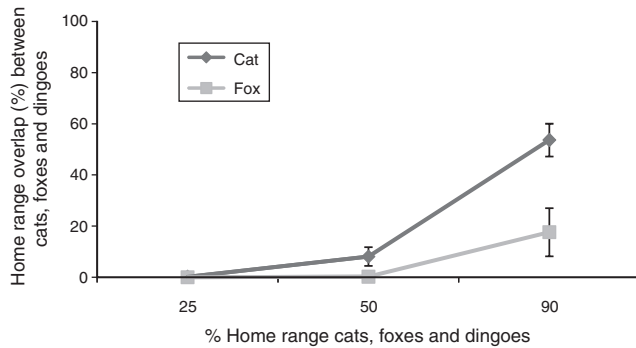


Fig. 4. Home-range overlap, showing proportional (%) overlap of cat and fox home ranges with equivalent dingo home-range sizes for each percentage of fixes for home-range calculation. Error bars indicate one standard error.

Habitat utilisation

Comparison of LME models by likelihood ratio tests showed that dingoes, cats and foxes expressed similar habitat preferences ($\chi^2(2)=0, P=1$). Swales and dunes were preferred habitats, followed by creeks and sandplains (Fig. 5).

Discussion

Results suggested that mechanisms of spatial rather than temporal avoidance were the main behavioural pattern underlying the relationship among dingoes, cats and foxes in the present study. Dingoes and cats, and dingoes and foxes neither avoided nor attracted each other at short temporal scales. However, there was a strong micro-spatial avoidance pattern at the core home-range level, suggesting that cats and foxes were avoiding areas of high use by dingoes (Johnson and VanDerWal 2009). Short-term delays in dynamic interactions owing to assumed olfactory communication patterns among the species, or changes in associations as a result of seasonal variability (e.g. as a result of the dingo pair’s breeding) were not detected, suggesting temporally independent movement patterns between dingoes and cats and dingoes and foxes. Significantly, all habitat types were similarly utilised by cats, foxes and dingoes, supporting the hypothesis that avoidance of core dingo areas is due to predatory competition mechanism and not due to habitat preferences.

All but one fox were killed the first time they came within 100 m of the male and/or female dingo (Moseby *et al.* 2012). Core

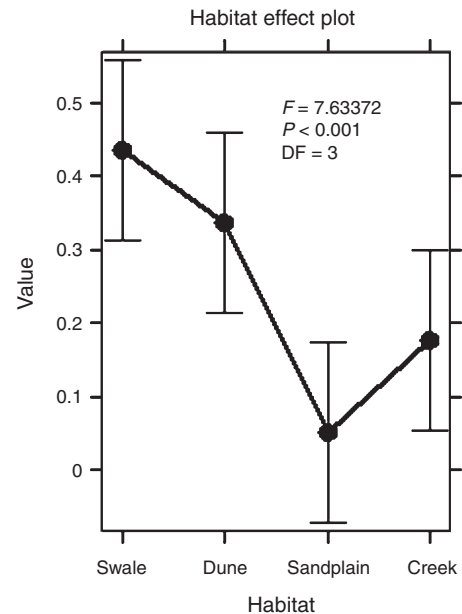


Fig. 5. Plot shows fixed effect ‘habitat type’. Statistical results given at the right-hand upper corner correspond to linear mixed effects (LME) model using each individual animal as random factor and ‘habitat type’ as fixed factors. Error bars indicate 95% CI (± 1.96 s.d.). Y-axis shows proportion of habitat usage.

home range of foxes did not overlap with core dingo range. Conversely, only ~50% of the cats were killed by dingoes if they came within a 100-m range of the apex predator (Moseby *et al.* 2012), and home-range overlap was greater than for foxes. This could suggest that dingoes are less tolerant of foxes than they are of cats, or that the feline predator is more effective at avoiding the dingo. The findings of the previous study support this, because foxes were killed within a shorter timeframe than were cats after introduction to the fenced enclosure (Moseby *et al.* 2012). Other research has found that, depending on resource availability, dingoes may perceive cats as a less threatening competitor for resources (Glen and Dickman 2005) and that cats might be more difficult to detect or catch (Edwards *et al.* 2001).

Dingoes mark home-range boundaries and core areas with olfactory signalling, providing clear signals for intruders to keep

out of the area (Allen *et al.* 1999; Purcell 2010). Minimal spatial overlap in core home ranges suggests that both mesopredators may have manipulated their behavioural patterns to avoid the dingo core centre of activity, possibly expecting that this will lead to avoidance of the dingoes themselves. This is in direct contrast to temporally avoiding dingoes at any particular point in time on the basis of knowledge of the dingo's current location (through howling, smell and visual cues). Olfactory signals could be the primary mechanism used by cats and foxes to avoid or limit direct interactions with dingoes, which appears to manifest at a broad spatial scale. Other studies have also found that foxes alter their spatial behavioural patterns to avoid interactions with dingoes (i.e. changed habitat preference when dingoes are present; Newsome *et al.* 2001; Southgate *et al.* 2007). Additionally, foxes can be excluded by dingoes as a result of dietary competition and avoidance behaviour (Mitchell and Banks 2005).

Similar species interaction patterns have been observed in several studies in the United States. Removal of coyotes led to increased activity of bobcats (*Felis rufus*; Engeman *et al.* 2000). Where coyotes are present, smaller predators such as opossums (*Didelphis virginiana*), feral cats and foxes are suppressed (Ritchie and Johnson 2009). Harrison *et al.* (1989) found that foxes avoided suitable habitats that lay within coyote territories. Some home-range overlap was reported, although this was restricted to the periphery of coyote territory and no overlap occurred at core areas. The authors concluded that foxes avoid core areas to reduce the potential of fatal encounters with coyotes. Many other studies have documented avoidance of coyote territories by foxes (Voigt and Earle 1983; Ralls and White 1995; Gosselink *et al.* 2003; Karki *et al.* 2007; Thompson and Gese 2007). This relationship is mirrored between wolves and coyotes, where wolves are the higher-order predator and exclude coyotes from their territories (Levi and Wilmsers 2012).

However, interactions among these three carnivores are complex, involving both intraguild predation (Marsack and Campbell 1990; Moseby *et al.* 2009) and interference competition mechanisms (Glen and Dickman 2005; Moseby *et al.* 2009). Dingoes prey on feral cats and foxes occasionally (Marsack and Campbell 1990; Dickman 1996), although they have also been found to tolerate cats (Smith and Quin 1996), and to provide carrion inadvertently (Dickman 1996). Additionally, dynamic interaction patterns among individual animals can be intricate and difficult to detect (Miller 2012). This may also apply for dynamic interactions between dingoes and cats, and dingoes and foxes. Therefore, when interpreting the results, one must consider the low sample size and temporal resolution, methodology used and the difficulty of detecting fine-scale interspecific interactions. The non-detection of a dynamic interaction for dyads might be due to the low temporal resolution of the spatial data (i.e. 2 hourly fixes) and/or the unsuitability of the methodology to detect complex, sporadic and short interactions between dingoes and cats, and dingoes and foxes. However, dynamic interaction analysis has been applied to data with a much lower temporal resolution (1 location/day) analysing cougar–wolf associations in North America, detecting slight avoidance (Jacobs index = -0.37 ; Ruth *et al.* 2003). Studies of intraspecies associations among avian species (*Accipiter gentilis* or *Buteo buteo*) also found sex-based

temporal avoidance on the basis of locations received from radio-tracking every 2–3 days (Kenward *et al.* 1993; Walls and Kenward 2001). Studies conducted with datasets with temporal resolution similar to this study (8 fixes per day) detected no association between wolverine and lynx, but strong attraction for male and female lynx dyads (Mattisson *et al.* 2011). We recorded strong association between male and female dingoes, suggesting that the resolution of fixes was sufficient to show interactions present.

Both the confined nature of the enclosure and the addition of only one dingo pair may have affected the results of the present experiment. In unconstrained situations, cats and foxes may be able to avoid a higher proportion of the dingo home range, and areas of home-range overlap may be less fragmented. However, the size of the enclosure (37 m²) was larger than the average home-range size of cats and foxes and, therefore, large enough to support many individuals, supported by the fact that at least four cats were present when the area was fenced (Moseby *et al.* 2009). The predator–interaction experiment may not represent real conditions because the dingo pair might not have been representative of common dingo pack structure and associated behaviour (Glen *et al.* 2007; Wallach *et al.* 2009). As a social carnivore, dingoes display a high degree of sociality and commonly occur in groups (Corbett and Newsome 1987). Advantages for maintaining a pack structure include shared rearing of young and increased hunting success for large prey. However, when resources are scarce, dingoes become more solitary (Thomson 1992). Dingoes have been known to adjust their pack structure and hunting strategies to increase hunting success on the most abundant and easily captured prey species (Corbett and Newsome 1987; Vernes *et al.* 2001). It is unknown how interactions with mesopredators change depending on whether dingoes are members of a pack or solitary. However, several factors suggest that the dingoes were behaving as wild dingoes. Field observations showed that the dingo pair was scent-marking and howling, suggesting normal pack behaviour. The pair successfully raised a pup during the first breeding season, after they were placed in the enclosure. The dingoes were taken from the wild in similar habitat and less than 100 km from the enclosure, suggesting they were familiar with local prey and habitats. Additionally, it should be noted that the dingoes killed some of the cats and foxes together, suggesting they were travelling as a pair (K. Moseby, unpubl. data). This is supported by the significant Jacobs index, showing high attraction between the male and female dingo.

Most importantly, dingoes proved to influence space-use patterns of mesopredators. This may benefit smaller prey species, because a mesopredator-free space reduces predation pressure (Crooks and Soulé 1999; Letnic *et al.* 2009b). Similarly, presence of coyotes was shown to benefit small-mammal and bird abundance and diversity by suppressing feral cats and foxes (Levi and Wilmsers 2012). Another study found that the dusky hopping mouse (*Notomys fuscus*) was more abundant in areas where dingoes were present (Letnic *et al.* 2009a). Dingo presence may also provide a net benefit for larger mammals such as the bilby (*Macrotis lagotis*) and the parma wallaby (*Macropus parma*) by reducing fox numbers, even though dingoes also prey on those medium-sized mammals (Paltridge 2002; Glen and Dickman 2005). The influence of dingoes on the spatial

distribution of cats and foxes might therefore provide refuge areas for small mammals that are not the preferred prey species for dingoes (Moseby *et al.* 2012). Dingo distribution in arid zones, in contrast to cats and foxes, is dependent on water availability; therefore, the ability to suppress mesopredators will be spatially and temporally restricted to areas providing sufficient water access (Wallach and O'Neill 2009; Moseby *et al.* 2012).

Conclusions

The results of the present study support recent hypotheses and evidence that dingoes can alter activity patterns of subordinate mesopredators. Cat and fox core home ranges were not located in areas of dingo high use, perhaps in an attempt to avoid direct encounters with dingoes. Avoidance was detected at micro-spatial scales over large areas, rather than at a temporal-spatial level, suggesting that cats and foxes do not locate and spatially avoid dingoes at particular points in time, but avoid high-use areas of dingoes perhaps through olfactory cues. Conversely, dingoes do not appear to actively seek out mesopredators, but kill them opportunistically when observed. If avoidance at core areas means that the presence of dingoes alters spatial behavioural patterns of cats and foxes so that they avoid being in dingo territory, it could be suggested that increasing dingo numbers could potentially reduce suitable habitat for cats and foxes and, therefore, suppress their population numbers. This could benefit native mammals and reptiles as predation pressures by cats and foxes are reduced.

However, further research needs to be conducted to tease out factors that influence interaction patterns and predation, such as prey availability and priority of occupancy.

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