

Space use and interactions of two introduced mesopredators, European red fox and feral cat, in an arid landscape

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Abstract. Introduced mammalian predators are drivers of species decline and extinction globally. The successful management and control of introduced mammalian predators is dependent on some knowledge of space use and movements in order to target a population and monitor outcomes. In Australia, these tasks are made complex as there is more than one significant introduced mammalian predator, namely the European red fox *Vulpes vulpes* and feral cat *Felis catus*, the landscapes are vast, and individual-level interactions between predators are little studied. The impact of these two introduced predators is large and a significant factor in the extinction of many of the country's small- to medium-sized mammals, either regionally or globally. In a three-year study, we used high-frequency location data, the deployment of the latest GPS tracking technologies, and recent advances in statistical modeling to examine how these two species distributed themselves in space, the degree to which individual distributions overlapped, intra- and interspecific interactions, and temporal patterns of activity in an arid landscape. In the absence of an apex predator, the two introduced mesopredators showed large differences in how they distribute themselves across the landscape and interact with conspecifics. The red fox mostly occupies defined territories, while most feral cats roam apparently independent of each other with occasional periods of frequent interaction with conspecifics of either sex. Intraspecific attraction was strongest in cats, while interspecific avoidance was observed in both directions. The home ranges of feral cats that were range-resident were 3–3.5 times larger than foxes in the same landscape. Notably, we observed long-distance movements in feral cats and some were displaced up to 164 km from their point of release. A greater portion of the feral cat population were non-sedentary and therefore likely less amenable to local control efforts than foxes. Given the different patterns of distribution in time and space, the reliable monitoring of population trends or estimates of abundance will necessarily differ in extent, intensity, or duration for the same level of precision and/or require a different method for monitoring each population.

Key words: dynamic interactions; European red fox; feral cat; GPS telemetry; invasive predators; predator management; space use.

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INTRODUCTION

Invasive mammalian predators are a leading cause of biodiversity decline and loss globally

(Long 2003, Doherty et al. 2016). In Australia, predation by two invasive carnivorous mammals is regarded as a major driver of the decline and extinction of many small vertebrate species

(Dickman 1996a, Woinarski et al. 2015) and the threat to extant fauna is ongoing (Kearney et al. 2019). Over the last 150 yr, the red fox (*Vulpes vulpes*) has become established in all Australian mainland habitats south of the tropics (Saunders et al. 1995) and it shares these areas with another invasive predator, the feral cat (*Felis catus*), which is distributed continent-wide and was introduced with European settlement through the 18th and 19th centuries (Abbott 2008). These invasive mesopredators have contributed to Australia experiencing the highest recent mammal extinction rate worldwide (McKenzie et al. 2007, Fleming et al. 2014c, Woinarski et al. 2015, 2019) with many of the country's small mammals now extinct, either regionally or globally (Moseby 2012, Woinarski et al. 2014). More effective and broad-scale management of these two invasive species is now a priority for the maintenance and recovery of many Australian threatened species (Australian Government 2015), but that management is constrained by some major knowledge gaps about the ecology and interactions of these predators.

Concern about Australia's biodiversity loss has heightened interest in the role of all predators, including the larger and much longer established dingo (*Canis dingo*) that has been present for at least 3000 yr (Balme et al. 2018). However, the extent and management implications of interactions between the dingo and the more recently established fox and cat has become a subject of vigorous debate (cf. Johnson and VanDerWal 2009, Wallach and O'Neill 2009, Allen 2010, Allen et al. 2011, Schroeder et al. 2015, Cooke and Sorriquer 2017, Morgan et al. 2017, Newsome et al. 2017a, Fancourt et al. 2019), in part because of inconsistent methodologies and approaches, and limited information (Bode 2019). There have been even fewer studies, and hence more uncertainty, about the interactions between the fox and cat (Greenville et al. 2014, Molsher et al. 2017), and the extent to which management of either or both of these predators is influenced by such interactions.

Few studies have examined space use in red foxes and feral cats simultaneously, notwithstanding theoretical grounds for assuming that the presence of one invasive mesopredator is likely to influence the distribution and behavior of another (Prugh et al. 2009). Two studies, in the arid north of South Australia, are notable exceptions (Moseby et al. 2009, Schroeder et al. 2015)

and another in the Simpson Desert (Greenville et al. 2014). Knowledge of space use and the interactions within and among species is crucial to conservation management, for example, by helping to identify which parts of a population are range-resident and those parts of a population that are non-sedentary. In the former group, knowledge of space use informs the scale and intensity required for management and/or control programs (e.g., Algar et al. 2011). By contrast, the latter group have a continually expanding range and their movements likely affect the rate of disease transmission, rate of repopulation of an area subject to lethal control, and other population-level processes, but are less amenable to local interventions (Thomson et al. 2000). Equally, knowledge of space use within the range of an individual can identify the characteristics and frequency of use of high visitation sites (Bracis et al. 2018), such as shelter or surface waters, that can facilitate targeted management or control across broad landscapes.

Red foxes have been studied via telemetry for more than 50 yr (Storm 1965), and estimates of home-range size are available for a wide variety of environments from across the world (Carter 2010). Estimates vary enormously from 6 ha (Marks and Bloomfield 2006) in urban areas (reviewed by Castañeda et al. 2019) to more than 40,000 ha in an Australian desert (Newsome et al. 2017b). To date, only six published studies have occurred in arid or semiarid environments, including two in Saudi Arabia (Macdonald et al. 1999, Lenain et al. 2004) and four in Australia (Marlow 1992, Burrows et al. 2003, Moseby et al. 2009, Newsome et al. 2017b). Across the literature on red foxes, reports of distinct territoriality outnumber studies that observed considerable overlap between adjacent home ranges. Exclusive use of space is most common where fox densities are high and home ranges small (Scott 1943, Ables 1969, Macdonald 1980, Poulle et al. 1994, Doncaster and Macdonald 1997, Adkins and Stott 1998). In arid New South Wales, Marlow (1992) concluded that foxes were primarily solitary with mostly non-overlapping home ranges, except for breeding pairs. A few studies present sufficient detail to assess home-range stability across seasons or years, but the results are equivocal. Some studies show that foxes, and family groups, maintained stable home-range

areas and did not appear to alter their centers of activity during the period of observation (Mulder 1985, Overskaug et al. 1995, White et al. 1996, Drygala and Zoller 2013), whereas other studies showed that foxes were not range-resident and moved their centers of activity during the study period (Dekker et al. 2001, Henry et al. 2005, Perrine 2005). Moreover, both scenarios have been identified in the same environment (suburban areas of Scotland and England) (Kolb 1984, Doncaster and Macdonald 1991).

Studies of space use for feral cats are fewer than for red fox. Estimates of home range start from <1 ha in urban environments (Mirmovitch 1995) to >6000 ha in environments as different as riverine ecosystems in New Zealand (Cruz et al. 2015) and the deserts of Western Australia (Comer et al. 2018). As with foxes, there are relatively few studies from semiarid and arid environments and all have been conducted in Australia (Jones and Coman 1982, Edwards et al. 2001, Burrows et al. 2003, Moseby et al. 2009, Johnston et al. 2013, Clausen et al. 2016, Comer et al. 2018), as reviewed by Doherty et al. (2014). Globally, the factors hypothesized to determine abundance and range size in feral cats are prey availability, shelter availability, predation and/or competition, and human resource subsidies (Doherty et al. 2014). A review of mostly Australian studies showed that home-range size scaled negatively with landscape productivity, a correlate for prey availability (Bengsen et al. 2016).

In this contribution, we examine the concurrent space use, movements, and interactions of the red fox and feral cat over three years in an extensive area of arid woodlands and shrublands in inland Australia. This region contains no apex predators as the dingo has been removed via exclusion fencing and lethal control. Our study comprises three broad steps: First, we examine space use with telemetry data collected at short intervals between location fixes. We use these data to model range extent in range-resident and non-sedentary individuals and identify sites of high visitation from the observed trajectories. Second, we use camera-trap data to examine activity patterns in both species. Finally, we identify individuals that overlap or are adjacent to each other, and use dynamic interaction models to examine interactions between conspecifics and

interspecific interactions between both mesopredators. Specifically, we ask how large are individual home ranges and to what extent do they overlap? Do individuals maintain stable home ranges year to year? What are the interactions between individuals? When are they most active? And critically, does the presence of one mesopredator modify the behavior of the other? The insights gained are relevant to understanding the behavior and management options for introduced predators in the study environment and elsewhere.

METHODS

Study area

Our study was conducted at Scotia Wildlife Sanctuary, a 64,659-ha private conservation reserve in south-western New South Wales, Australia (-33.15° S, 141.06° E; Fig. 1), owned and managed by the Australian Wildlife Conservancy. The climate is semiarid with low and highly variable rainfall (spatially and temporally) that averages 230 mm per year with high evapotranspiration (1500 mm per year) and low relative humidity (average: 20%) (Australian Wildlife Conservancy, *unpublished data*). The site is characterized by cool winters (average daily maxima of 17° C in July) and hot summers (average daily maxima of 30° C in February), with annual temperature extremes ranging from -6° C to 48° C. Vegetation is dominated by three main communities: mallee *Eucalyptus* spp. open shrubland with a spinifex (*Triodia scariosa*) understory, mallee open shrubland with a mixed-shrub understory (e.g., *Senna*, *Dodonaea* and *Eremophila* spp.), and *Casuarina pauper* woodland (Westbrooke et al. 1998).

Approximately 8000 ha of the sanctuary is surrounded by an electrified conservation fence, within which foxes and cats have been excluded since 2007, and five threatened mammals have been reintroduced successfully (Roshier et al. 2020). A combination of poison baits and Canid Pest Ejectors is used to suppress foxes in a 36,000-ha area to the south of the conservation fence at Scotia. However, for the duration of this study, lethal fox control was suspended across most of this area and there was no control activity within 10 km of the study area. Foxes and cats were trapped (details below) across an area

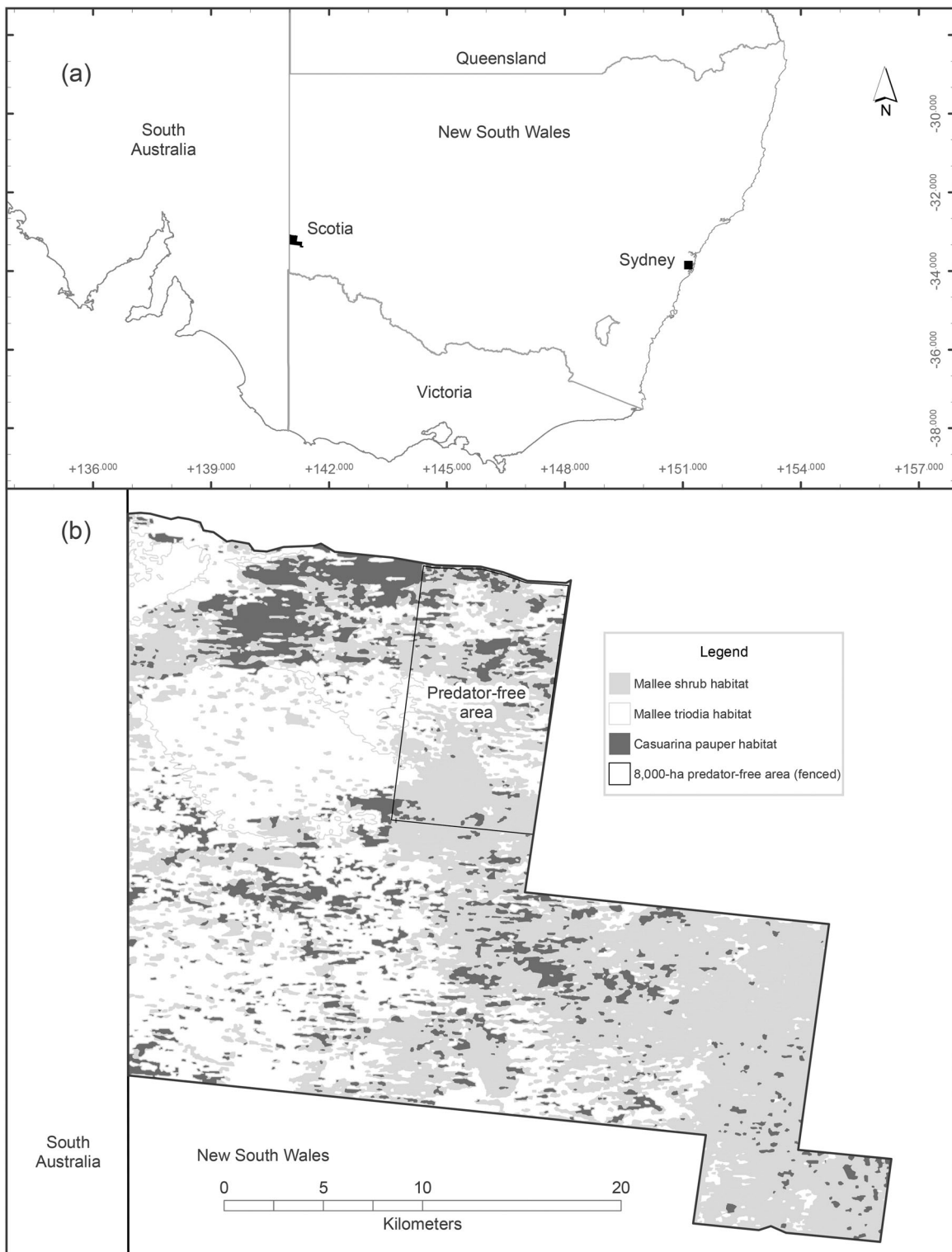


Fig. 1. Location of (a) Scotia Wildlife Sanctuary and (b) the predator-free area and main habitats across the property.

of approximately 19,000 ha to the west of the fenced area, where no lethal control had occurred for more than six years prior to this study. No permanent free water is available within the study area, although during our study, two artificial dams held water periodically.

As part of a related (A. Carter et al.) study, a lethal population control program targeting foxes was implemented across the study area from October 2017 onward. This control program was subsequent to the deployment of GPS collars on foxes and occurred throughout the deployment of Iridium collars on feral cats in the final year (see next section).

Animal capture and handling

Cats and foxes were each trapped in three consecutive years during the following months: October–November (2015; foxes only); July–August (2016); June–July (2017); and May–June (2018; cats only). Trapping periods were chosen to facilitate the capture of adult foxes only so that seasonal dispersal by juvenile foxes (i.e., <1 yr old) did not bias our results. Three types of traps were used: (1) number 1.5 Victor Soft-Catch foothold traps (Woodstream, Lititz, PA, USA) fitted with in-line springs and swivels, tethered with chain to two steel stakes (500 mm long) driven below ground level beneath the trap; (2) custom-made box traps that were buried in the ground with an entrance resembling the burrow of a European Rabbit (*Oryctolagus cuniculus*) and a trap door activated by a treadle plate; and (3) cage traps measuring 740 × 300 × 300 mm (Wiretainers, Preston, Victoria, Australia). Numerous attractants were used including chicken pieces, rabbit meat, fox/cat scats, commercial scent lures, and visual lures (e.g., feathers and novelty items such as compact disks). Traps were checked for captures at dawn and dusk, with trapped animals subdued either using an animal-restraining pole (Ketch-all, San Luis Obispo, California, USA) and blankets (when in foothold traps), or by being transferred from the box/cage traps into a wire crush cage (Wiretainers). Once restrained, animals were anesthetized with an intramuscular injection of a tiletamine/zolazepam combination (Zoletil 100, Virbac, Peakhurst, New South Wales, Australia) at a rate of 8–10 mg/kg body mass for foxes and 6–

8 mg/kg body mass for cats. All methods conformed to standard operating procedures for fox and cat trapping in Australia (Sharp 2016a, b, c).

Sedated cats and foxes were weighed, sexed, and inspected for injuries and condition, and then, a 2-mm tissue sample was collected from their ear to permit micro-satellite DNA analyses. Animals of sufficient weight and condition were subsequently fitted with a GPS collar. All foxes were fitted with Quantum 4000E GPS collars (Telemetry Solutions, Concord, California, USA) that weighed 170 g, which was <5% of the foxes' bodyweight. In 2016 and 2017, cats were fitted with Q4000E GPS collars (Telemetry Solutions) that weighed 116 g. These collars permitted remote data downloads via a UHF antenna at distances of approximately 50 m from the animal. In 2018, cats received newly available prototype GPS collars (Iridium 3.0; Telemetry Solutions) that weighed 134 g and transmitted data automatically via the Iridium satellite network at eight-day intervals. All collars weighed <5% of the cats' bodyweight. Fox collars contained remote drop-off mechanisms that were activated after approximately four months of data collection. Cat collars did not contain drop-off mechanisms, and GPS batteries operated for approximately 8–9 months. No animals sustained serious injuries during trapping, and after receiving their collars were placed in the nearest available cover and monitored to ensure recovery from anesthesia.

The age of any collared animals that were recovered deceased was determined by counting the cementum annuli of cross-sectioned lower canine teeth (Matson's Laboratory 2020).

Data acquisition and filtering

All GPS units were programmed to operate for the first 25 d of each month, recording location fixes at 20-min intervals between 17:00 h and 09:00 h and at 96-min intervals between 09:00 h and 17:00 h. Units were programmed to search for satellites for a maximum of 60 s at each time interval. In 2016 and 2017, with a couple of exceptions, all GPS collars were programmed to commence data acquisition on the same date.

We determined the accuracy of GPS collars from 10 stationary collars located throughout the study area (two collars in 2015; five collars in 2016; and three collars in 2017). Accuracy was

assessed from 106 location attempts (i.e., the equivalent of two full days of data collection) using the same collection schedule as collars placed on foxes and cats. Fix success rate across the 10 collars was 99.6% (i.e., 1056 successful fixes from 1060 attempts). The “true” locations were estimated by calculating the mean latitude and longitude of the 106 location attempts made by each stationary collar using the Mean Center tool in ArcMAP 10.5 (Environmental Systems Research Institute, Redlands, California, USA). The Euclidean distance between each location recorded and the mean center latitude and longitude were calculated. Using this method, the average distance between the mean center and fixes recorded by stationary GPS collars (i.e., location error) was 3.3 m (± 4.5 m SD; range 0.1–75.9 m). All fixes were managed in Movebank (Kranstauber et al. 2011) and the data filtered by removing locations with HDOP = 9.9 (max. value) and elevations >200 m above mean sea level and negative values of mean sea level, noting that the terrain is generally flat and elevations range from approximately 30 to 100 m across the study area. We then removed location fixes for which the rate of movement from the previous fix was implausible or the turning angle was between 166° and 194° (after Bjørneraas et al. 2010). For foxes, we used a rate of movement of 5 m/s and for cats 2 m/s. These rates of movement were determined by examining the tracking data and selecting a plausible upper threshold for sustained rates for a minimum of 20 min. Note these rates of movement are not the maximum speeds recorded for either species. For foxes, this combined filtering process removed 1444 of 95,413 location fixes, retaining 98.5% of the original data, while for cats, this removed 2685 of 112,858 location fixes and retained 97.6% of the original data.

Home-range estimation and overlap

The frequency of location fixes (every 20 min, predominantly) in our study meant that any location fix was likely correlated with the previous or subsequent fix as individuals maintain directional movement or repeat behaviors. Therefore, methods of home-range estimation that assume data are independent and identically distributed, such as the widely used kernel density estimation (KDE), are not appropriate.

Relocation data can be modeled as a continuous-time stochastic process (Calabrese et al. 2016) and the autocorrelated data structures incorporated into the estimation process using autocorrelated kernel density estimation (AKDE; Fleming et al. 2015). We used the continuous-time movement modeling (ctmm) package (version 0.5.9; Calabrese et al. 2016) in R (version 3.6.2, R Core Team 2019) to model a utilization distribution within an animal’s home range. We followed the recommended workflow of Calabrese et al. (2016) and first determined whether individuals were range-resident by fitting a semi-variance function to the data. Only those individuals for which the semi-variance of time-lags was asymptotic were used in comparison with home-range area (Calabrese et al. 2016, Morato et al. 2016, Fleming and Calabrese 2017). Specifically, we used the `ctmm.select` function to generate candidate models using maximum likelihood (Fleming et al. 2014b) and selected the best model based on the Akaike information criterion (AIC; Akaike 1973, Akaike 1974). In all cases, the best model for range-resident individuals that exhibit restricted space use and correlated velocities was the anisotropic Ornstein-Uhlenbeck F (OUF) process model (Calabrese et al. 2016). We then calculated the utilization distribution using the `akde` function with `weights = TRUE`, as individual data sets included two duty cycles each day. Given that the period of observation for individuals varied in start and finish date, where possible we calculated both the utilization distribution and home range by austral season. For some individuals, the data did not coincide with the full three months of a season and the utilization distribution and home range were calculated for the entire data set if the animal was range-resident. For individuals that were not range-resident, we simply present the 95% MCP (minimum convex polygon) for the entire period they were tracked. MCP was calculated using the `mcp` function in the `adehabitatHR` package (Calenge 2006) in R (version 3.6.2, R Core Team 2019).

The degree of overlap of adjacent ranges was determined using the Bhattacharyya coefficient (BC) calculated using the `ctmm` R package as above, following the methods of Winner et al. (2018). The use of AKDE corrects for biases due to autocorrelation and enables valid comparisons

across sites and individuals, generating confidence limits that can be extended to measures of range overlap.

Identification of sites of high visitation

We used the *recurse* package (version 1.1.0; Bracis et al. 2018) in R (version 3.6.2; R Core Team 2019) to determine the location and frequency of visits to sites of high use. The *recurse* package enables users to specify a circle of a particular radius around location fixes. It then counts the number of trajectory segments of the movement paths of one or many individuals that intersect the circle. Each such intersection is classified as one visit. The package uses linear interpolation to estimate the entrance and exit times and calculates other metrics such as visit duration and time since previous visit. For this analysis, we used a radius of 25 m and a threshold of 20 visitations. Dens and lairs are specific locations that are visited often; therefore, we selected a radius larger than the observed accuracy of the GPS but not so large that visits to such sites could be confused with other activities. All times are Australian Eastern Standard Time and take no account of daylight-saving time. To determine changes in activity over time, we used calendar month and hour of the day to aggregate the data over a season or daily period of activity.

Temporal activity as measured by camera traps

As part of a related study, we placed 107 camera traps with passive-infrared sensors (HC600; Reconyx, Holmen, Wisconsin, USA) across 14,000 ha within the study area (for full details, refer to Carter et al. 2019). Camera traps operated 24 h per day, for the first 25 d of each month to synchronize data collection periods with GPS collars. Surveys were conducted monthly for four years (October 2015–September 2019), and all independent images of foxes and cats were extracted for analysis. Photographs of the same species recorded ≤ 60 min apart at the same camera were considered to be the same individual and not included in analysis unless body markings or GPS collars enabled clear distinction between individuals within this time period, or there was a second individual in a photograph. For the current study, we used camera-trap data to investigate the temporal activity of foxes and cats using the *camtrapR* package (Niedballa et al.

2016) in R (version 3.6.2; R Core Team 2019). To compare cat and fox activity, we used the *activityDensity* function to plot a kernel density estimate of both species' diel activity. Further, to investigate the impact of seasonality on the activity of foxes and cats we generated histograms of both species' diel activity in 1-h intervals for each month of the year using data from the four-year study period.

Dynamic interactions between individuals

The spatial distribution of location fixes and range overlaps can suggest discrete boundaries between individuals or attraction in individuals that share large parts of their range with another individual, among other possible interactions. Temporal trends can be used to identify periods of cohesive or opposing movement in dyads where there is some expectation of interaction, such as adjacent or overlapping ranges (Long et al. 2014). To examine this further, we used the *amt* package (version 1.1.0; Bracis et al. 2018) in R (version 3.6.2; R Core Team 2019) to model movement responses for fox–fox, cat–cat, and fox–cat dyads. The *amt* package fits step-selection functions (SSF) to investigate whether the movements of one individual are influenced by another (Schlägel et al. 2019). Individuals may be attracted to another, display avoidance behaviors, or be neutral to the presence or movements of another individual. In addition, these behaviors might be reciprocated, or not, depending on sex, age, and other factors. Selection coefficients are estimated for each step of a movement path relative to a subset of steps and occurrence distribution of the other individual before, after, or either side of the current time stamp. That is, instead of asking how is the animal responding to the overall (i.e., complete) space use of the other individual, the model looks at it within rolling time slices. In our case, we modeled the movement decisions of animal *i* to the space use of animal *j* in the last 400 min, or 6.6 h, being a multiple of the nominal duty cycle of the collars. Also, to define the position of animal *i* we used a maximum time of 40 min, being the first multiple of the duty cycle, as variation in the timing of location fix by a few seconds can affect the computation of the step-selection function if using the nominal duty cycle of 20 min. It should be noted that these methods might not be robust to

methodological choices such as data time steps (U. Schlägel, *personal communication*), and we tested the sensitivity of the results in pairs of animals that we knew to be interacting. Having settled on the parameters above, they were applied consistently to all dyad pairs. We applied this analysis of dyad pairs of cats, foxes, and cat and fox for those pairs with a Bhattacharyya coefficient of range overlap >0.10 .

In addition, we calculated the distance of nearest approach for pairs of individuals with adjacent or overlapping ranges. We could do this with accuracy because all collars were synchronized for both cats and foxes. Thus, all location data from deployed collars have the same time stamps to within a few seconds, except when a location fix was not obtained. We calculated nearest approach in meters for pairs of location fixes that were one minute or less apart for cats, foxes, and individuals of either species that had overlapping ranges.

RESULTS

Twenty-six adult foxes (10 σ and 16 ♀) were captured and fitted with GPS collars across three years, including four individuals that were captured and collared in two consecutive years (1 σ and 3 ♀). On average, foxes were tracked for 88 d (± 34 SD) and provided 3588 GPS locations (± 1397 SD) (Table 1). In total, 93,969 GPS locations were obtained on foxes (Fig. 2), with a maximum displacement distance, from point of capture, of 45 km.

Twenty-eight adult cats (20 σ , 8 ♀) were captured and fitted with GPS collars across three years, including two individuals that were captured and collared in two consecutive years (1 σ and 1 ♀) and one male that was collared in three consecutive years. Cats were tracked for an average of 100 d (± 118 SD) and provided 4024 GPS locations (± 5055 SD). In total, 110,173 GPS locations were obtained on cats (Fig. 2), with maximum displacement distances (from point of capture) exceeding 100 km for three individuals (Table 1).

Home-range area and range overlap

Foxes.—For foxes, some individuals were range-resident with narrow confidence limits defining discrete boundaries (Fig. 3), while

others were non-sedentary (Fig. 4) and wandered through and between the territories of other individuals (Fig. 5). Only 13 of the 22 foxes that were tracked with GPS collars for >30 d were range-resident throughout the entire period of deployment. For these animals, the core area of their home range (AKDE50) was 371 ± 119 ha (mean \pm SD) and their extended home range (AKDE95) was 1648 ± 518 ha, on average (Table 2). For females, there were more sedentary ($n = 8$) than non-sedentary individuals ($n = 4$), while there were equal numbers of sedentary and non-sedentary males. It was unclear whether age influenced movement behavior, although sedentary individuals were slightly heavier (average 4.3 kg, ± 0.5 SD) than non-sedentary individuals (average 3.9 kg, ± 0.5 SD). When data were considered separately by season, an additional two individuals were range-resident throughout spring only. Core and extended home ranges in spring and summer were smaller than overall ranges (Table 2). In spring, average core area (AKDE50) was 261 ± 111 ha (mean \pm SD, $n = 7$) and the extended home range (AKDE95) was 1279 ± 522 ha ($n = 7$), while in summer, the average core area (AKDE50) was 297 ± 55 ha ($n = 3$) and the extended home range (AKDE95) was 1379 ± 289 ha ($n = 3$) (Table 2). As adult foxes only were fitted with GPS collars, our results were not biased by the seasonal dispersal of juvenile foxes (i.e., <1 yr old), which occurs annually (cf. Coman et al. 1991, Allen and Sargeant 1993, Gosselink et al. 2010).

In any particular year, the ranges of individuals differed in the degree of overlap—including almost complete overlap, to partial overlap, to apparent discrete boundaries between territories for range-resident individuals. Among adjacent range-resident individuals, the proportion of range overlap was low for $\text{♀}:\text{♀}$ (range 0.01–0.06, $n = 2$) and higher for $\text{♀}:\sigma$ (range 0.02–0.42, $n = 3$) and there were no observed instances of range-resident male foxes having adjacent home ranges (Table 3). In addition, data were available for four range-resident individuals (FF963-, 2015 and 2016; FF369-, FF569-, and MF654-, 2016 and 2017) across two consecutive years. In all instances, the proportion of overlap year to year was 0.80 or greater (Table 4). Among individuals that were non-sedentary, six (4 ♀ and 2 σ) shifted

Table 1. Summary of red foxes and feral cats tracked with GPS collars at Scotia Wildlife Sanctuary (2015–2018).

ID	Sex	Age	Weight (kg)	Deployment date†	No. days tracked	No. locations	Max. displacement (km)
Foxes							
MF663	♂		4.8	8/10/2015	117	4395	5.8
MF546	♂		4.0	14/10/2015	104	4003	23.6
FF549	♀		4.0	20/10/2015	114	4267	10.1
FF546	♀		5.0	9/11/2015	25	974	2.7
FF636	♀		3.4	24/11/2015	63	2218	11.0
FF963-15	♀	1	4.0	24/11/2015	108	3792	4.1
FF266	♀		4.0	1/12/2015	101	4032	7.9
FF232-A	♀	2	3.6	1/08/2016	105	4520	6.1
FF232-B	♀		3.6	1/08/2016	116	5131	10.9
MF654-16	♂	1	4.4	1/08/2016	116	5145	5.7
FF228	♀	4	4.7	1/08/2016	22	837	3.2
FF963-16	♀	2	3.7	1/08/2016	22	1148	4.4
FF369-16	♀	6	4.6	1/08/2016	115	3732	3.7
MF262	♂	1	4.8	1/08/2016	33	1422	8.4
MF734	♂	5	4.4	1/08/2016	116	4405	7.6
FF825	♀		3.6	1/09/2016	114	4219	6.2
FF569-16	♀	5	3.8	1/09/2016	113	4047	4.5
MF654-17	♂	2	4.9	1/08/2017	91	4237	6.2
FF767	♀	1	4.0	1/08/2017	87	3983	7.5
FF536	♀	2	4.1	1/08/2017	91	3909	3.3
FF369-17	♀	7	4.4	1/08/2017	15	740	3.8
MF536	♂		4.3	1/08/2017	112	4687	31.7
MF568	♂		3.4	1/08/2017	112	5285	45.3
MF366	♂		5.4	1/08/2017	112	5058	10.2
MF376	♂	2	4.6	1/08/2017	87	3933	4.0
FF569-17	♀	6	3.6	1/08/2017	87	3168	18.7
Cats							
MC533	♂	4	3.9	1/08/2016	7	349	2.0
MC266	♂		3.9	1/09/2016	146	6557	30.8
MC536-16	♂	4	4.0	1/09/2016	480	20,996	14.0
MC566	♂	5	3.8	1/09/2016	54	2591	5.9
MC937	♂		4.4	1/12/2016	114	4789	7.7
MC839	♂		4.6	13/06/2017	37	1694	14.7
FC489	♀		3.2	18/06/2017	269	11,576	5.6
MC729	♂		3.6	21/06/2017	235	9768	13.4
MC236	♂		5.0	1/07/2017	225	9634	7.1
MC793	♂		4.0	3/07/2017	10	475	5.1
MC629	♂		4.8	7/07/2017	14	693	5.0
MC769	♂	6	3.8	9/07/2017	318	13,804	9.9
FC329	♀	8	3.0	11/07/2017	10	502	3.2
FC642	♀		2.6	15/07/2017	6	266	4.1
MC833	♂	6	4.6	1/06/2018	47	2041	79.6
MC922	♂		4.2	2/06/2018	104	3981	164.0
MC274	♂	6	3.6	25/06/2018	51	2310	70.8
FC596	♀		3.0	4/06/2018	4	165	12.4
MC265	♂	7	4.4	5/06/2018	49	2266	9.7
MC536	♂	6	3.8	6/06/2018	28	1120	5.5
MC536-18	♂	6	3.9	7/06/2018	30	1187	148.7
MC925	♂		4.8	12/06/2018	160	6897	10.2
FC726	♀		3.0	15/06/2018	2	56	5.4
FC232	♀		3.6	16/06/2018	172	1980	108.3
MC769-18	♂	7	3.6	18/06/2018	15	539	69.5

(Table 1. Continued.)

ID	Sex	Age	Weight (kg)	Deployment date†	No. days tracked	No. locations	Max. displacement (km)
MC842	♂		4.4	18/06/2018	170	4939	11.9
FC489-18	♀		3.6	18/06/2018	16	410	4.1
FC321	♀		3.6	19/06/2018	27	1092	78.2

†Dates are provided in day/month/year format.

their centers of activity at least once in the tracking period and undertook what could be characterized as a “range shift,” and two males (MF546, MF568) wandered back and forth across an area of 100s of square kilometers. The range of these non-sedentary individuals showed a high degree of overlap with other foxes, both range-resident and non-sedentary (Fig. 5).

Finally, kinship group appears to influence the subsequent range occupied by offspring and siblings, depending on sex. Across the three years of the study, there were four kinship groups identified using micro-satellite markers (*unpublished data*, AWC).

1. Group 1—FF266 (♀, 2015), FF228 (♀, 2016), and FF536 (♀, 2017).
2. Group 2—FF636 (♀, 2015) and FF232-B (♀, 2016).
3. Group 3—FF546 (♀, 2015) and MF654- (♂, 2016 and 2017).
4. Group 4—FF825 (♀, 2016) and MF262 (♂, 2016).

There was observed overlap in range for all members of Group 1 (0.21–0.71, BC) and Group 2 (0.46, BC) and no overlap in kinship groups 3 and 4, which contained males.

Cats.—In contrast to foxes, most cats were non-sedentary and traveled large distances from their point of release. Only seven of the 17 cats that were tracked for >30 d were range-resident throughout the entire period of GPS collar deployment. For these individuals, the average core area of their home range (AKDE50) was 1372 ± 687 ha (mean \pm SD) and their extended home range (AKDE95) was 5089 ± 2363 ha (Table 5). When data were considered separately by season, an additional two individuals were range-resident throughout spring only. Core and extended home ranges in spring were comparable to overall ranges, while summer ranges were markedly smaller (Table 5). For spring, core area

(AKDE50) was 1527 ± 1123 ha (mean \pm SD, $n = 7$) and the extended home range (AKDE95) was 5318 ± 3731 ha ($n = 4$) (Table 5). For summer, core area (AKDE50) was 715 ± 272 ha (mean \pm SD, $n = 4$) and the extended home range (AKDE95) was 2842 ± 1066 ha ($n = 4$) (Table 5).

In 2018, 12 cats were tracked via the Iridium network for between 15 and 170 d, revealing maximum displacement distances up to 164 km traveled over 12–22 d. Two of the tagged cats (1♂ and 1♀) traveled to the only large river in the region, up to 150 km distant, and the female returned to the vicinity it was trapped at Scotia 16 weeks later. Another male (MC922) ventured 164 km to the southeast of Scotia over a period of 16 d before settling in an area of farmland covering approximately 1100 ha where it remained for three months before the batteries expired in its GPS collar. Eight months later, this male was recorded by a camera trap back at Scotia, only 11 km from where it was captured and released the previous year.

Analyses of range overlap were only appropriate for the few individuals that were range-resident with adjacent territories. In those individuals, both high and low (or no) proportions of range overlap were identified in ♀:♂ and ♂:♂ pairings (Table 6).

Visitation of high-use sites

Foxes.—Individual foxes typically had one or two sites that were used frequently (Table 7), and the duration of stay at these sites was notably longer than at any other location within the animals' home range (Fig. 6). The location and number of sites that were used changed over time, although some individuals had a single high visitation site that they visited more than 100 times during the course of the study, while others had none. All foxes had one or many preferred sites that were revisited, but not all individuals had a site that could be characterized as high use.

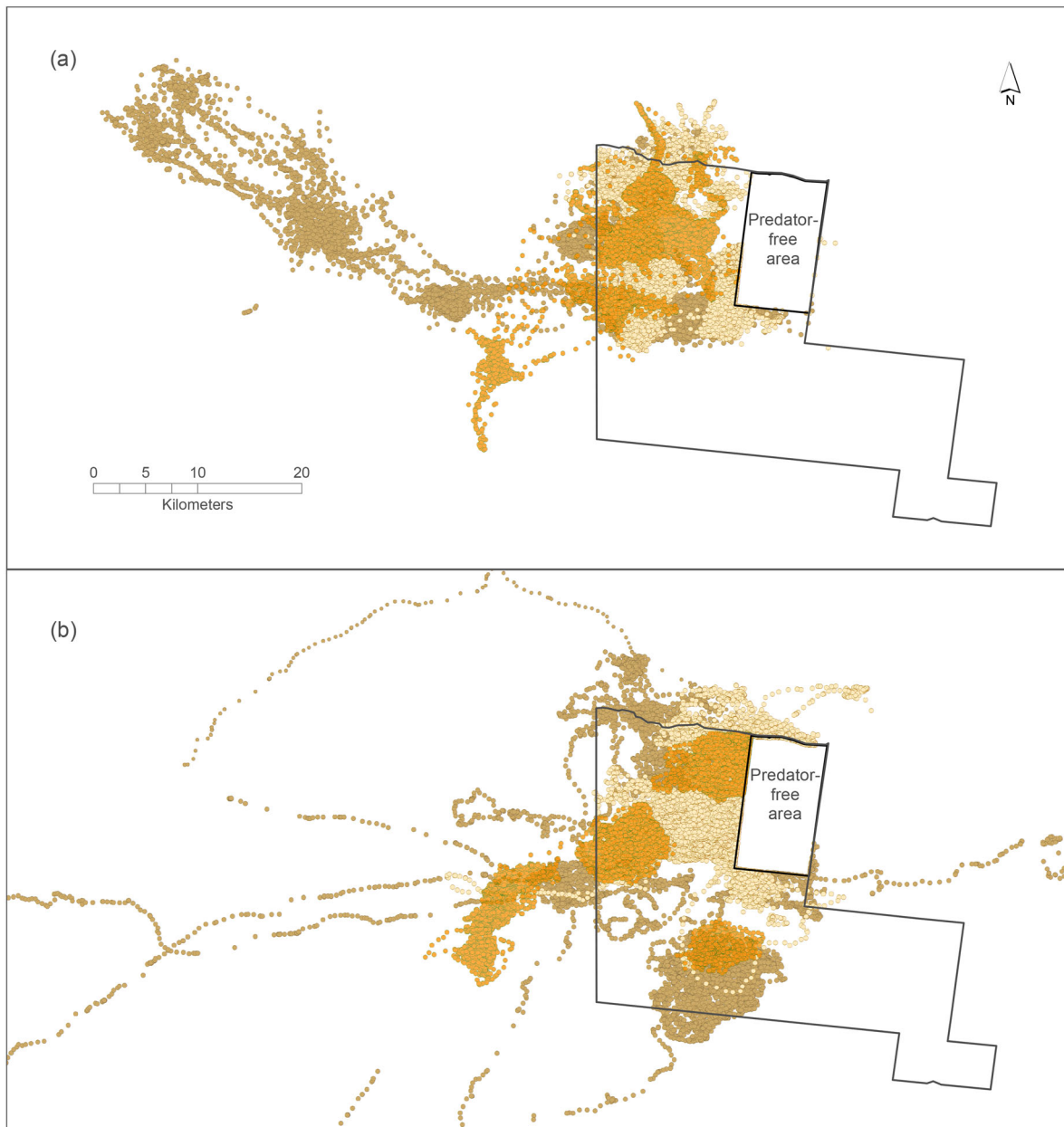


Fig. 2. Maps showing GPS location data obtained from 26 foxes (a) and 28 feral cats (b) fitted with telemetry collars at Scotia Wildlife Sanctuary, 2015–2018. The three different color shades represent the combined data for an entire calendar year.

Cats.—As for foxes, among the feral cats tracked for more than 60 d, approximately half had individual lairs that were used more than 20 times during the study (Table 8). Similarly, when lairs were used repeatedly, cats typically used one or two such sites only during the three to nine

months that they were observed. In two range-resident males MC236 and MC729, this was a single high visitation site that in each case was a vacant rabbit burrow adjacent to a road. The one exception was MC536-16, a male feral cat that had three to four high visitation sites in each of the

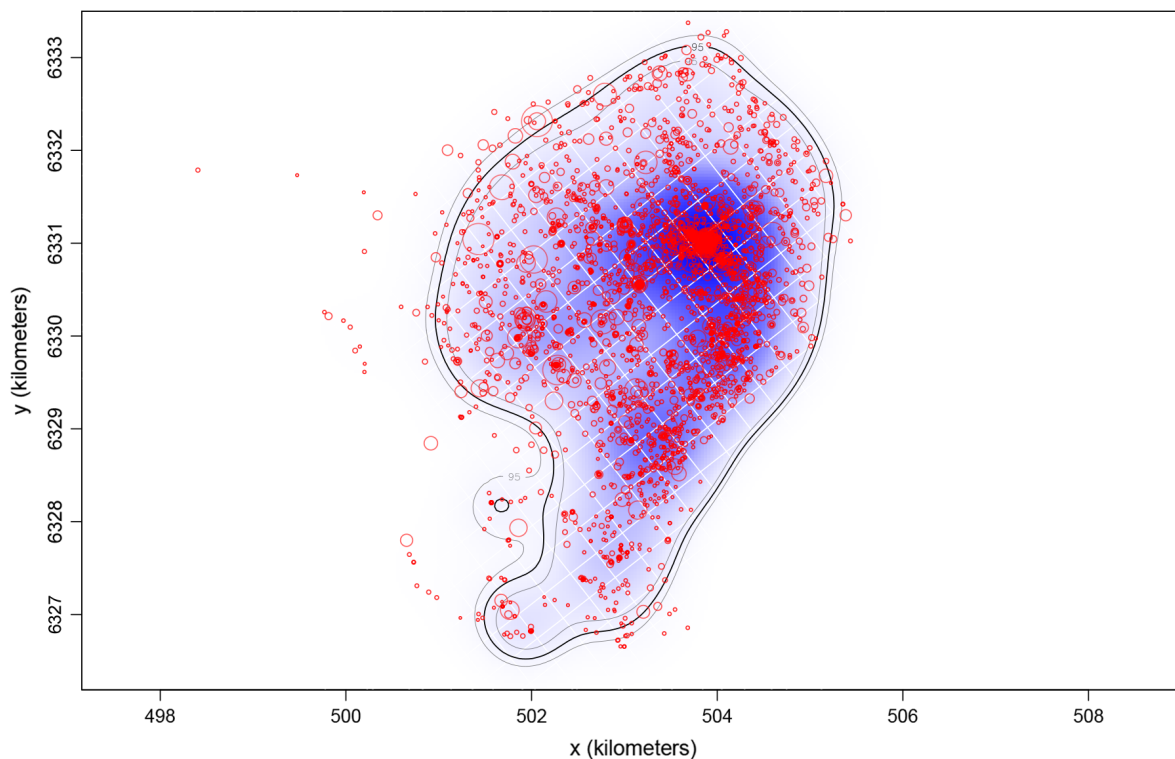


Fig. 3. An example of an individual (FF825) that was strongly range-resident. Red circles are GPS location fixes ($n = 4219$), and blue is the AKDE utilization distribution. Black line is 95% utilization distribution with 95% confidence interval (CI) shown as gray line.

summer months of 2016/17. Some sites were visited by this cat >60 times during the period of observation and >30 times in a single month, as occurred in December 2016. The following summer, this individual maintained the same approximate home range but, in contrast to the previous year, had no individual sites of high visitation.

Temporal activity as measured by camera traps

Across the first two years of the study, camera traps recorded 2898 independent images of foxes and 958 independent images of cats. When data from all months were pooled together, fox and cat activity showed a high degree of overlap throughout the diel period ($Dhat4 = 0.85$). Analyzing the data separately by month showed that foxes were largely nocturnal, with relatively few photographs recorded during the day between 09:00 h and 17:00 h (Fig. 7). The activity of cats was more varied, particularly during the cooler months (May–August) when the proportion of

photographs recorded during hours of daylight was greater than in the summer months and overlap in fox and cat activity was lowest in June ($Dhat4 = 0.64$). In the hottest months (January–February), most activity of both species was in the pre-dawn (Fig. 7), while in the cooler months (May–September), most activity was in the early evening (Fig. 8).

Dynamic interactions between individuals

Foxes.—Most interactions between individual foxes were neutral, that is, neither attraction nor avoidance (Table 9). There was one significant interaction of mutual attraction between two females (FF636 and FF963-15). These two individuals had a range overlap of 0.85 and had apparent contact with each other most weeks over a period of two months from late November 2016, prior to FF636 shifting range in the third week of January (Fig. 9). This pair were recorded to occur within 4 m of each other. Two other

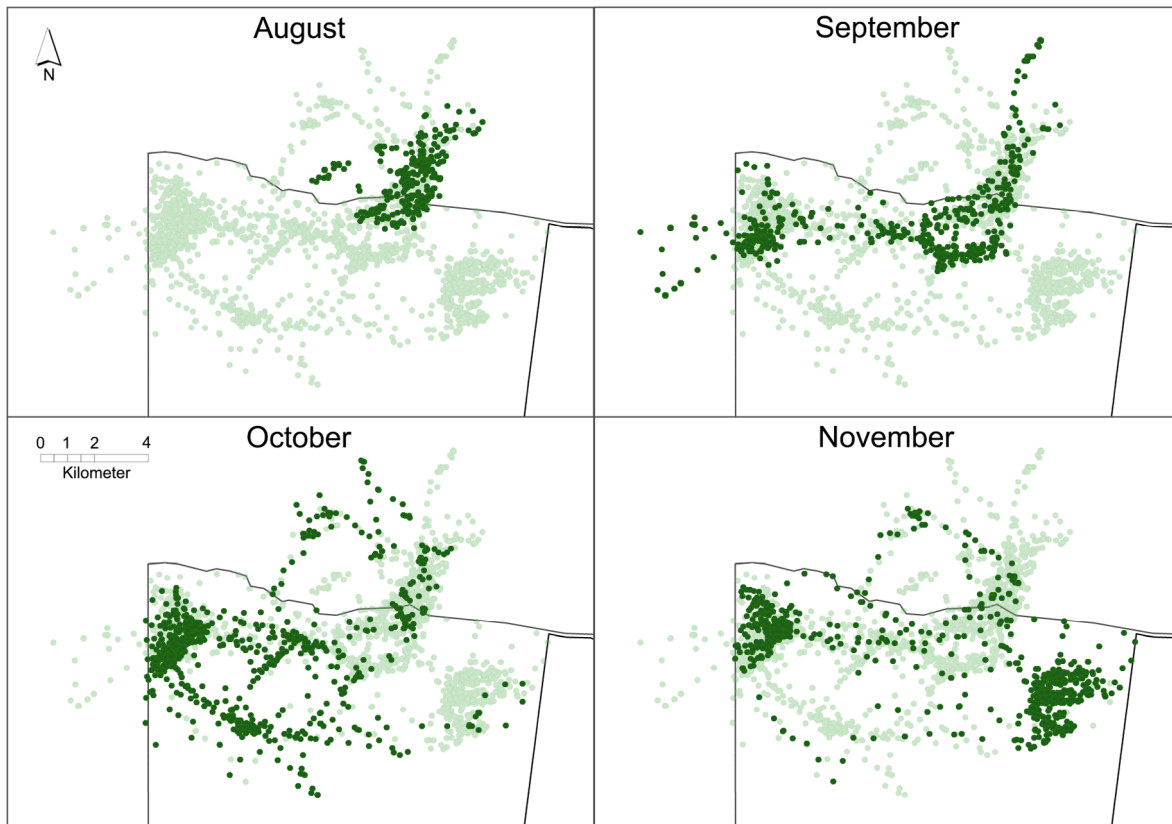


Fig. 4. An example of an individual fox (FF636) that was non-sedentary, shifting centers of activity at irregular intervals over a large area (9038 ha (MCP95)). Changes in distribution shown by month of the year starting in August 2016. Pale green dots ($n = 2218$) show all location fixes, while dark green dots are location fixes for the current month.

females (FF232-A, FF232-B) shared a large portion of their range (0.51), and there was a marginally significant attraction of the latter for the former. Elsewhere, there were two other significant interactions of attraction between male and female foxes. In both instances, the pair shared a large portion of their ranges (0.27 and 0.94), but the attraction was only significant in one direction, being neutral in the other direction (Table 9).

Cats.—Feral cats roamed over larger areas than foxes (Table 5, Fig. 2) and were typically non-sedentary, and most did not co-occur. While movement trajectories of individual cats did cross, this did not occur in the same time frame and cats caught and released in the same location and period appeared to move largely independently of each other. However, when individuals were range-resident they had frequent contact

and shared a large portion of their range with other range-resident individuals (Table 10). Although the sample is small, this was true for both ♀:♂ and ♂:♂ interactions. All individuals that shared a portion of their range had frequent contact with the other, regardless of sex, being recorded with 1 m of each other on numerous occasions. This included the female cat (FC489) that had frequent contact with both males with whom she shared a range (Fig. 10). This female was located within 100 m of the first male (MC236) >180 times in the 20 weeks from early September 2016, and within 100 m of the second male (MC536-16) >80 times in the 10 weeks from early October of the same year. The two males had similar close contact >20 times over the same 10 weeks. For non-sedentary individuals, there were 25 dyad pairs of feral cats whose trajectories intersected in space and time. Of these dyad

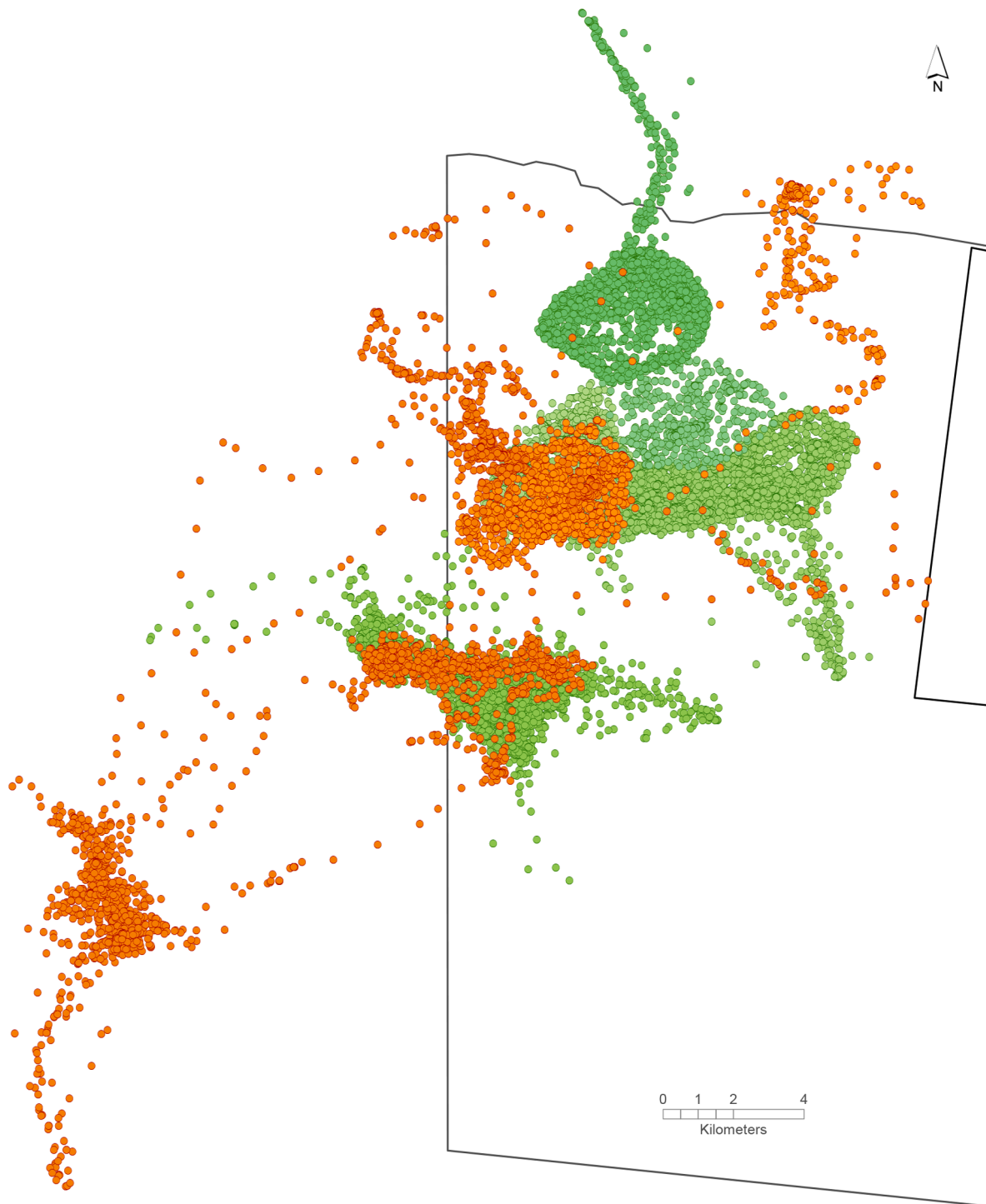


Fig. 5. Spatial overlap of range-resident (green tones, $n = 5$) and non-sedentary foxes (ochre tones, $n = 2$) in the first year of the study, October 2015 to March 2016.

Table 2. For foxes, estimated core area (AKDE50) and extended home range (AKDE95) in hectares for the full deployment and seasons.

Animal ID	Sex	MCP95 (ha)	All data		Season: Spring		Season: Summer	
			AKDE50 (ha)	AKDE95 (ha)	AKDE50 (ha)	AKDE95 (ha)	AKDE50 (ha)	AKDE95 (ha)
FF266	♀	1202	234	1455			242	1517
MF546	♂	18,329						
FF549	♀	2343	353	1680			351	1573
FF636	♀	6405						
MF663	♂	2122	473	2033				
FF963-15	♀	981	288	1037			298	1047
FF232-A	♀	2823			75	450		
FF232-B	♀	9038						
MF262	♂	506						
FF369-16	♀	1329	407	1466	348	1275		
FF569-16†	♀	1706	400	1729	362	1687		
MF654-16†	♂	1470	233	1341	166	738		
MF734	♂	4348			306	1765		
FF825	♀	1788	331	1733	215	1255		
MF366	♂	2581	475	2282	357	1783		
MF376	♂	1172	381	1211				
FF536	♀	705	166	735				
FF569-17†	♀	2251						
MF536	♂	8520						
MF568	♂	25,645						
MF654-17†	♂	2715	559	2537				
FF767	♀	2323	529	2196				

Notes: To facilitate comparison with previous studies, minimum convex polygon (MCP 95) home-range area, using all data for each individual, is presented also. Only animals tracked for more than 30 d are shown. A blank cell denotes that the individual was not “range-resident” and estimation of AKDE was not appropriate.

† Denotes an individual tracked in more than one year.

Table 3. For range-resident foxes, the proportion of range overlap as measured by Bhattacharyya coefficient (BC) and the upper and lower 95% confidence interval (CI).

Year	Animal <i>i</i>	Animal <i>j</i>	Sex	BC	95% CI	
					Lower	Upper
2015	FF266	FF963-15	♀:♀	0.01	0.01	0.01
	MF663	FF963-15	♂:♀	0.17	0.14	0.20
2016	FF369-16	FF825	♀:♀	0.06	0.05	0.07
2017	MF654-17	FF536	♂:♀	0.42	0.38	0.47
	MF376	FF767	♂:♀	0.02	0.02	0.03

pairs, one pair only came within 100 m of each other (median 3318 m, range 19–94,750 m).

Interactions between foxes and cats

Unlike intraspecific analyses of foxes and cats, we detected significant avoidance behaviors in both directions in the interactions of foxes and cats with overlapping ranges (Table 11). In 2016,

Table 4. For range-resident foxes tagged in consecutive years, the proportion of range overlap year to year as measured by Bhattacharyya coefficient (BC) and the upper and lower 95% confidence interval (CI).

Years	Animal ID	Sex	BC	95% CI	
				Lower	Upper
2015–2016	FF963-	♀	0.80	0.72	0.87
2016–2017	FF369-	♀	0.86	0.81	0.90
	FF569-	♀	0.80	0.76	0.83
	MF654-	♂	0.91	0.89	0.93

a male cat MC536-16 shared its range with three foxes—displaying strong avoidance behavior toward a female fox FF369-16 and neutral interactions with the other two foxes (1♂ and 1♀). At the same time, the male fox in this dyad displayed significant avoidance behavior toward the male cat MC536-16. In 2017, there were 11 dyad pairs of cats and foxes that shared their

Table 5. For cats, estimated core area (AKDE50) and extended home range (AKDE95) in hectares.

Year	Animal ID	Sex	MCP95 (ha)	All data AKDE50 (ha)	All data AKDE95 (ha)	Spring AKDE50 (ha)	Spring AKDE95 (ha)	Summer AKDE50 (ha)	Summer AKDE95 (ha)
2016	MC937	♂	2898	1044	3705			1038	3687
	MC536-16†	♂	3362	965	3466	1385	4287	534	2090
	MC266	♂	4858	1601	6148	534	1917		
	MC566	♂	1869						
2017	FC489†	♀	1871	500	1895	318	1566	450	1765
	MC236	♂	4586	1382	5056	1073	4030		
	MC729	♂	4288						
	MC839	♂	16,494						
	MC769†	♂	6214	1422	6218	1400	4651	839	3826
2018	MC274	♂	331,351						
	FC232	♀	196,566						
	MC265	♂	2292						
	MC536-18†	♂	123,947						
	MC833	♂	41,797						
	MC842	♂	12,894			3539	11,678		
	MC925	♂	7282	2691	9133	2440	9096		
MC922	♂	227,560							

Notes: To facilitate comparison with previous studies, minimum convex polygon (MCP 95) home-range area, using all data for each individual, is presented also. Only animals tracked for more than 30 d shown. A blank cell denotes that the individual was not “range-resident” and estimation of AKDE was not appropriate.

† Denotes an individual tracked in more than one year. Not shown are seven cats that were tracked for less than two weeks and the winter AKDE for MC536-16 (AKDE50 = 523 ha; AKDE95 = 2221 ha).

Table 6. For range-resident cats with adjacent territories in Spring 2017, the proportion of range overlap as measured by BC and the upper and lower 95% confidence interval (CI).

Animal <i>i</i>	Animal <i>j</i>	Sex	Proportion overlap	95% CI	
				Lower	Upper
MC236	FC489	♂:♀	0.81	0.71	0.89
MC536-16	FC489	♂:♀	0.33	0.24	0.43
MC236	MC536-16	♂:♂	0.35	0.27	0.44
MC236	MC769	♂:♂	0.07	0.03	0.14
FC489	MC769	♂:♀	0.00	0.00	0.00

range (Table 11). Unlike the previous year, all significant interactions were attraction of one animal to the other in the dyad pair. This attraction between species was evident in the movements of two foxes (♂fox → ♂cat; ♀fox → ♀cat) and one cat (♂cat → ♂fox).

DISCUSSION

This study is the most complete analysis for any environment of the spatial distribution, movement

patterns, and interactions of two co-occurring mesopredators—the red fox and feral cat—providing new insight into the long-distance movements of cats in Australia, and the interactions within and between these species. These analyses were made possible by the collection of high-frequency location data, the deployment of the latest tracking technologies, and recent advances in statistical modeling. Importantly, synchronization of location fixes from all animals enabled us to observe directly the spatial separation of all pairs of animals at 20-min intervals through the study. A priori, we expected the presence of one invasive mesopredator to influence the distribution and behavior of another. While observed avoidance behaviors between cats and foxes were not common, when they were observed they were strong. Interactions within and between species were most commonly neutral, against a background of considerable variation in individual patterns of residency (Tables 8, 10).

Home-range estimation and overlap

In this environment, throughout the duration of the study, only a portion of fox and cat

Table 7. Number of sites of high visitation (>20 visits) for foxes tracked for more than 60 d.

Animal ID	Sex	Range-resident	Unique sites	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
FF266	♀	Yes	3	2	1	1	1
MF546	♂	No	2	1	1	1	0
FF549	♀	Yes	0	0	0	0	0	0
FF636	♀	No	1	1	1	1
MF663	♂	Yes	0	0	0	0	0
FF963-15	♀	Yes	1	0	0	0	1	1
FF232-A	♀	Yes	1	...	0	1	1	1
FF232-B	♀	No	0	...	0	0	0	0
FF369-16	♀	Yes	1	...	1	1	1	1
FF569-16	♀	Yes	3	1	2	2	1
MF654-16	♂	Yes	0	...	0	0	0	0
MF734	♂	Yes	0	...	0	0	0	0
FF825	♀	Yes	2	1	1	2	1
MF366	♂	Yes	1	...	1	1	1	1
MF376	♂	Yes	0	...	0	0	0
FF536	♀	Yes	2	...	0	2	2
FF569-17	♀	No	0	...	0	0	0
MF536	♂	No	2	...	2	2	2	2
MF568	♂	No	0	...	0	0	0	0
MF654-17	♂	Yes	1	...	1	1	0
FF767	♀	Yes	0	...	0	0	0

Note: An ellipsis (...) signifies no data.

populations were range-resident (Tables 3, 6). Fewer cats (41%) than foxes (59%) were range-resident, and among cats that remained within a home range, core and extended range size was 3–3.5 times larger than that observed for foxes. In both populations, there were individuals for whom the semi-variance function continued to increase with longer time-lags; that is, range extent continues to expand over time and the animal is not range-resident (Fleming et al. 2014a). Indeed, this was true for most cats as individuals moved up to 164 km from their point of release. Long-distance movements that resulted in displacement >100 km have been observed in foxes (Ables 1969, Walton et al. 2017) and rarely in feral cats. The only other accounts are of an adult male that traveled 130 km from its point of release and returned in 19 d (Clausen et al. 2016) and another that traveled 200 km (Newsome 1991). These long-distance movements in feral cats can best be characterized as *ranging* behavior (Dingle 2014) as individuals move over broad scales in response to condition-dependent factors such as competition, predation risk, breeding status, energy reserves or other factors (Roshier et al. 2008). This description of the observed

movement behavior in our study is supported further by the fact that three of the individual cats (2♂ and 1♀) that made extensive movements from their release point returned to the study site up to eleven months post-release. In assessing these observed behaviors, it should be noted that most cats in this study were male (20 of 28), which is consistent with other studies of feral cats in semiarid and arid Australia (combined 26♂, 9♀; Jones and Coman 1982, Edwards et al. 2001, Burrows et al. 2003, Moseby et al. 2009, Johnston et al. 2013), presumably because males are less risk averse and more likely to be trapped (Molsher 2001).

The observed core and extended home-range areas were on average larger for cats and similar for foxes to that observed in the only comparable study of co-occurring foxes and cats (Moseby et al. 2009). In that study, the extended home range for foxes and cats was, on average, similar in both species (1660 and 1741 ha, respectively). In our study, average home-range size (AKDE95) for range-resident foxes was the same as Moseby et al. (2009), while range-resident feral cats at Scotia had substantially larger home ranges. Large differences between individuals were

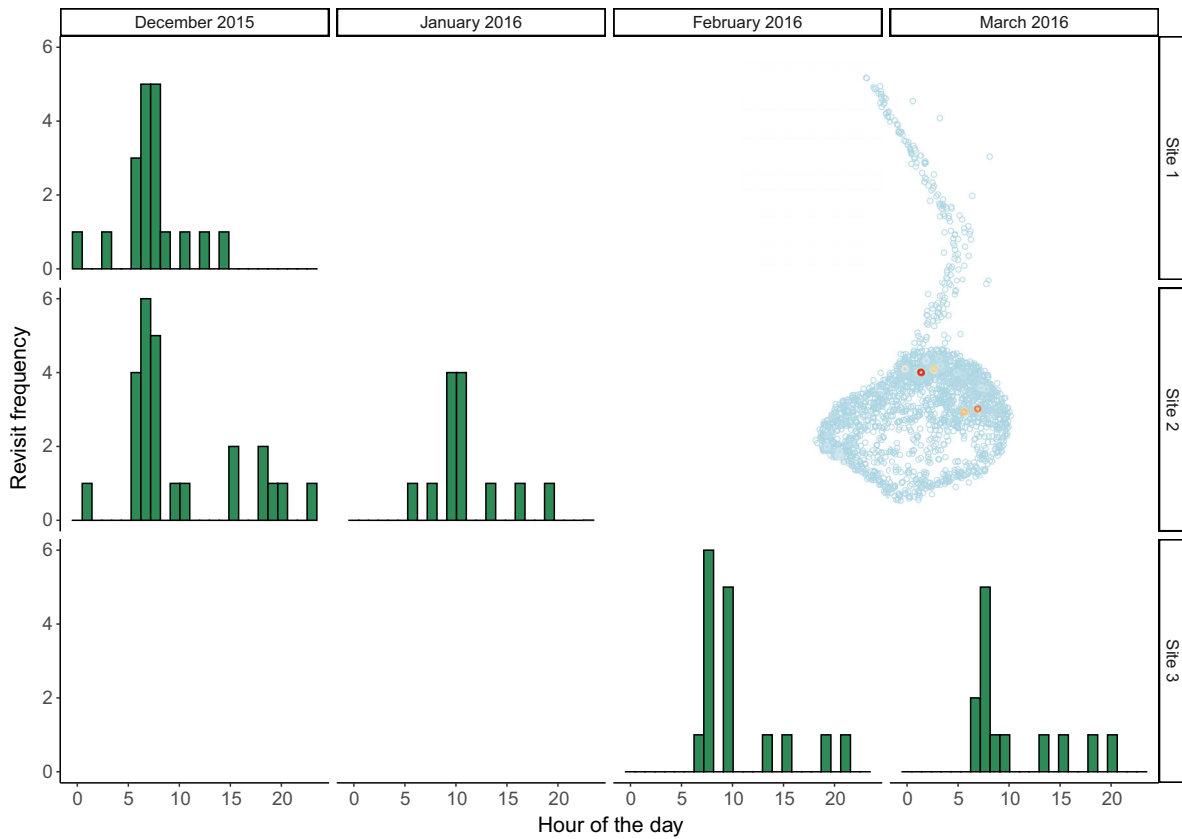


Fig. 6. The frequency of visitation of high-use sites ($n = 3$) by a female fox FF266, according to month and hour of the day. The inset map shows the location of every GPS fix (denoted by a circle) collected throughout the observation period—the redder the color of the circle, the higher the frequency of visitation.

Table 8. Number of sites of high visitation (>20 visits) for cats tracked for more than 60 d.

Animal ID	Sex	Range-resident	Unique sites	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
MC937	♂	Yes	0	0	0	0	0
MC536-16	♂	Yes	7	4	3	4	2	6	6	4	7	5	3	1	0
MC266	♂	Yes	0	...	0	0	0	0	0	0
FC489	♀	Yes	2	0	1	1	1	0	1	2	1	1
MC236	♂	Yes	1	0	0	1	0	1	1	1	1
MC729	♂	Yes	2	2	2	2	1	2	2	1
MC769	♂	Yes	4	2	3	3	3	3	2	3	3	3	2	4	...
FC232	♀	No	0	0	0	0	0	0	0
MC842	♂	No	0	0	0	0	0	0
MC925	♂	Yes	0	0	0	0	0	0
MC922	♂	No	0	0	0	0

Note: An ellipsis (...) signifies no data.

observed in non-sedentary foxes that had ranges (MCP95) as large as 25,645 ha, although this was still smaller than the 41,201 ha reported from the Simpson Desert in central Australia (Newsome

et al. 2017b). In other biomes, variation in the size of fox home ranges is well known (Voigt and Macdonald 1984, Cavallini 1996). We would expect home range to scale negatively with

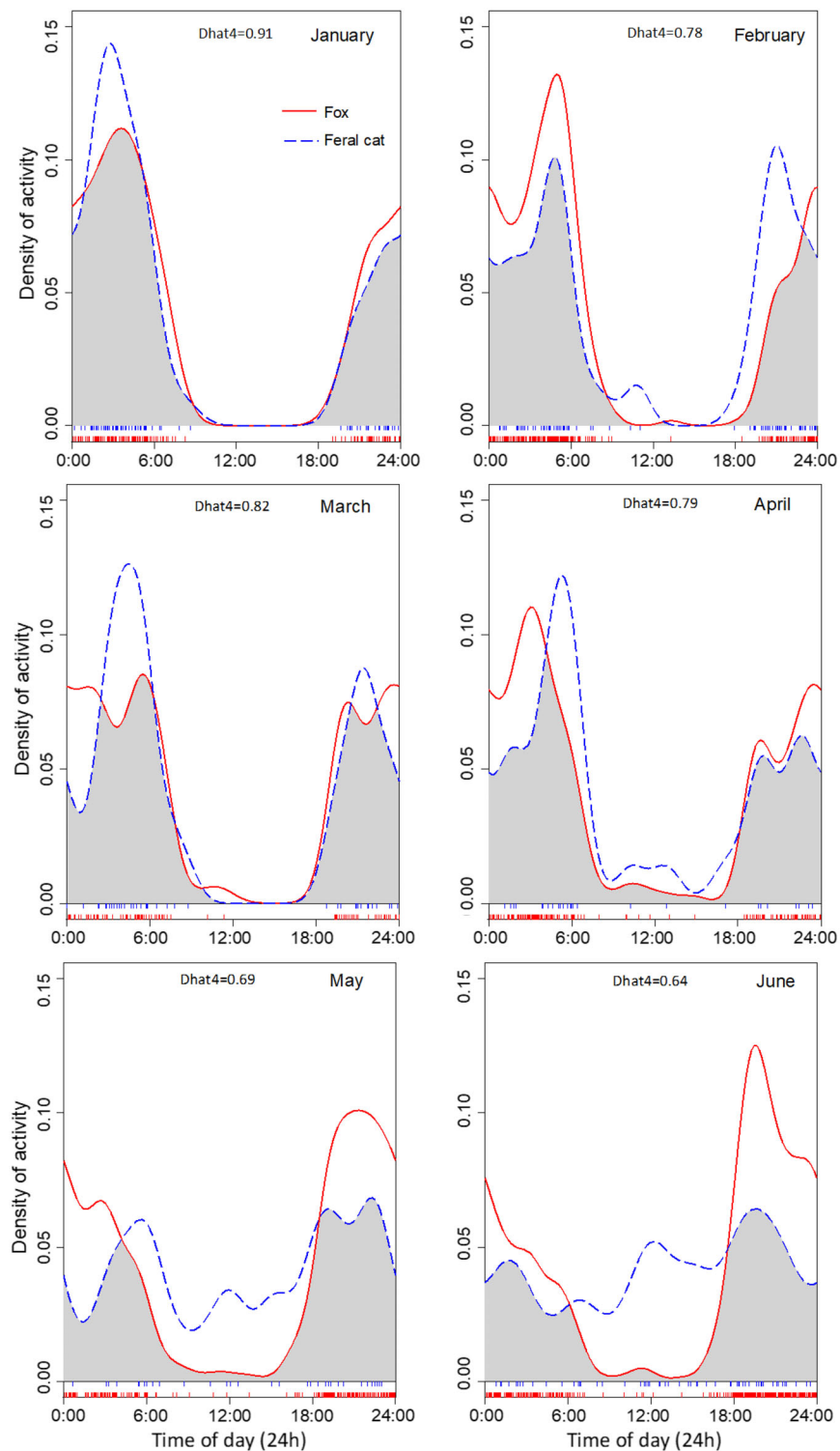


Fig. 7. Monthly dial activity (January–June) of foxes and cats derived from 2903 and 958 independent camera-trap images, respectively, for the period October 2015 to September 2017. The solid gray area shows the area of overlap between both species (all data $Dhat4 = 0.85$).

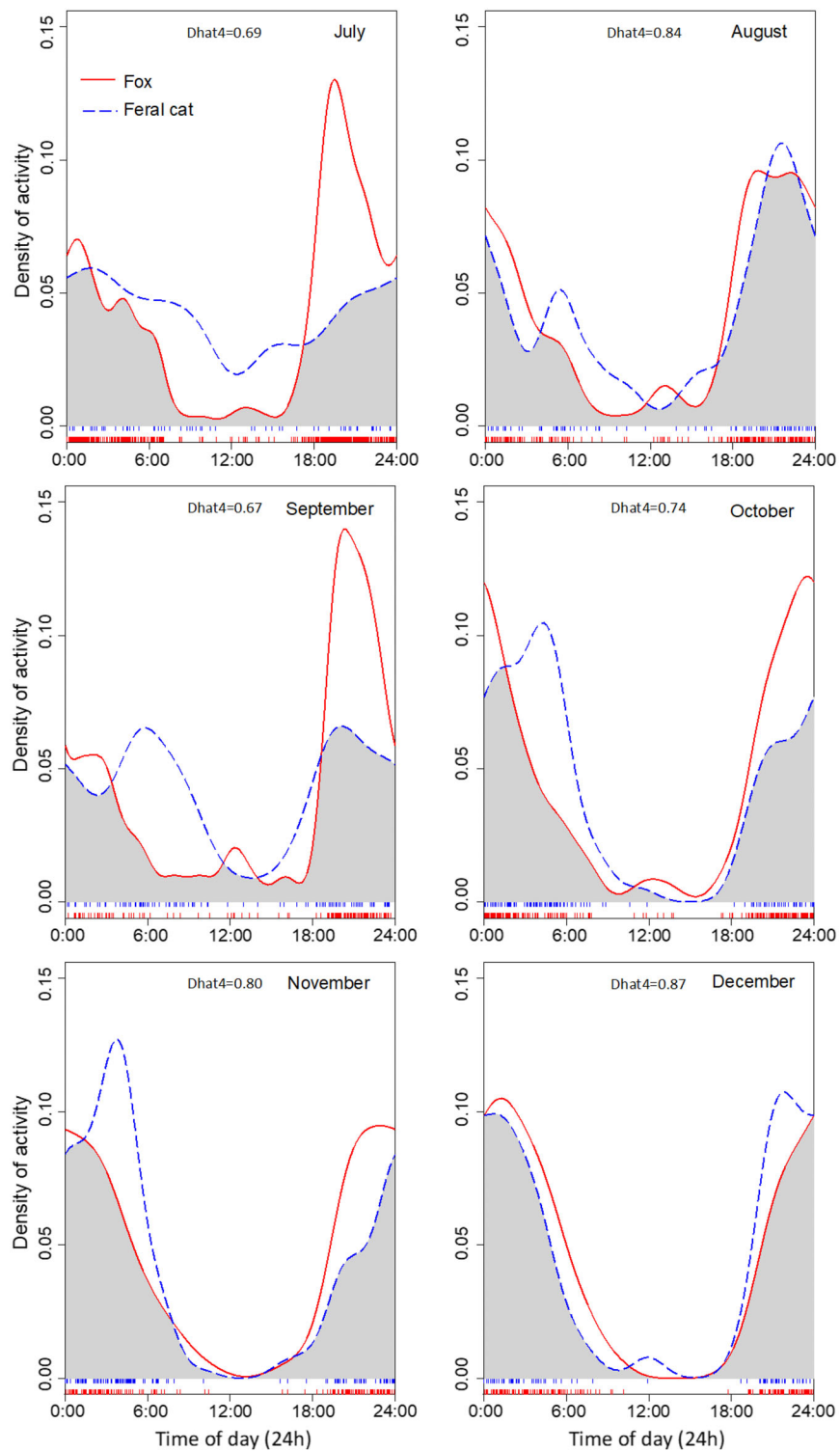


Fig. 8. Monthly dial activity (July–December) of foxes and cats derived from 2903 and 958 independent camera-trap images, respectively, for the period October 2015 to September 2017. The solid gray area shows the area of overlap between both species (all data $D_{hat4} = 0.85$).

Table 9. Coefficients of interaction and *P* value for all fox dyads (animal *i*, *j*) with a Bhattacharyya coefficient (BC) for range overlap of 0.10 or greater, and observed nearest approach (meters) for simultaneous GPS location fixes.

Year	Animal <i>i</i>	Animal <i>j</i>	Sex	BC	Nearest approach (m)	Coeff. <i>i</i> on <i>j</i>	<i>P</i>	Coeff. <i>j</i> on <i>i</i>	<i>P</i>
2015	FF546	FF636	♀:♀	0.10	1856	−55.7	0.581	−4.7	0.676
	FF546	MF663	♀:♂	0.15	476	−6.0	0.222	−52.1	0.066
	FF636	MF663	♀:♂	0.28	186	−3.2	0.227	−2.9	0.258
	FF636	FF963-15	♀:♀	0.85	4	0.9	0.002*	1.0	0.002*
	MF663	FF963-15	♂:♀	0.17	60	−1.6	0.284	−1.8	0.197
2016	FF232-A	FF232-B	♀:♀	0.51	6	1.4	0.050*	−0.3	0.769
	MF262	FF569-16	♂:♀	0.27	348	3.0	0.339	−1.0	0.787
	FF232-B	MF654-16	♀:♂	0.45	49	−1.2	0.260	−0.8	0.559
	FF228	MF654-16	♀:♂	0.94	26	1.0	0.070	1.3	0.032*
	FF369-16	MF734	♀:♂	0.32	271	−3.5	0.132	−1.8	0.107
	FF369-16	FF825	♀:♀	0.10	63	0.9	0.585	−0.8	0.493
	FF232-A	FF963-16	♀:♀	0.28	50	0.3	0.747	1.1	0.129
	MF366	FF369-17	♂:♀	0.14	49	0.0	0.982	0.8	0.321
2017	MF376	MF536	♂:♂	0.14	154	0.3	0.840	−0.3	0.854
	FF369-17	MF536	♀:♂	0.10	2489	38.0	0.777	−416.8	0.706
	FF536	MF654-17	♀:♂	0.42	27	1.1	0.002*	0.1	0.865
	FF569-17	FF767	♀:♀	0.19	372	−0.2	0.831	−2.9	0.239

Notes: This analysis includes both range-resident and non-sedentary individuals. Interaction models for two dyads (FF232-B–FF228; FF232-B–FF963-16) did not converge (results not shown).

Bold values are significant interactions, **P* < 0.05; ***P* < 0.01.

landscape productivity (e.g., McNab 1963) as has been suggested for foxes (Walton et al. 2017) and cats (Bengsen et al. 2016). Comparing the two mesopredator populations in our study environment revealed that a greater proportion of the fox population were range-resident, their home ranges were smaller, and the extent of the range (AKDE95) was larger relative to the core home range (AKDE50)—the ratio of extended range to core range in foxes was 4.53 ± 0.86 (mean \pm SD, $n = 13$) and in cats was 3.74 ± 0.32 ($n = 7$). This larger “buffer” around the core home range suggests that, in addition to resource constraints, in this environment there is a social constraint on range use in foxes that is greater than in cats (also see later). For range-resident feral cats, the observed extended home range (AKDE95) was about double the size of home ranges estimated for feral cats in another arid region of Western Australia (Wysong et al. 2020), about three times that estimated for arid South Australia (Moseby et al. 2009), and four times that estimated for subtropical savannas in northern Australia (McGregor et al. 2015). This suggests that prey resources are more limiting in the semiarid woodland environments of our study area

compared to regions with greater rainfall and/or more diverse reptile and small mammal faunas, for instance, rodents (see Roshier et al. 2020). The near-constant movement by non-sedentary feral cats observed in this study has been observed in previous studies in semiarid or arid environments and has been attributed to nutritional stress (Jones and Coman 1982, Edwards et al. 2001, Moseby et al. 2009).

The stability of a home range can be characterized in several ways: the narrowness of the confidence limits that describe its spatial extent (Fig. 2), the extent of overlap with adjacent conspecifics (Tables 4, 7), the congruence in spatial extent of an individual’s range seasonally or year to year (Table 5), and the degree to which other members of a familial group share the same range over time. While we have no data on the last point for cats, based on the other metrics, we can characterize stability of home range as being more evident in foxes than cats. Individual foxes maintained tight distributions, and the utilization distribution was weighted toward the boundary of the range, while overlap with adjacent individuals was near zero (Table 4), suggesting the boundary of the range is maintained

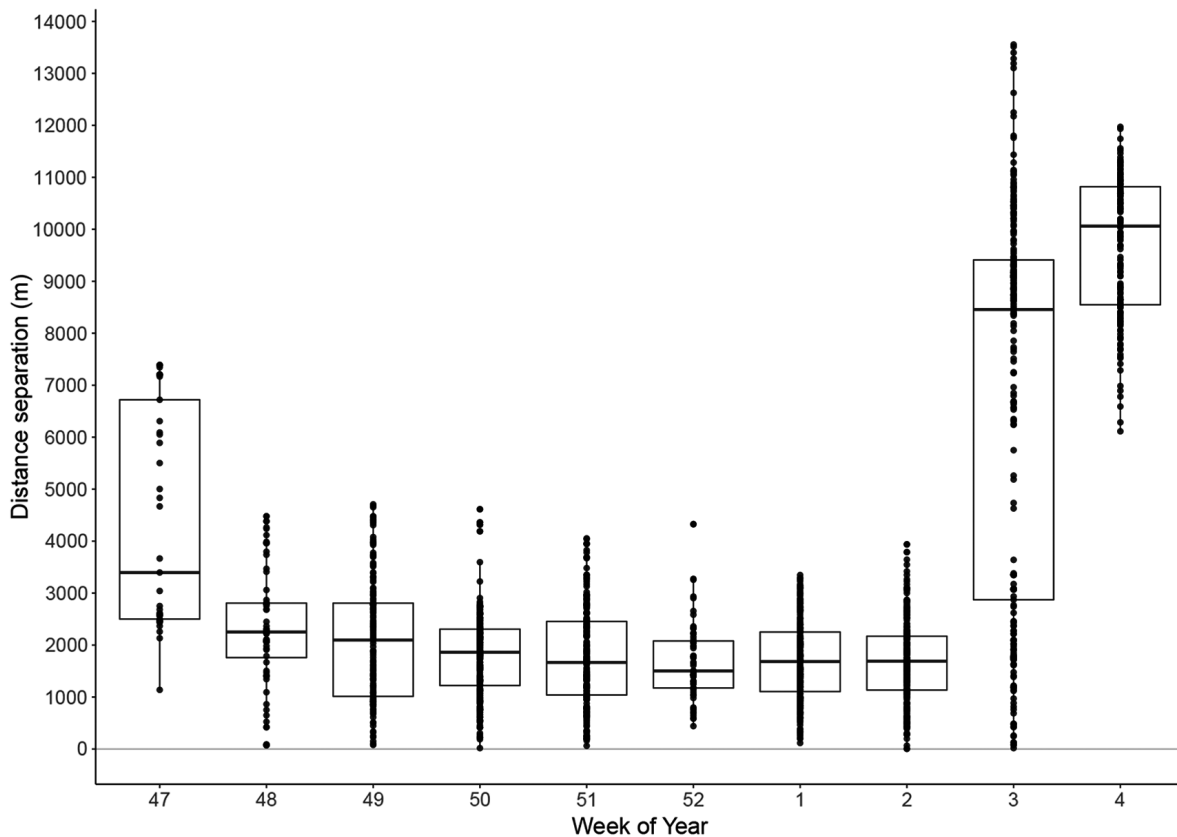


Fig. 9. Observed distance between two individual foxes, FF636 and FF963-15, in the summer of 2015/16. Data are grouped by week of the year.

Table 10. Coefficients of interaction and *P* value for all cat dyads (animal *i,j*) with a Bhattacharyya coefficient (BC) for range overlap of 0.10 or greater, and observed nearest approach (meters) for simultaneous locations in 2016.

Animal <i>i</i>	Animal <i>j</i>	Sex	BC	Nearest approach (m)	Coeff <i>i</i> on <i>j</i>	<i>P</i>	Coeff <i>j</i> on <i>i</i>	<i>P</i>
MC236	FC489	♂:♀	0.81	<1	2.2	0.000***	1.3	0.000***
MC236	MC536-16	♂:♂	0.35	<1	1.3	0.001***	1.2	0.001***
FC489	MC536-16	♀:♂	0.33	<1	1.5	0.000***	2.2	0.000***

Note: This analysis includes range-resident individuals only. Bold values are significant interactions, ****P* < 0.01.

closely and the range can be characterized as a territory. This contrasts with the observations of space use in foxes in the arid landscapes of Saudi Arabia where extensive range overlap was observed (Macdonald et al. 1999), although the methods of range estimation differ between the studies. Territorial behaviors are well known in fox populations from more mesic environments (Ables 1969, Macdonald 1980, Poulle et al. 1994,

Adkins and Stott 1998), and the data presented here suggest that these behaviors are maintained in relatively resource-poor arid landscapes.

In contrast, feral cats in our study area were mostly non-sedentary and ranged over larger areas. Some individuals were range-resident for many months to more than a year and switched to ranging behavior thereafter. In the case of MC536-, this male cat maintained a home range

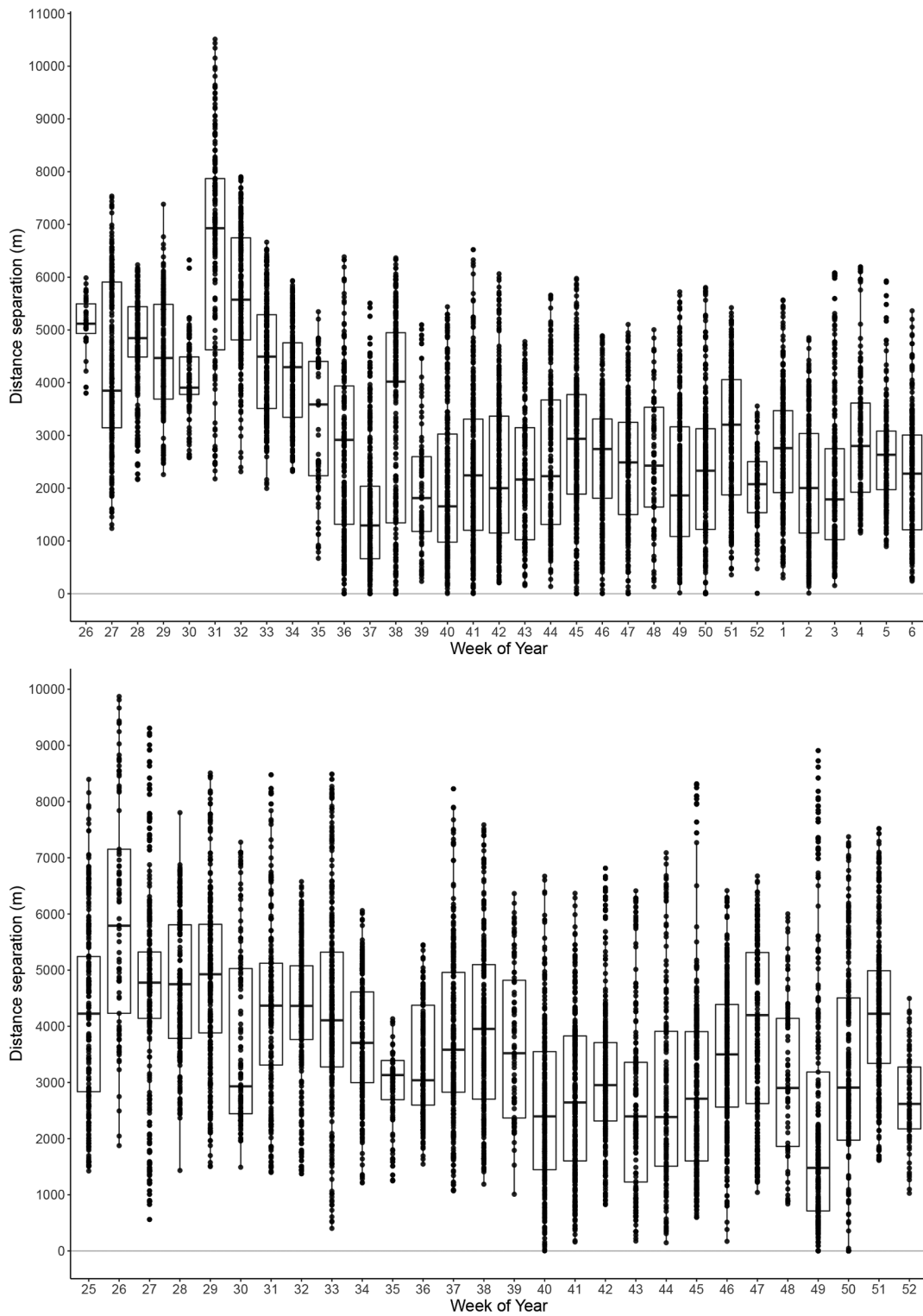


Fig. 10. Observed distance between individual feral cats, FC489 (♀) and MC236 (♂) (top) and FC489 and MC536-16 (♂) (bottom), in the spring and summer of 2016/17. Data are grouped by week of the year.

Table 11. Coefficients of interaction and *P* value for all dyads (feral cat *i*, fox *j*) with a Bhattacharyya coefficient (BC) for range overlap of 0.10 or greater, and observed nearest approach (meters) for simultaneous locations.

Year	Feral cat <i>i</i>	Fox <i>j</i>	BC	Nearest approach (m)	Coeff. <i>i</i> on <i>j</i>	<i>P</i>	Coeff. <i>j</i> on <i>i</i>	<i>P</i>
2016	MC536-16	FF369-16	0.41	100	-2.75	0.002*	-1.46	0.126
	MC536-16	MF734	0.42	198	-1.18	0.374	-3.28	0.026*
	MC536-16	FF825	0.44	171	-0.02	0.214	-0.04	0.564
2017	MC536-16	MF376	0.23	610	-2.00	0.582	0.37	0.781
	MC536-16	MF366	0.22	74	0.60	0.500	-0.27	0.894
	MC536-16	MF536	0.21	172	-0.58	0.736	4.23	0.005*
	FC489	FF369-17	0.69	296	-0.81	0.497	-87.20	0.248
	FC489	FF569-17	0.19	249	0.87	0.842	3.27	0.012*
	MC236	MF366	0.25	104	1.82	0.004*	-1.1	0.498
	MC236	FF369-17	0.59	758	-28.77	0.486	-2.16	0.559
	MC236	FF569-17	0.18	970	-6.09	0.522	-3.38	0.602
	MC729	FF569-17	0.94	42	-0.06	0.856	0.26	0.718
	MC729	FF369-17	0.19	2106	184.30	0.520	-	-
	MC729	FF767	0.24	358	-18.87	0.150	0.48	0.805

Note: This analysis includes both range-resident and non-sedentary individuals. Bold values are significant interactions, **P* < 0.05; ***P* < 0.01.

of ~2000–4000 ha for 16 months, then ranged over more than 120,000 ha in 29 d in the final year of the study. The most extreme case of ranging behavior was observed in male MC274 who roamed over more than 330,000 ha (MCP95) in 51 d and was 71 km from its point of release on day 20. This solitary-like behavior has been observed in feral cat populations in New Zealand (Recio and Seddon 2013). While feral cats in our study also maintained non-exclusive ranges, range-resident cats frequently came into close contact with each other (see later). In resource-rich urban areas, cats can form colonies and share resources throughout the year (Liberg et al. 2000). Away from urban environments, the nature of the range sharing relationship by the sexes in cats appears more complex and equivocal. In New Zealand, all pairings (σ : σ , σ : φ , φ : φ) were observed, but the extent of sharing was dependent on sex and season (Recio and Seddon 2013). In northern Australia, range overlap has been recorded in σ : σ and σ : φ pairings—being extensive in the latter and limited in the former (McGregor et al. 2015). We restricted our analyses of space use to individuals that were range-resident, and therefore, our sample is small. Nonetheless, in contrast to both aforementioned studies, we observed extensive overlap in the ranges of both σ : φ and σ : σ through spring and early summer (Table 9, Fig. 10).

Comparisons of space use with previous studies are made more difficult by several factors including varying periods of tracking, non-sedentary behaviors, and the different methods used to estimate home range. The frequency, duration, and accuracy of location fixes among studies vary greatly from one to several fixes per day that are separated by days or weeks (Edwards et al. 2001, Burrows et al. 2003), to hourly fixes for several consecutive weeks (Comer et al. 2018). The increase in frequency of location fixes reflects advances in telemetry and battery technologies, yet analyses of space use remain mostly unchanged—predominantly MCP and kernel density estimation (KDE)—the “workhorses” of home-range estimation. Both of these methods are biased by outliers and/or make assumptions of independence that increasingly do not apply to modern telemetry data sets (Fleming et al. 2015). The availability of methods to explicitly incorporate autocorrelated data structures into models of space use (Calabrese et al. 2016) and statistical means to identify individuals that are not range-resident (Fleming et al. 2014b) will facilitate more robust comparisons of space use (Noonan et al. 2019).

Sites of high visitation

We know of no similar analysis of recurrent site use identified from the movement trajectory

in either feral cats or foxes. In this study, sites of high visitation are shelter sites—dens or lairs—used during breeding or as refuge from extreme weather conditions. There is no obvious difference between foxes and cats in usage of high visitation sites. A similar portion of both species used such sites, 43% and 45% for foxes and cats, respectively. Male foxes (0.7 ± 0.9 [mean \pm SD], $n = 9$) had, on average, fewer high visitation sites than female foxes (1.2 ± 1.1 , $n = 12$). The reverse was true for feral cats, in which male cats (1.6 ± 2.5 , $n = 9$) had, on average, more high visitation sites than female feral cats (1.0 ± 1.4 , $n = 2$), although the sample of female cats is small. Post-analysis, we visited a subset of high visitation sites and found they were of three broad types: burrows dug into sandy soils, runs pushed under spinifex (*Triodia scariosa*), and piles of timber and sand adjacent to roads. In addition, foxes utilized lay-up sites under shrubs and feral cats used dense *Callitris* spp. stands—both of which provide deep shade. Our study area has hot summers and subfreezing conditions overnight in the winter, plus, there is no permanent water within the study area, except distant sources on adjacent properties. In addition to providing shelter for breeding females, such sites can buffer species against extreme heat, cold, humidity, or other stressors (Reside et al. 2019) and enable species to persist in a location (Kepel et al. 2012). Fidelity to shade sites has been reported in foxes in other arid environments (Macdonald et al. 1999), as have “temporary focal points” that cats and foxes use repeatedly over short periods (<7 d) before being vacated for a new area within their home range (Moseby et al. 2009).

Temporal activity as measured by camera traps

Overall, the temporal activity patterns of foxes and feral cat in this study are similar, both species being predominantly nocturnal, as has been described elsewhere (Van Rensburg 1986, Langham and Porter 1991, Travaini et al. 1993, Weber et al. 1994, Forsyth et al. 2014, Fancourt et al. 2019). However, feral cats are more diurnal in their activity patterns in winter (Fig. 7). This mirrors the findings of Geyle et al. (2020) in western Victoria, but contrasts with the results of Fancourt et al. (2019) that found little diurnal activity by feral cats during winter months. Elsewhere,

feral cat diel activity has also been shown to vary with seasonality (Wang and Fisher 2012). Our results suggest that feral cats are physiologically constrained during the hotter months and/or that there is a change in prey availability as the weather cools—causing them to switch prey or expend more time to secure sufficient food resources. There is considerable overlap in the diet of feral cats and foxes in Australia (Catling 1988, Risbey et al. 1999, Glen et al. 2011, Molsher et al. 2017), although feral cats are thought to prefer live prey (Dickman 1996b) and foxes have been shown to consume more carrion (Catling 1988). Reptiles are an important dietary component for cats in arid environments (Spencer et al. 2014, Doherty 2015), and while there is a diverse reptile fauna at Scotia (Roshier et al. 2020), they exhibit strong seasonality in the semiarid mallee region (Spence-Bailey et al. 2010) with suppressed activity during the cooler months of the year (Read and Moseby 2001, Roshier et al. 2020).

Dynamic interactions between individuals

The analyses of home range presented above show that, in terms of static interactions, foxes mostly maintain non-overlapping ranges, while cats occupy non-exclusive ranges and range over much larger areas. Given the large area over which some individuals range, there is no expectation that individuals with overlapping ranges are necessarily aware of the presence of others that pass through a location at a different time. We therefore restricted our analysis of dynamic interactions to dyads that had a range overlap of at least 0.10, as measured by Bhattacharyya coefficient, and additionally for cats to range-resident individuals only. Within both populations, observed significant interactions were all positive, including between- and same-sex interactions. In foxes, this attraction was mostly asymmetrical, while in cats, the attraction was mutual in all observed cases. It is worth noting that these asymmetrical interactions would not be detected using classic point-based dyad analyses that necessitate simultaneous fixes or path-based analyses that rely on correlation or cohesion of movement (Schlägel et al. 2019). The observed positive interactions in our study occurred against a background of mostly neutral interactions in foxes and only occurred in dyads

that shared a large proportion (>0.40) of their ranges, highlighting a level of spatial and social organization in foxes that is not evident in feral cats in this environment. Elsewhere, it has been observed that contacts between neighboring foxes occupying large ranges appear sporadic at most, despite the frequent encroachment of animals onto adjacent areas (Keenan 1981). In arid environments specifically, in contrast to our study, Macdonald et al. (1999) found considerable static overlap between the ranges of foxes from neighboring groups in Saudi Arabia and frequent contact between social groups, perhaps facilitated by the presence of additional food sources from urban areas.

In cats, dynamic interactions between individuals were strong when they occurred, being highly significant and shown to occur on a frequent basis over many weeks. Two of the three cat dyads shared only a third of their range and were observed to be as much as 9 km apart in the same weeks that they were also observed together (Fig. 10), suggesting a highly developed spatial and social awareness that may be facilitated by scent marking (Feldman 1994) or spatial memory (Fagan et al. 2013).

Models of competition and facilitation between co-occurring predators assume a level of interaction between species sufficient for the fitness of one to be enhanced or compromised (Prugh and Sivy 2020). Other researchers have noted the potential for competition and intraguild predation between foxes and feral cats (Molsher et al. 2017) given the high degree of dietary overlap between the two species (Catling 1988, Risbey et al. 1999, Glen et al. 2011), with the findings from several studies, suggesting that cats are likely subordinate to foxes (Catling and Burt 1995, Christensen and Burrows 1995, Read and Bowen 2001). Moreover, Molsher (1999) identified spatial segregation between cats and foxes, reporting mutually exclusive core home-range areas despite overlapping extended ranges. Molsher et al. (2017) also studied cat and fox interactions in an area free of dingoes using dietary analysis, activity indices, and telemetry on feral cats. These authors found no evidence of intraguild predation between the two species, but concluded that the red fox does affect some aspects of resource use by feral cats, noting modest shifts in the diet, range size, and habitat use

of cats following fox control (Molsher et al. 2017). By contrast, in the more arid landscapes of our study we found a large portion of the populations of both species is non-sedentary and intraspecific interactions between individuals are mostly brief or neutral despite sharing parts of their range. Among significant dynamic interactions in fox–cat dyads, observed nearest approach distances were further apart than for either foxes or cats separately and all interactions were asymmetrical. It is notable that all significant interspecific dynamic interactions in 2016 were negative (avoidance, $n = 2$), and in 2017, all interactions were positive (attraction, $n = 3$), suggesting a possible broad seasonal effect to how predator species interact—although the numbers are small.

CONCLUSIONS

Little is known about how mesopredators interact with each other in the absence of apex predators (Fancourt et al. 2015, Molsher et al. 2017). Taken together, our analyses provide a comprehensive insight into the spatial distribution, movement, and interactions of the red fox and feral cat in an environment free from apex predators and anthropogenic food sources. In the absence of these elements, the two introduced mesopredators showed large differences in how they distribute themselves across the landscape and interact with conspecifics. In our study, the red fox was found to mostly occupy defined territories, while most feral cats roam apparently independent of each other with occasional periods of frequent interaction with conspecifics of either sex. While interactions were shown to occur in a few fox–cat dyads, overall, we found no strong evidence that the activity patterns or distribution of either species was influenced by the presence of the other. As such, in the absence of higher-order predators, the extent of territories and ranges of both cats and foxes in this environment are likely determined by prey and shelter availability (Heithaus 2001) or intraspecific social dynamics.

A greater portion of the feral cats in this study were non-sedentary and therefore likely less amenable to local control efforts than foxes as a result of emigration and immigration from the area of control. Individual cats familiar with the

study area left for extended periods and returned up to 11 months later. Given the different patterns of distribution in time and space, the reliable monitoring of population trends or estimates of abundance will necessarily differ in extent, intensity, or duration for the same level of precision and/or require a different method for monitoring each population. Some methods of abundance estimation assume that survey sites are spatially independent, for example, N-mixture models (Royle 2004), while spatial capture–recapture and mark–resight methods (Borchers and Efford 2008, Royle et al. 2013) require redetection events of individuals between survey sites to estimate density. That is, the precision of all abundance estimation methods will be strongly influenced by the grain of the spatial array deployed to detect individuals in the population. Thus, knowledge of how foxes and feral cats distribute themselves in any particular environment is a prerequisite to reliable estimation of population densities.

Our study provides an analytical framework to quantify objectively the interactions between predators. Currently, there is growing interest in the role of apex predators in the restoration of ecosystems and the nature of interactions between different predator guilds (Allen et al. 2011, Ritchie et al. 2012). Foxes and cats are known to be disturbed and killed by dingoes (Moseby et al. 2012), but what is currently the subject of vigorous debate is whether the presence of the dingo affects the activity of these invasive mesopredators in a manner that will benefit the conservation of native species (cf. Johnson and VanDerWal 2009, Wallach and O'Neill 2009, Allen 2010, Allen et al. 2011, Schroeder et al. 2015, Cooke and Soriguer 2017, Morgan et al. 2017, Newsome et al. 2017a, Fancourt et al. 2019). The analytical framework presented here can readily be applied to landscapes with dingoes, foxes, and cats, and inform the current debate, and subsequently guide management options for introduced predators throughout Australia and elsewhere.

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