

Foxes at your front door? Habitat selection and home range of urban red foxes (*Vulpes vulpes*)

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Abstract

The red fox (*Vulpes vulpes*) is one of the most adaptable carnivorans, thriving in cities across the globe. Understanding movement patterns and habitat use by urban foxes will assist with their management to address wildlife conservation and public health concerns. Here we tracked five foxes across the suburbs of Perth, Western Australia. Three females had a core home range (50% kernel density estimate; KDE) averaging 37 ± 20 ha (range 22–60 ha) or a 95% KDE averaging 174 ± 130 ha (range 92–324 ha). One male had a core home range of 95 ha or a 95% KDE covering 352 ha. The other male covered an area of ~ 4 or ~ 6 times this: having a core home range of 371 ha or 95% KDE of 2,062 ha. All five foxes showed statistically significant avoidance of residential locations and significant preference for parkland. Bushland reserves, golf courses, and water reserves were especially preferred locations. Foxes moved quickest (i.e. commuting) when they were in close proximity to roads and slowest (i.e. foraging) when they were further from roads. We compare these findings with a review of the literature for urban fox home ranges. The movement patterns we describe are likely to be common for urban foxes, with half of the published home range estimates for urban foxes (principally based on VHF data) excluding data for 'lost' individuals or animals that showed 'excursions'. It is likely that the home range estimates for these urban exploiters have therefore been grossly underestimated to date. Further application of GPS trackers that allow remote download will vastly improve our understanding of the space use of urban foxes.

Introduction

The red fox (*Vulpes vulpes*) is one of the most adaptable mammal carnivores, with native and non-native populations across all continents except Antarctica. Its generalist ecology, with few specific habitat requirements and opportunistic use of a diverse range of foods (Forbes-Harper et al., 2017; Harris, 1981b; Reynolds and Tapper, 1995), has undoubtedly contributed to success of the red fox in urban landscapes (Bateman and Fleming, 2012). Around the world, red foxes have been reported in at least 114 cities (Soulsbury et al., 2010), supported by an abundance of anthropogenic resources (Bateman and Fleming, 2012). Some urban and peri-urban locations have very high fox densities. For example, in Melbourne (Victoria, Australia), up to 16 individuals·km⁻² have been recorded (Marks and Bloomfield, 1999), which is 2–5 times the densities recorded for rural areas of Victoria (Coman et al., 1991). In Bristol (UK), urban areas support fox densities of up to 20 or 37 individuals·km⁻² (Baker et al., 2001; Harris, 1981a).

Red foxes were introduced into Australia from Europe during the second half of the 19th century (Turner, 2017). Just as in parts of its native range, in Australia, the fox has actively colonised urban habitats (Soulsbury et al., 2010; Wilkinson and Smith, 2001) and has been recorded in six Australian cities (Soulsbury et al., 2010), including Perth, Western Australia (Fleming and Crawford, 2019). Urban fox management is a matter of concern across many parts of the globe, not only due to their predatory impact, but also due to risk of disease transmission and human and animal health. For example, a potentially fatal parasite of pet dogs, canine heartworm (*Dirofilaria immitis*), the larval stages of which are transmitted via mosquitoes, has been identified in foxes in Sydney and Melbourne (Marks and Bloomfield, 1998; Mulley and Starr, 1984). Urban foxes can also act as a definitive host for many zoonotic intestinal helminths, including *Echinococcus granulosus*, *Toxocara canis* and hookworms (Brochier et al., 2007; Fischer et al., 2005; Hofer et al., 2000; Jenkins and Craig, 1992) as well as viral diseases such as rabies (Rosatte and Allan, 2009; Rosatte et al., 1992). Understanding movements and habitat preference of urban foxes can, therefore, inform how they are managed for wildlife conservation as well as public health reasons (Pluemer et al., 2019).

Foxes require secluded and secure daytime rest sites in urban areas, and can have a number (two to five) of diurnal shelter sites used in each home-range, generally located in areas without human access, or where access is restricted to daylight hours (Baker et al., 2000; Marks and Bloomfield, 2006). Foxes make use of thickets of dense vegetation (Marks and Bloomfield, 2006; White et al., 2006), but novel artificial habitat is also used, including spaces beneath buildings (Harris and Rayner, 1986), drainage culverts (Marks and Bloomfield, 2006), or debris such as disused boiler units (Marks and Bloomfield, 2006) or abandoned car bodies (this study). Foxes also need natal den sites in which they leave young, and will generally dig earths (Harris and Rayner, 1986). Of 72 natal dens within a 20 km radius of the Melbourne GPO, burrows that had been dug by foxes were most common (92%), although rabbit warrens and artificial structures were also used.

Red foxes have an opportunist diet and readily exploit a diversity of high-nutrition food in human-modified landscapes (Bateman and Fleming, 2012; Contesse et al., 2004). In addition to items that rural foxes consume (i.e. small mammals, fruit, earthworms, etc.), urban foxes often rely heavily on scavenged anthropogenic food (Baker et al., 2000; Doncaster et al., 1990; Saunders et al., 1993). For example, in Zurich, over 50% of fox stomachs examined contained anthropogenic food and this increased from suburban to city centre zones (Contesse et al., 2004). Synanthropic rodents (house mice *Mus musculus* and rats, e.g. black rat *Rattus rattus*), and chicken coops provide important resources for foxes (Contesse et al., 2004), while many invasive and garden plants also provide easily sourced fruit (e.g. olives, figs, blackberries, mulberries, grapes) (Fleming and Crawford, 2019; Forbes-Harper et al., 2017). Even in more rural landscapes human

mediated food sources (orchard crops, livestock, introduced rodents) are utilised by foxes, with 97.4% of 230 scats analysed around the town of Bindoon, Western Australia containing anthropogenic sources of food (Dawson et al., 2016).

Home range analyses for red foxes have been carried out across the globe, with smaller home ranges in urban than rural locations (Main et al., 2020), presumably due to more reliable access to high quality food. But even within urban areas, there is a large degree of variability, with published home range sizes varying by orders of magnitude; between 3.6–460 ha (Table 1 and references therein). Understanding habitat selection would help understand the factors that contribute to this marked variability in space use. The aim of our study was, therefore, to investigate the home range and movement patterns of suburban red foxes in Perth, Western Australia.

Table 1
Global summary of home range (HR) studies for urban red foxes (*Vulpes vulpes*).

Method	Measure €	n, sex†	When tracked	Avg. time tracked	HR area (range); ha	Signals lost ¥	Country	Location	Same‡	Ref.
GPS	95% AKDE _c	5 (2M,3F)	both	102 d	1,626 ± 3,150 (92–7,257)		Australia	Perth		This study
GPS	95% KDE	17	both	2 y	198 ± 142 (76–623)		Australia	Sunshine Coast	a	(O'Connor et al., 2021)
GPS	95% KDE	6F	both		237 (82–623)		Australia	Sunshine Coast	a	(O'Connor et al., 2021)
GPS	95% KDE	5M	both		189 (84–415)		Australia	Sunshine Coast	a	(O'Connor et al., 2021)
VHF	MCP	11 (3M,6F,1m,1f)	evening	12–20 w	27 ± 12 (5.5–46)		Australia	Melbourne		(Marks and Bloomfield, 2006)
VHF	MCP	9 (6M,3F)	day = night	32 w	44.6 ± 13.2 (19.2–152.6)		Australia	Melbourne	bb	(White et al., 2006)
VHF	95% harmonic mean	9 (6M,3F)	day = night	32 w	23.9 ± 5.7 (11.6–63.5)		Australia	Melbourne	bb	(White et al., 2006)
VHF	MCP	2M,1F	most night	?	90 ± 36 (60–130)		Australia	Bendigo		(Coman et al., 1991)
VHF	KDE (Ranges)	10 (5M,5F)	night	~ 12 mo	325 ± 207 (114–718)	L(9)	Canada	Toronto	cc	(Rosatte and Allan, 2009)
VHF	KDE (Ranges)	18 (6m,12f)	night	~ 12 mo	165 ± 176 (21–541)	E	Canada	Toronto	cc	(Rosatte and Allan, 2009)
VHF	95% KDE	17	both	193 d	139 ± 86	L(8)	Germany	Starnberg	dd	(Janko et al., 2012)
VHF	MCP	17 (3M,3F,6m,5f)	both		76.6 ± 44.1	L(8)	Germany	Starnberg	dd	(Janko et al., 2012)
VHF	MCP	15M	most night	20 w	207 ± 146 (42–460)	L(7)	UK	Edinburgh	ee	(Kolb, 1984)

€ Measures of home range: AKDE_c autocorrelation corrected kernel density estimate, MCP minimum convex polygon, KDE kernel density estimate, Grid e estimate based on occupancy of a grid

† Caps adults or unknown; lowercase juveniles (where known).

¥ L signals lost (number of individuals); E 'excursions' excluded in estimating home range area.

‡ Potentially same animals (or same animals but different measure recorded).

Method	Measure €	n, sex†	When tracked	Avg. time tracked	HR area (range); ha	Signals lost ¥	Country	Location	Same‡	Ref.
VHF	MCP	9F,3f	most night	20 w	103 ± 50 (31–233)		UK	Edinburgh	ee	(Kolb, 1986)
VHF	SubjP	7F	?	4/5 mo	45.4 ± 6.9 (25.7–78.2)		UK	Bristol		(Harris, 1980)
VHF	MCP	9M	night	639 d	52	E,L	UK	Bristol		(Woollard and Harris, 1990)
VHF	MCP	3M	night	15 mo	33.9 ± 3.9	L(3)	UK	Bristol	ff	(Saunders et al., 1993)
VHF	MCP	3F	night	15 mo	25.9 ± 1.5		UK	Bristol		(Saunders et al., 1993)
VHF	MCP	8 (4M,2F,2f)	active	10 mo	36 ± 16 (17–70)		UK	Bristol		(White et al., 2006)
VHF	MCP	6M,6F	night	3 d	32.3 ± 19.1		UK	Bristol	gg	(Arnold et al., 2011)
VHF	MCP	5M,6F	night	3 d	20.8 ± 8.6		UK	Bristol	gg	(Arnold et al., 2011)
GPS	95% KDE	13 (7M,6F)	both	54 d	14.2 ± 3.26	L(1)	UK	Briton/Hove		(Tolhurst et al., 2020)
VHF	Grid e	17 (F,M)	night	319 d	93.4 ± 10.7 (41.8–197.8)	E	UK	Oxford	hh	(Doncaster and Macdonald, 1991)
VHF	Grid e	11 (4M,7F)	night	50 d	17.6 ± 0.2		UK	Oxford	hh	(Ward et al., 1997)
VHF	Grid e	29 (F,M)	night	320 d	54.3 ± 5.3 (14.7–107.3)	E	UK	Boar's Hill		(Doncaster and Macdonald, 1991)
VHF	MCP	4 (2M,2F)	both	5.3 mo	258 ± 139 (147–460)		USA	Newport News Park		(Rountree, 2004)
€ Measures of home range: AKDE _c autocorrelation corrected kernel density estimate, MCP minimum convex polygon, KDE kernel density estimate, Grid e estimate based on occupancy of a grid										
† Caps adults or unknown; lowercase juveniles (where known).										
¥ L signals lost (number of individuals); E 'excursions' excluded in estimating home range area.										
‡ Potentially same animals (or same animals but different measure recorded).										

Methods

Our study was approved by the Murdoch University Animal Ethics Committee (Permit number RW2612/13). We had approval to work under Scientific License Number U6 2014-2016 and worked in accordance with the Department of Primary Industries and Regional Development (DPIRD) Permit to trap a Vertebrate Pest (r45).

Animal capture and study sites

Tracking

Site selection was largely based on local knowledge. A three-week period trialling cage traps to capture foxes resulted in no captures, and therefore we moved to leg hold trapping. Padded jaw leg hold traps were set in vegetated areas that were likely to be attractive fox habitat where animals would be funnelled through a small space (e.g. along fences, around gaps in fences, adjacent to road underpasses). Traps were checked and cleared within 3 hours of sunrise and on days forecast to be over 30°C, traps were re-checked mid-morning to ensure that no animals were re-trapped after they had already been cleared.

Between December 2015 and July 2016, we captured and equipped six red foxes with ATS W500 Wildlink GPS logging collars (Advanced Telemetry Solutions Australia, Queensland, Australia). All foxes were caught using Victor Softcatch® #1.5 padded jaw leg hold traps (Woodstream Corporation, USA). Traps were buried just below ground level and positioned along game trails or in areas frequented by foxes and incorporated a scent (e.g. fox anal glands, urine) or visual (e.g. bird feathers, mammal fur) lure to entice foxes into the traps. Traps were checked once every 12 hours (i.e. early in the morning and late afternoon). A 1.5 m noose pole (Ketch-All, USA) was used to physically restrain trapped foxes and transfer them to a covered crush cage (W.A. Poultry Equipment & Coast to Coast Vermin Traps, Australia) for observation and holding before processing. Captured foxes were chemically immobilised using 0.14 mg/kg Medetomidine (Troy Laboratories, Australia) administered I.M. by hand injection. Once effectively immobilised, foxes were removed from the crush cage and examined for injuries. Sex for each animal was recorded, and the weight and morphometrics assessed to support visual estimates that all animals were in good body condition. During recumbency, body temperature, respiration and heart rate were monitored. GPS collars (Fig. 1) were only fitted to animals >4 kg body weight. Once collars were fitted, foxes were replaced into the covered crush cage and sedation was reversed by administering 0.4 mg/kg of Atipamezole (Troy Laboratories, Australia) I.M. by hand injection. Foxes were allowed to fully recover inside the covered crush cage for 15–20 min, prior to being transported and released at the site of capture. GPS collars were programmed to take 33 positions every 24 hours, with a focus of greater fix frequency during nocturnal times to capture fox roaming activity in more detail: 30 min fix interval between 18:00–08:00 h (28 location fixes daily), 60 min fix interval between 08:00–09:00 h and between 17:00–18:00 h (2 location fixes daily), and 120 min fix interval between 09:00–17:00 h (3 location fixes daily).

Location data was recovered from GPS collars remotely by radio tracking collared foxes via VHF signal to within approximately 200 m of their current den or rest site, before establishing a UHF connection to a portable base station which downloaded the location data from the collar. The metropolitan landscape in which foxes were collared resulted in significant interference to receiving and establishing both VHF and UHF signals, and as such remote download of location data from collars in the field was possible on only a few occasions. The majority of location data was retrieved when collared foxes were re-caught as part of ongoing City Council pest management operations.

Statistical analyses

Tracking

We used the 'rhr' package (Signer and Balkenhol, 2015) in R to estimate site fidelity for each individual. Site fidelity was determined based on suggested methods by Spencer et al. (1990), where site fidelity exists (and therefore the animal possesses a home range) if the observed area an animal uses is smaller than the area used if an individual's movement was random (Munger 1984). We then used three packages to calculate home range estimates. We used the 'rhr' (Signer and Balkenhol, 2015) and 'adehabitatHR' (Calenge, 2019) packages in R to calculate 50% and 95% kernel density home range estimates (KDE), and the 'ctmm' package in R to calculate the Autocorrelation-corrected Kernel Density Estimator AKDE_c (Calabrese et al., 2016; Fleming et al., 2015) for 50% and 95% kernels using the model of best fit to each individual's data and accounting for error using HDOP (horizontal dilution of precision) values (Fleming et al., 2020). Fox #1.FJ displayed a significant range shift and to accommodate AKDE_c analysis we subset the data to northern and southern home ranges using the 'segclust2d' package (Patin et al., 2018) using the home-range mode.

For habitat selection analyses, all GPS locations were compared with available geospatial databases, from which we extracted data for land use category (residential, industrial, parkland, transport corridors, water bodies, commercial/education facilities) (Geoscience Australia, 2018). We extracted the Euclidean distance to the nearest road (Main Roads Department of Western Australia, 2018). Each location was classified according to vegetation presence (Caccetta et al., 2012) ('veg_raw': classifies pixels into either 1=green growing vegetation, or 0=everything else), vegetation height ('vht_all': height of vegetation pixels relative to the ground in millimetres) and presence of grass ('grs_all': a mask of all the vegetation below 0.5 m in height) for each location by comparing with each animal sighting (Caccetta et al., 2012). We compared the proportion of fox locations in each land use category with expected proportions calculated for 1 km and 3 km radius buffers centred about the geometric median point of the animal's home range with Pearson's χ^2 analyses. For Fox #1.FJ, who

exploited a thin coastal reserve between his southern and northern home ranges, we divided his data into four sections and calculated potential land use categories for each of these sections for comparison with the observed data.

We estimated minimal speed of movement (m/h) from consecutive fixes (i.e. every 30 minutes overnight, every 2 h during daylight) by trigonometry and converted for differences in the fix schedules or missed data by calculating an hourly displacement as a surrogate of animal speed. Using the *glm* function in 'lme4' package in R (Bates et al., 2012), we carried out generalised linear regression analyses with speed as dependent variable and time of day (day 06:00 h-18:00 h or night 19:00 h-05:00 h), temperature (records from the collar), land use, distance to nearest road, whether the site was on a road reserve, grass presence, vegetation presence, and vegetation height as predictor variables. To identify which factors made the strongest contribution to model fit for each individual, a set of best-fit models was generated using combinations of predictor variables using the *dredge* function in the 'MuMIn' package (Barton and Barton, 2015) in R. We compared models using Akaike Information Criterion (AIC) (Burnham & Anderson, 2002) and calculated model weights (w_i) for each of the top models (DAIC<2). Each predictor variable was mean-standardised, allowing calculation of standardised β values, but raw values were also calculated to evaluate effects for each individual variable (where the other variables were held constant) using *ggemmeans* in the 'ggeffects' package (Lüdtke, 2018) in R. Model assumptions were checked and final models were validated by examining the residuals using the 'DHARMA' package (Hartig, 2020) in R. Values are presented as means \pm 1SD.

Results

The five foxes were tracked for an average of 102 ± 81 (range 25–226) days (Table 2). Four individuals had stationary home ranges and showed site fidelity using both the linearity index and the mean squared distance from the centre of activity. Two individuals did not show site fidelity (#1.FJ, #3.ES). Female #3.ES moved her core activity area mid-way through the monitoring period and was found dead after 1 month, away from the centre of her previous home range. Male #1.FJ was tracked for the longest and across the greatest distance and showed a distinct range shift from a southern to a northern home range, making extensive use of a narrow coastal reserve to move north-south (Fig. 2) for at least part of the tracking period.

Table 2. Summary of the tracking data for five red foxes (*Vulpes vulpes*) tracked with GPS collars across the metropolitan area of Perth, Western Australia.

ID	Sex	Dates	Days	2016												# independent points	Distance moved		AKDE, Home range area (range); ha			Obvious movements*
				D	J	F	M	A	M	J	J	A	Total (km)	Average (km/day)	50%		70%	95%				
#1.FJ	M	20/12/2015–2/8/2016	226												7,499	2,504	11.08	1,598 (1,323–1,897)	2,864 (2,372–3,401)	7,257 (6,011–8,618)	ES (many)	
" south		20/12/2015–22/07/2016	215												1,577	389	-	391 (289–509)	762 (562–992)	2,276 (1,679–2,962)		
" north		28/01/2016–02/08/2016	187												6,010	2,104	-	351 (314–389)	681 (611–755)	1,847 (1,657–2,048)		
#3.HX	M	26/2/2016–15/7/2016	140												569	62	0.44	95 (64–132)	159 (107–220)	352 (238–488)	E	
#2.ES	F	15/1/2016–15/7/2016	60												1,650	54	0.89	60 (29–100)	119 (59–200)	324 (160–545)	ES	
#4.CC	F	4/6/2016–2/8/2016	59												897	157	2.66	30 (26–33)	49 (44–55)	105 (93–116)		
#5.DB	F	8/7/2016–2/8/2016	25												559	74	2.96	22 (18–26)	39 (32–47)	92 (75–110)		

*Movements obvious in GPS data: E excursions, S shifts.

All GPS location data used in analyses had a horizontal dilution of precision (HDOP) of < 3, and were therefore considered to be reliable estimates of location. Using these data to calculate autocorrelated-corrected home ranges, the three females had a core home range (50% kernel) averaging 37 ± 20 ha (range 22–60ha) or a 95% kernel averaging 174 ± 130 ha (range 92–324 ha) (Table 2). Male #3.HX had a core home range of 95 ha or a 95% kernel covering 352 ha and largely remained within a bushland reserve, only occasionally moving along road reserves or exploring adjacent industrial properties. By contrast, male #1.FJ covered an area ~ 4 or ~ 6 times this: having a core home range of 371 ha or 95% kernel of 2,062 ha (the average of area estimates for the northern and southern parts of his home range estimated separately). He frequently moved between locations, remaining around core patches for days or weeks before moving again. This animal travelled a minimum of 2,500 km in the 7.5 months it was tracked, covering a total area (95%AKDE_c) of 7,257 ha (CI 6,011–8,618 ha).

These movements were not dispersal movements, because he regularly retraced his tracks. Instead, they conform to the definition of shifts (sensu Cavallini, 1996), where the animal moved between activity centres. He regularly travelled many kilometres overnight to return to a previously-used diurnal rest site. Sighting of this animal on camera trap (Fig. 3c) around a wetland where 13 swans had been found beheaded showed that he was in excellent condition. He was eventually trapped as part of pest animal control (after the collar battery life had expired) and euthanised.

There was a strong correlation between the three methods of home range assessment used, although we found that AKDE_c yielded values that were 5–104% greater than adehabitatHR or rhr for the two animals that moved during the study period (#1.FJ and #3.ES) compared with values that were 17% smaller than adehabitatHR or rhr for the other three animals (Table 3).

Table 3. Summary of home range area estimates, calculated using three statistical methods, for five red foxes (*Vulpes vulpes*) tracked with GPS collars across the metropolitan area of Perth, Western Australia.

Sex	Fox	Home range area (ha)						adehabitathR vs AKDEc	rhr vs AKDEc
		adehabitathR		rhr		Autocorrelation-corrected (CTMM)			
		50%KDE	95% KDE	50% KDE	95% KDE	50% AKDEc	95% AKDEc		
Males	#1.FJ	742	5,532	936.4	4,618.40	1,598	7,257	31%	57%
	south	289	2,176	315	2073.2	391	2,276	5%	10%
	north	209	1,734	284.4	1628.7	351	1,847	7%	13%
Females	#3.HX	90	400	98.9	437.3	95	352	-12%	-20%
	#2.ES	14	159	23.9	187.2	60	324	104%	73%
	#4.CC	24	115	24.1	123.2	30	105	-9%	-15%
	#5.DB	25	109	23.9	130.2	22	92	-16%	-29%

Compared with the land use categories present in a 1 km and 3 km radius buffers centred about the geometric median point of the animal's home range, all five foxes showed statistically significant avoidance of residential locations and significant preference for parkland (Table 4). Bushland reserves, golf courses, and water reserves were especially preferred locations. Four golf courses were used by two individuals (Fig. 4), where their activities were focussed around the native vegetation between the greens. Waterbodies were also preferred sites (Fig. 3) where foxes were recorded consuming waterbirds during the course of this study (Jo Taylor, City of Stirling).

Table 4. Percentage of area available across different land use categories within a 1 km and 3 km radius centred about the geometric median point of the animal's home range compared with the percentage of location datapoints ('used') for five red fox individuals. Foxes show a significant preference for parkland ('used'; green), and significant avoidance of residential areas ('avoided'; orange).

Land use category	Males #1.FJ*			#3.HX			Females #2.ES			#4.CC			#5.DB		
	1km	3km	%	1km	3km	%	1km	3km	%	1km	3km	%	1km	3km	%
Residential	57	67	3	38	59	0	55	60	44	65	77	2	68	78	1
Parkland	37	21	87	43	20	99	19	25	81	19	17	61	24	15	96
Industrial		6	0	15	11	1	13	7	0						
Education	2	3	0	3	5	0	3	0	0	10	4	13	6	4	2
Transport	-0.5	1	1				13	2	14	ns					
Commercial	-0.5	2	0	4	0	0	2	0	0	4	2	18	2	0	0
Water	4	<0.5	9				1	1	-						
Hospital/Medical		<0.5	0												
Other										2		6			

* summed across four locations across total home range for #1.FJ.

blanks indicate absence of that land use category (<10 incidents) within the 1 km and 3 km radius buffers centred about the geometric median point of the animal's home range.

Significance values are for χ^2 tests comparing percentages for used with available data: - insufficient data for statistical analysis, ns not statistically significant, * p<0.05, ** P<0.01, *** P<0.001.

Blue shading represents land use categories available, with the darkest colouring representing the most common. Green colouring represents significant preference for a particular land use category by a fox individual; orange colouring represents significant avoidance of that particular land use category.

A summary of the modelling of describing speed of movements (minimum displacement distance between consecutive locations) for each fox is shown in Fig. 5. All five foxes showed a significant effect of time of day (day/night) on speed, remaining reasonably immobile during daylight hours. The inclusion of collar temperature improved model fit, reinforcing that foxes only moved overnight, when temperatures were lowest (shown for one individual in Fig. 6a). The two males (#1.FJ and #3.HX) showed a *time of day x distance to road* interaction term, moving fastest (i.e. commuting) when they were in close proximity to the roads and slowest (i.e. foraging) when they were further from the road (Fig. 6b). Fox #4.CC showed overall faster movement when closer to the roads. Foxes #1.FJ and #5.DB were significantly slower when moving through vegetated areas, but showed a positive relationship with vegetation height, suggesting that they were more likely foraging amongst lower vegetation than tall canopy. Foxes #2.ES and #3.HX moved significantly slower when located on grassed areas. There were few data for land use that was not parkland, and therefore the effect of land use on speed of movement was not significant for any of the foxes. Fox #2.ES showed faster movements around water bodies (but there were very few datapoints for this female. Fox #5.DB showed fastest speed around residential areas and slower around parkland (compared with the baseline of education land use). Fox #3.HX showed faster movement around road reserves and slowest movements across parkland.

Discussion

Red foxes in urban Perth showed significant preference for urban parkland and significant avoidance of residential areas. Home range estimates for four individuals tracked were reasonably consistent with some of the larger published values for red foxes (Table 1), but one of the animals we tracked covered an enormous distance, far greater than previous estimates of home range for urban foxes. We also noted that individuals with larger home ranges moved faster when they were in proximity to roads.

Comparison with published urban fox home range studies

Our largest home range estimate (7,257 [6,011–8,618] ha or 72 km²) stands out from the remaining data. This is partly due to the shape of the home range, with this fox using a narrow 25 km-long north-south coastal reserve. We applied a range of home range estimators, but all methods yielded similarly large values for this animal. Even segmenting the home range to a southern and northern distribution provided estimates up to an order of magnitude larger than the other foxes tracked. The average home range across 16 urban fox studies we reviewed was 86 ha, with a maximum of 718 ha recorded for a fox in urban Toronto, Canada (Rosatte and Allan, 2009) (Table 1). However, foxes are capable of using larger home ranges. In a study tracking 52 foxes across Sweden and Norway using GPS collars, Walton et al. (2017) reported three fox home ranges located in their three southern study areas – where there was greater incidence of agriculture and anthropogenic disturbance – were larger than 10 km² (90% LoCoH-k, n = 44), whilst in their northern study area all, bar one, fox home ranges were larger than 10 km² (90% LoCoH-k, average 1,950 ± 1,180 ha, n = 8). Similarly in Toronto, Canada, Rosatte and Allan (2009) reported a juvenile male fox that dispersed twice and did not settle down, resulting in an annual range of 18,285 ha (182.9 km²) (data excluded from their calculation of home range analysis).

'Excursions' beyond the normal home range may represent exploration preceding natal dispersal. Of nine foxes in Bristol, UK, six were recorded making exploratory trips prior to dispersal (Woollard and Harris, 1990). These trips, lasting one night to one week, were made to areas that were never revisited, and exploratory trips were also carried out by foxes that did not eventually disperse. Disappearances and excursions were also recorded for non-dispersing animals, for example, by males searching for a mate, or directed towards specific food sources by lactating vixens (Niewold, 1980). In a review of fox home ranges, Cavallini (1996) recorded a fraction of the red fox population acting as 'transient', 'nomadic' or 'floating', and recognised that few authors report information about these animals because they were difficult to follow and study (Lovari et al., 1994; Zabel and Taggart, 1989; Zimen, 1984).

Published home range and space use calculations derived from VHF tracking are highly likely to have underestimated fox home ranges. Six (of 15) published urban fox studies using VHF collars reported issues with lost signals (Table 1). While some are due to transmitter or receiver malfunction, missing data is likely to reflect times when the animal moved beyond the receiver range. For example, Kolb (1984) noted that 7 of 15 foxes tracked with VHF 'disappeared' and long distance unpredictable 'expeditions' away from their home ranges were reported on numerous occasions. Also, Marks and Bloomfield (2006) fitted 20 foxes with VHF collars, but insufficient data were collected from nine foxes to permit reliable home-range estimates; only their daytime positions and diurnal shelter locations could be analysed for home range estimates. Half the published home range estimates have similarly ignored data for animals that moved beyond receiver range or excluded 'excursions' in estimating average ranges (Table 1). The description of methods for the remaining studies do not indicate how excursions or lost signals were handled.

A study comparing the home ranges of 10 VHF- and 3 GPS-tracked red foxes indicated that the GPS data revealed home ranges around 10 times larger than those derived from VHF technology (Towerton et al., 2016). Using GPS trackers, Hradsky et al. (2017) recorded home range estimates between 33 to >2,500 ha in a predominately forested landscape and this technology enabled tracking of foxes that 'commuted' more than 5 km between daytime refuge and farmland or towns at night. GPS tracking has also revealed substantially longer dispersal distances for red foxes than had been reported previously, with distances of 132–1,036 km recorded and cumulative distances moved five times longer than straight-line distances (recorded using fewer data points, such as collected through VHF) (Walton et al., 2018). These findings reinforce the value of fine-scale temporal position data in revealing aspects of the biology of tracked animals.

The GPS devices we used required proximity to download data remotely but we were successful only three times for #1.FJ and only once each for the other four animals. It would have been informative to have had seasonal data for our animals to determine whether there were changes in space use over the year. Such questions may be achievable with satellite technology that do not rely on base station downloads. Analytical methods will also result in a difference in home range area estimates. We found differences in home range area estimates using different statistical methods. Compared with estimates that ignore temporal autocorrelation, the use of autocorrelation-corrected analysis yields larger home range estimates for animals that move across their home range over a matter of hours or days.

Habitat preference

Foxes show preference for parkland over built-up urban spaces

Perth foxes preferentially used parkland and water reserves. Marks and Bloomfield (2006) report that 61% of natal dens used by 20 tracked foxes in Melbourne were in secluded places where public access was restricted, including schools, cemeteries, industrial and commercial lands, fenced parks, sporting clubs and lands maintained by the National Trust, councils, port authorities and areas maintained by the Commonwealth Government where public entry was prohibited. To this list of preferred locations, we add coastal reserves and golf

courses. O'Connor et al., (2021) similarly report extensive use of coastal reserves at the Sunshine Coast, Queensland, Australia. These reserves provide extensive linear connectivity and there is likely to be minimal disturbance from people over night. Similarly, golf courses are usually quiet at night, with little disturbance, while some golf courses also support potential prey, such as introduced European rabbit (*Oryctolagus cuniculus*) or waterbird populations. Similarly, Rosatte and Allan (2009) reported that half the foxes for which they had sufficient data (14/28 foxes) made extensive use of golf courses in Toronto, and Kolb (1984) noted that 75% of locations for one male fox in Edinburgh, UK were on a golf course.

Foxes avoid residential areas

Red foxes have an opportunist diet and exploit many anthropogenic food sources, and are regarded as well-adapted to urban areas. We were therefore surprised to observe that the tracked foxes showed strong avoidance of residential areas, and when they did pass through such areas, it was often when travelling rapidly between foraging areas. Similar avoidance of high human densities has been found for foxes in Toronto, Canada (Adkins and Stott, 1998) and in Virginia, USA (Rountree, 2004). By contrast, regular exploitation of gardens has been recorded in Bristol, UK, where foxes visited gardens where they were most frequently provided with food by residents (Dorning and Harris, 2017).

Foxes are likely to be avoiding people, but they may also be showing an aversion to pet dogs (*Canis familiaris*). Marks and Bloomfield (2006) noted that natal dens around Melbourne were more likely to be associated with properties that did not contain domestic dogs, while O'Connor et al. (2021) noted antagonistic behaviour by domestic dogs towards foxes on camera traps positioned around dens. We found foxes using sites with more cover, but in North America where they co-exist with coyotes, which prefer natural vegetation, foxes avoid these locations and select for more open areas (Mueller et al., 2018), or show no specific habitat preference (Pluemer et al., 2019). The habitat preference of foxes could therefore reflect the probability of encountering other canids and is likely to vary between sites accordingly.

Foxes avoid urban roads

The two male foxes we tracked, which moved beyond the boundaries of a single urban reserve, avoided roads or sped up when they were in proximity to roads. We also noted that home ranges appeared to be bounded by roads. Some of these roads were busy highways, which could be acting as barriers to movements; however, many roads were small residential streets that would have minimal traffic. Roads may therefore form natural boundaries to territorial foxes.

Roadstrike is a leading cause of mortality for red foxes in the UK and USA (Gosselink et al., 2007; Harris, 1981a; Harris and Smith, 1987; Lewis et al., 1993; Soulsbury et al., 2007). In Bristol, UK, there is evidence that foxes change their activity patterns, avoiding roads prior to midnight when traffic volume is greater (Baker et al., 2007). Road death is likely to be biased towards individuals that disperse further, e.g. males and juveniles (Baker et al., 2007), and resident animals occupying high quality sites may therefore avoid using roads where possible. Rather than using roads, quieter corridors such as railway and road reserves (Lewis et al., 1993; Rosatte and Allan, 2009), ravines associated with waterways (Rosatte and Allan, 2009) or coastal reserves (this study) provide important access and are therefore important focal points to target for management.

Management implications of this study

As is likely for cities across the world, Perth fox populations are controlled on an *ad hoc* basis by pest management services contracted to Shire or City Councils. Implementation of control measures is costly, limiting the scope of control and therefore its success. Furthermore, control measures necessarily require live trapping to avoid risk to stray and domestic pets, and this requires local knowledge of the home ranges and dispersal patterns. Sound understanding of how foxes use resources and habitat across the urban landscape should assist with targeting management to improve success in controlling populations of this cryptic predator.

Conclusions

The difficulties of tracking animals across private property in urban landscapes has been particularly challenging. Improvements in tracking technology have a great deal of value in revealing how urban exploiters adapt to these landscapes. Robust data for locations and regular time sampling through GPS tracking are likely to confirm that we have been vastly underestimating the movements of urban foxes. Understanding the movement patterns of these cryptic carnivores will benefit management for wildlife conservation and disease transmission.

Declarations

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Conflicts of interest: None.

Availability of data and material: data available from movebank.org.

Code availability: Not applicable.

Author's contribution: HK spatial data analysis and manuscript writing, ES and PA fieldwork, data analysis and manuscript writing, PB data analysis and manuscript writing, JS data analysis and manuscript writing, PF original design of the study and manuscript writing.

Ethics approval

Our study was approved by the Murdoch University Animal Ethics Committee (Permit number RW2612/13). We had approval to work under Scientific License Number U6 2014-2016 and worked in accordance with the Department of Primary Industries and Regional Development (DPIRD) Permit to trap a Vertebrate Pest (r45).

References

- Adkins, C.A., Stott, P., 1998. Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada.
- Arnold, J., Soulsbury, C.D., Harris, S., 2011. Spatial and behavioral changes by red foxes (*Vulpes vulpes*) in response to artificial territory intrusion. *Can. J. Zool.* 89, 808-815.
- Baker, P., Newman, T., Harris, S., 2001. Bristol's foxes - 40 years of change. *British Wildlife* 12, 411-417.
- Baker, P.J., Dowding, C.V., Molony, S.E., White, P.C.L., Harris, S., 2007. Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behav. Ecol.* 18, 716-724.
- Baker, P.J., Funk, S.M., Harris, S., White, P.C.L., 2000. Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Anim. Behav.* 59, 127-146.
- Barton, K., Barton, M.K., 2015. Package 'MuMIn' Version 1.43.17.
- Bateman, P.W., Fleming, P.A., 2012. Big city life: carnivores in urban environments. *J. Zool., Lond.* 287, 1-23.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., 2012. Package 'lme4', CRAN. R Foundation for Statistical Computing, Vienna, Austria.
- Brochier, B., De Blander, H., Hanosset, R., Berkvens, D., Losson, B., Saegerman, C., 2007. *Echinococcus multilocularis* and *Toxocara canis* in urban red foxes (*Vulpes vulpes*) in Brussels, Belgium. *Prev. Vet. Med.* 80, 65-73.
- Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edn. Springer, Berlin.
- Caccetta, P., Collings, S., Devereux, A., Hingee, K., McFarlane, D., Traylen, A., Wu, X., Zhou, Z., 2012. Urban Monitor: Enabling effective monitoring and management of urban and coastal environments using digital aerial photography; Final Report – Transformation of aerial photography into digital raster information product. CSIRO, Australia.
- Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution* 7, 1124-1132.
- Calenge, C., 2019. Home range estimation in R: the adehabitatHR package.
- Cavallini, P., 1996. Variation in the social system of the red fox. *Ethology Ecology & Evolution* 8, 323-342.

- Coman, B.J., Robinson, J., Beaumont, C., 1991. Home range, dispersal and density of red foxes (*Vulpes vulpes* L.) in central Victoria. *Wildl. Res.* 18, 215-223.
- Contesse, P., Hegglin, D., Gloor, S., Bontadina, F., Deplazes, P., 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm. Biol.* 69, 81-95.
- Dawson, S.J., Crawford, H.M., Huston, R.M., Adams, P.J., Fleming, P.A., 2016. How to catch red foxes red handed: identifying predation of freshwater turtles and nests. *Wildl. Res.* 43, 615-622.
- Doncaster, C.P., Dickman, C.R., MacDonald, D.W., 1990. Feeding ecology of red foxes (*Vulpes vulpes*) in the city of Oxford, England. *J. Mammal.* 71, 188-194.
- Doncaster, C.P., Macdonald, D.W., 1991. Drifting territoriality in the red fox *Vulpes vulpes*. *J. Anim. Ecol.* 60, 423-439.
- Dorning, J., Harris, S., 2017. Dominance, gender, and season influence food patch use in a group-living, solitary foraging canid. *Behav. Ecol.* 28, 1302-1313.
- Fischer, C., Reperant, L.A., Weber, J., Hegglin, D., Deplazes, P., 2005. *Echinococcus multilocularis* infections of rural, residential and urban foxes (*Vulpes vulpes*) in the canton of Geneva, Switzerland. *Parasite* 12, 339-346.
- Fleming, C.H., Drescher-Lehman, J., Noonan, M.J., Akre, T.S.B., Brown, D.J., Cochrane, M.M., Dejid, N., DeNicola, V., DePerno, C.S., Dunlop, J.N., 2020. A comprehensive framework for handling location error in animal tracking data. *bioRxiv*.
- Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96, 1182-1188.
- Fleming, P.A., Crawford, H.M., 2019. Invasive predators in urban bushland – corridors and cover for conservation, in: Lambers, H. (Ed.), *A jewel in the crown of a global biodiversity hotspot*. Kwongan Foundation and the Western Australian Naturalist Club, Perth, Western Australia.
- Forbes-Harper, J.L., Crawford, H.M., Dundas, S.J., Warburton, N.M., Adams, P.J., Bateman, P.W., Calver, M.C., Fleming, P.A., 2017. Diet and bite force in red foxes: ontogenetic and sex differences in an invasive carnivore. *J. Zool., Lond.* 303, 54-63.
- Geoscience Australia, 2018. Digital Topographic Maps.
- Gosselink, T.E., Van Deelen, T.R., Warner, R.E., Mankin, P.C., 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. *J. Wildl. Man.* 71, 1862-1873.
- Harris, S., 1980. Home ranges and patterns of distribution of foxes (*Vulpes vulpes*) in an urban area, as revealed by radio tracking, in: Amlaner, C.J., Macdonald, D.W. (Eds.), *A Handbook on Biotelemetry and Radiotracking*. Elsevier, Oxford, UK, pp. 685-690.
- Harris, S., 1981a. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *J. Appl. Ecol.* 18, 455-465.
- Harris, S., 1981b. The food of suburban foxes (*Vulpes vulpes*), with special reference to London. *Mamm. Rev.* 11, 151-168.
- Harris, S., Rayner, J.M.V., 1986. Urban fox (*Vulpes vulpes*) population estimates and habitat requirements in several British cities. *J. Anim. Ecol.* 55, 575-591.
- Harris, S., Smith, G.C., 1987. Demography of two urban fox (*Vulpes vulpes*) populations. *J. Appl. Ecol.* 24, 75-86.
- Hartig, F., 2020. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models, version 0.3.3.0 ed. R package.
- Hofer, S., Gloor, S., Muller, U., Mathis, A., Hegglin, D., Deplazes, P., 2000. High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zurich, Switzerland. *Parasitology* 120, 135-142.
- Hradsky, B.A., Robley, A., Alexander, R., Ritchie, E.G., York, A., Di Stefano, J., 2017. Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes*. *Sci. Rep.* 7, 12291.

- Janko, C., Schröder, W., Linke, S., König, A., 2012. Space use and resting site selection of red foxes (*Vulpes vulpes*) living near villages and small towns in Southern Germany. *Acta Theriologica* 57, 245-250.
- Jenkins, D. J., and Craig, N. A., 1992. The role of foxes *Vulpes vulpes* in the epidemiology of *Echinococcus granulosus* in urban environments. *Medical Journal of Australia* 157, 754-756.
- Kolb, H.H., 1984. Factors affecting the movements of dog foxes in Edinburgh. *J. Appl. Ecol.* 21, 161-173.
- Kolb, H.H., 1986. Some observations on the home ranges of vixens (*Vulpes vulpes*) in the suburbs of Edinburgh. *J. Zool., Lond.* 210, 636-639.
- Lewis, J.C., Sallee, K.L., Golightly, R.T.J., 1993. Introduced red fox in California, Nongame Bird and Mammal Section Report. The Resources Agency, State of California. Department of Fish and Game, Wildlife Management Division, p. 74.
- Lovari, S., Valier, P., Lucchi, M.R., 1994. Ranging behaviour and activity of red foxes (*Vulpes vulpes*: Mammalia) in relation to environmental variables, in a Mediterranean mixed pinewood. *J. Zool., Lond.* 232, 323-339.
- Lüdecke, D., 2018. ggeffects: Tidy data frames of marginal effects from regression models. *J. Open Source Software* 3, 772.
- Main, M.T., Davis, R.A., Blake, D., Mills, H., Doherty, T.S., 2020. Human impact overrides bioclimatic drivers of red fox home range size globally. *Div. Dist.* 26, 1083-1092.
- Main Roads Department of Western Australia, 2018. Road Network.
- Marks, C.A., Bloomfield, T.E., 1998. Canine heartworm (*Dirofilaria immitis*) detected in red foxes (*Vulpes vulpes*) in urban Melbourne. *Vet. Parasitol.* 78, 147-154.
- Marks, C.A., Bloomfield, T.E., 1999. Distribution and density estimates for urban foxes (*Vulpes vulpes*) in Melbourne: Implications for rabies control. *Wildl. Res.* 26, 763-775.
- Marks, C.A., Bloomfield, T.E., 2006. Home-range size and selection of natal den and diurnal shelter sites by urban red foxes (*Vulpes vulpes*) in Melbourne. *Wildl. Res.* 33, 339-347.
- Mueller, M.A., Drake, D., Allen, M.L., 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. *PLoS one* 13, e0190971.
- Mulley, R.C., Starr, T.W., 1984. *Dirofilaria immitis* in red foxes (*Vulpes vulpes*) in an endemic area near Sydney, Australia. *J. Wildl. Dis.* 20, 152-153.
- Munger, J. C. 1984. Home ranges of horned lizards (*Phrynosoma*): circumscribed and exclusive? *Oecologia* (Berlin) 62:351-360.
- Niewold, F.J.J., 1980. Aspects of the social structure of red fox populations: a summary, in: Zimen, E. (Ed.), *Biogeographica - The Red Fox*. Springer, Dordrecht, pp. 185-193.
- O'Connor, J. M., Srivastava, S. K., Brunton, E. A., and Burnett, S. E., 2021. Urban fringe dweller: the European red fox (*Vulpes vulpes*) in an urban coastal ecosystem. *Australian Journal of Zoology*, <https://doi.org/10.1071/ZO20069>
- Patin, R., Etienne, M.P., Lebarbier, E., Benhamou, S., 2018. segclust2d: bivariate segmentation/clustering methods and tools. R package version 0.2.0.
- Pluemer, M., Dubay, S., Drake, D., Crimmins, S., Veverka, T., Hovanec, H., Torkelson, M., Mueller, M., 2019. Red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) in an urban landscape: prevalence and risk factors for disease. *J Urban Ecol.* 5, juz022.
- Reynolds, J.C., Tapper, S.C., 1995. The ecology of the red fox *Vulpes vulpes* in relation to small game in rural southern England. *Wildl. Biol.* 1, 105-119.
- Rosatte, R., Allan, M., 2009. The ecology of red foxes, *Vulpes vulpes*, in metropolitan Toronto, Ontario: disease management implications. *The Canadian Field-Naturalist* 123, 215-220.

- Rosatte, R.C., Power, M.J., Machines, C.D., Campbell, J.B., 1992. Trap-vaccinate-release and oral vaccination for rabies control in urban skunks, raccoons and foxes. *J. Wildl. Dis.* 28, 562-571.
- Rountree, G.H., 2004. Comparative study of the home range and habitat usage of red foxes and gray foxes in an urban setting: a preliminary report, in: Shaw, W.W., Harris, L.K., L, v.D. (Eds.), *Proc. 4th International Urban Wildlife Symposium*, pp. 238-244.
- Saunders, G., White, P.C.L., Harris, S., Rayner, J.M.V., 1993. Urban foxes (*Vulpes vulpes*): food acquisition, time and energy budgeting of a generalized predator. *Symposia of the Zoological Society of London* 65, 215-234. Cited by Baker et al. 2000.
- Signer, J., Balkenhol, N., 2015. Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildl. Soc. Bull.* 39, 358-363.
- Soulsbury, C.D., Baker, P.J., Iossa, G., Harris, S., 2010. Red foxes (*Vulpes vulpes*), in: Gehrt, S.D., Riley, S.P.D., Cypher, B.L. (Eds.), *Urban carnivores*. The John Hopkins University Press, Baltimore, pp. 63-75.
- Soulsbury, C.D., Iossa, G., Baker, P.J., Cole, N.C., Funk, S.M., Harris, S., 2007. The impact of sarcoptic mange *Sarcoptes scabiei* on the British fox *Vulpes vulpes* population. *Mamm. Rev.* 37, 278-296.
- Spencer, S. R., Cameron, G. N., and Swihart, R. K. 1990. Operationally defining home range: temporal dependence exhibited by Hispid Cotton Rats. *Ecology* 71, 1817-1822.
- Tolhurst, B.A., Baker, R.J., Cagnacci, F., Scott, D.M., 2020. Spatial aspects of gardens drive ranging in urban foxes (*Vulpes vulpes*): The Resource Dispersion Hypothesis revisited. *Animals* 10, 1167.
- Towerton, A.L., Kavanagh, R.P., Penman, T.D., Dickman, C.R., 2016. Ranging behaviour and movements of the red fox in remnant forest habitats. *Wildl. Res.* 43, 492-506.
- Turner, D.C., 2017. A review of over three decades of research on cat-human and human-cat interactions and relationships. *Behav. Proc.* 141, 297-304.
- Walton, Z., Samelius, G., Odden, M., Willebrand, T., 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS one* 12, e0175291.
- Walton, Z., Samelius, G., Odden, M., Willebrand, T., 2018. Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking. *Eur. J. Wildl. Res.* 64, 64.
- Ward, J.F., MacDonald, D.W., Doncaster, C.P., 1997. Responses of foraging hedgehogs to badger odour. *Anim. Behav.* 53, 709-720.
- White, J.G., Gubiani, R., Smallman, N., Snell, K., Morton, A., 2006. Home range, habitat selection and diet of foxes (*Vulpes vulpes*) in a semi-urban riparian environment. *Wildl. Res.* 33, 175-180.
- Wilkinson, D., Smith, G.C., 2001. A preliminary survey for changes in urban Fox (*Vulpes vulpes*) densities in England and Wales, and implication for rabies control. *Mamm. Rev.* 31, 107-110.
- Woollard, T., Harris, S., 1990. A behavioural comparison of dispersing and non-dispersing foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypotheses. *J. An. Ecol.* 59, 709-722.
- Zabel, C.J., Taggart, S.J., 1989. Shift in red fox (*Vulpes vulpes*) mating system associated with El Niño in the Bering Sea. *An. Behav.* 38, 830-838.
- Zimen, E., 1984. Long range movements of the red fox, *Vulpes vulpes* L. *Acta Zoologica Fennica* 171, 267-270.

Figures



Figure 1

Attaching a collar to a red fox (*Vulpes vulpes*) in Perth, Western Australia.

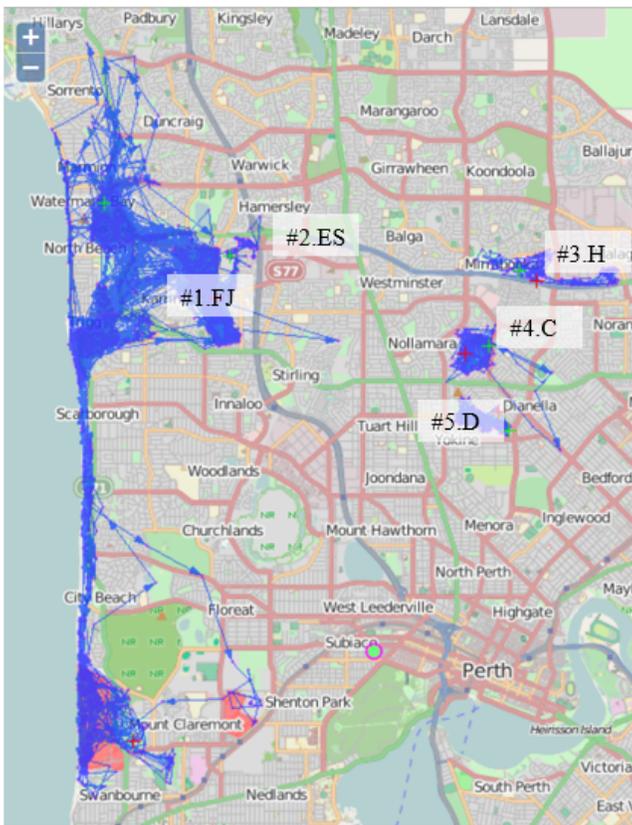


Figure 2

Map of movements of five foxes.

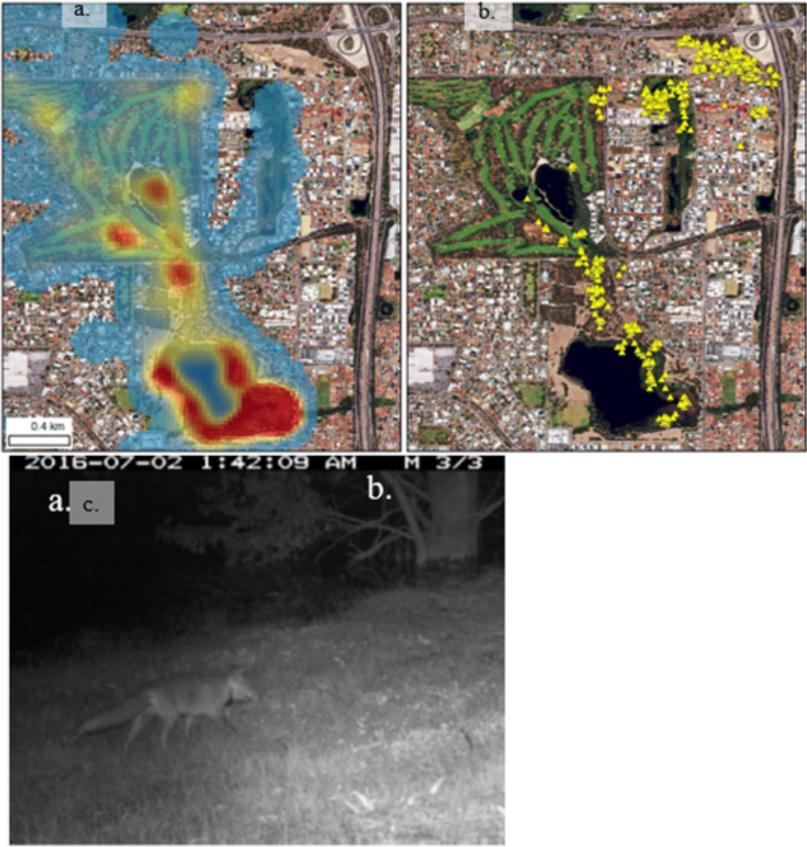


Figure 3

(a) The home range estimated (red colours show the 50% core of the KDE surface) for male #1.FJ at a lakeside reserve (Lake Gwelup, Perth, Western Australia) where he was captured on camera trap (c) and later trapped. (b) Female #2.ES was present at this location, although she had moved away at the time #1.FJ was recorded. Imagery sources: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.



Figure 4

Three golf courses used by one male (#1.FJ) and one used by a female (#5.DB) (bottom right) red fox in Perth, Western Australia showing GPS locations (yellow triangles) situated within the bushland between the fairways. Imagery sources: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

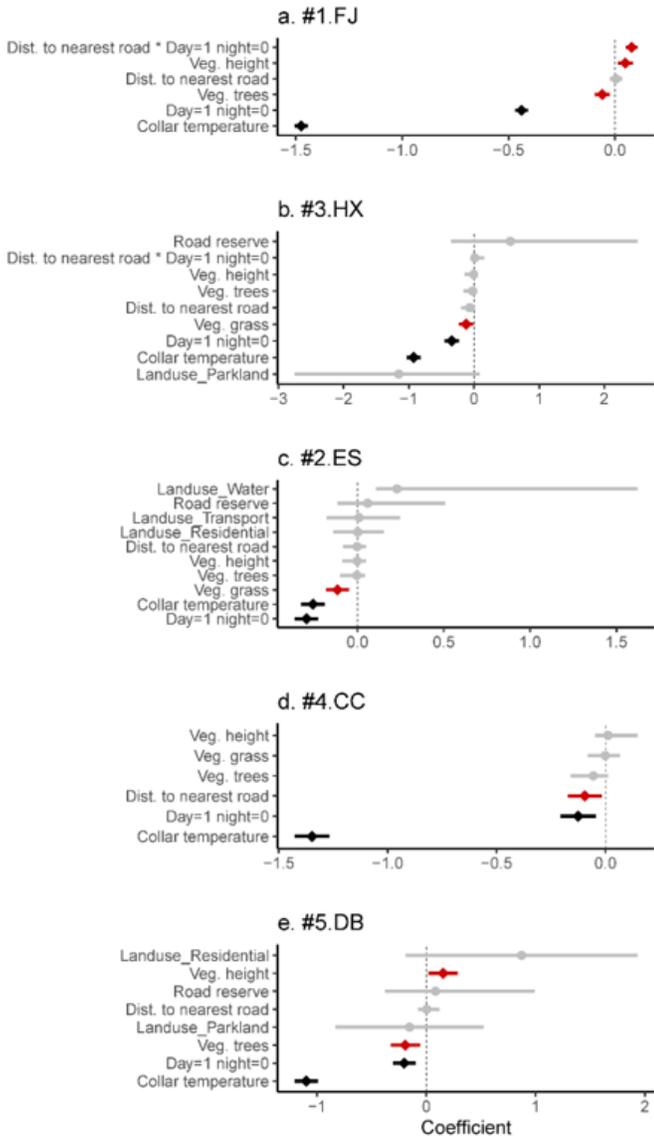


Figure 5

Beta estimates \pm 95% confidence intervals for predictor variables that were retained in the top modelset (AICc/t-AIC <2) describing their speed of movements (minimum displacement distance for half-hour intervals at night, and 1- or 2-hour intervals during day) for each of five red fox (*Vulpes vulpes*) (a-e). Variables with confidence intervals that do not overlap with zero are considered influential; those with significant p-values are indicated with bold lines. Collar temperature was linked with time of day (day=1/night=0) for all five individuals; these values are shown in black. There was a single top model describing speed of movements (minimum displacement distance between consecutive locations) for Fox #1.FJ which likely accounts for the small confidence intervals on estimates for this fox (a); the other four foxes required model averaging amongst the top model set.

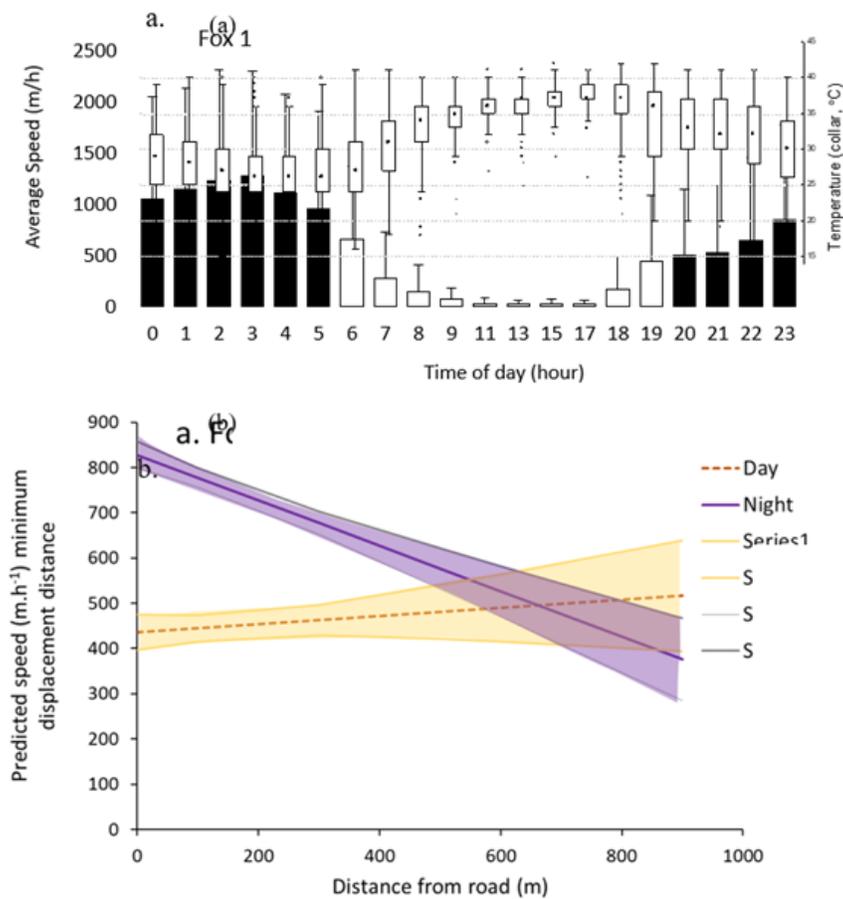


Figure 6

Comparison of minimum speed and predictor variables for Fox #1.FJ. (a) Average speed was significantly correlated with time of day (fastest speeds were during the early morning hours, especially pre-dawn – presumably on return to diurnal rest sites – while there was limited mobility during the middle of the day) and collar temperature (which is likely to reflect that foxes showed minimal movement during the day). (b) Predicted nocturnal speeds (from modelling, when other predictor variables were held constant) were influenced by distance from the road, while diurnal speeds were not influenced by distance from roads.