Foxes at your front door? Habitat selection and home range estimation of suburban 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. We used GPS-tracking of five suburban foxes across high-density residential suburbs of Perth, Western Australia to quantify (1) their habitat selection and (2) home range area. All five foxes showed statistically significant avoidance of residential locations ($p < 0.001$) and preference for parkland ($p < 0.001$), with native vegetation reserves, golf courses, and water reserves showing disproportionately greater use. Landuse category also influenced their movements, with foxes moving quickest (i.e., commuting) in proximity to roads and slowest (i.e., foraging) when they were further from roads. Three females had core home ranges (50% autocorrelated-corrected kernel density estimate; $AKDE_c$) averaging 37 ± 20 ha or 95% $AKDE_c$ averaging 208 ± 196 ha. One male had a 95 ha core home range and 349 ha 95% $AKDE_c$ but the other male covered an area ~20 times this: using a 371 ha core home range and 7,368 ha 95% $AKDE_c$. The extensive movement patterns we describe are likely to be common for urban foxes, with half of 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 habitat preference and exploitation of resources by urban foxes.

Keywords Invasive animal · Urban exploiter · Autocorrelated KDE ($AKDE_c$) · Home range · Tracking data · Utilisation distribution

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 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) and it is now a declared pest. 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

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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) as well as viral diseases such as rabies (Rosatte and Allan 2009; Rosatte et al. 1992). A greater understanding of habitat preference and movements of urban foxes can therefore indicate areas of increased human-wildlife or domestic and wild animal overlap, movement patterns between resources, and areas of species conservation or management concern. Such data could inform how foxes 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 (General Post Office), burrows that had been dug by foxes were most common (92%), although rabbit warrens and artificial structures were also used (Marks and Bloomfield 2006). Understanding which habitat foxes use for diurnal rest sites can therefore inform what resources they are using for cover and would make a powerful contribution to fox management where their control is warranted.

Red foxes have an opportunist diet (Fleming et al. 2021) 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, invertebrates, fruit, etc.) (Fleming et al. 2021; Soe et al. 2017), urban foxes often rely heavily on food derived from anthropogenic sources (Baker et al. 2000; Doncaster et al. 1990; Saunders et al. 1993). For example, in Zurich, over 50% of fox stomachs examined contained food derived from anthropogenic sources (mainly scavenged meat from human refuse, but also pets and domestic stock, pet food, and bird seed), and the proportion of anthropogenic food 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). Diet observations therefore suggest that some foxes are likely to exploit residential gardens as they move through the urban matrix.

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 and 460 ha (Table 1 and references therein). This flexibility in resource use is challenging when designing effective control of declared pest species and suggests that a regionally specific understanding of drivers of habitat selection are required to inform and improve population management. Understanding space use may suggest locations that are bottlenecks or population sinks, providing opportunities to direct control activities in cities such as Perth, where the red fox is a declared pest under biosecurity legislation (s22(2) of the *Biosecurity Agriculture Management Act 2007*), and therefore is the target of population control.

The first aim of our study was to quantify diurnal (resting) and nocturnal (foraging) habitat selection by foxes in suburban Perth, Western Australia. Based on previous studies, we predicted that Perth foxes would exploit residential gardens as they move through the urban matrix. We compared locations used with the availability of different landuses within a radius around the centre of each individual's home range. We also investigated how urban landuse type influenced the behaviour (movement speed) of foxes to better understand their adaptability to the urban landscape. Second, we quantified home range area for these foxes for comparison with published studies and compared different home range estimators to understand their application for urban animals that show habitat avoidance across the urban matrix.

Methods

Our study was approved by the Murdoch University Animal Ethics Committee (Permit number RW2612/13). We

Table 1 Global summary of home range (HR) studies for urban red foxes (*Vulpes vulpes*). Data are sorted by tracking (VHF or GPS) and estimate method. Multiple data are presented for some studies where the authors gave different measures, or separated animals by sex or age

Measure €	n, sex†	When tracked	Avg. time tracked	HR area (range); ha	Sig-nals lost ¥	Location	Same‡	Ref.
VHF								
SubjP	7 F	?	4/5 mo	45.4 ± 6.9 (25.7–78.2)		Bristol, UK		Harris (1980)
Grid e	17 (F,M)	night	10.5 mo	93.4 ± 10.7 (41.8–197.8)	E	Oxford, UK	a	Doncaster and Macdonald (1991)
Grid e	29 (F,M)	night	10.5 mo	54.3 ± 5.3 (14.7–107.3)	E	Boar's Hill, UK		Doncaster and Macdonald (1991)
Grid e	11 (4 M,7 F)	night	50 d	17.6 ± 0.2		Oxford, UK	a	Ward et al. (1997)
MCP	15 M	most night	5 mo	207 ± 146 (42–460)	L(7)	Edinburgh, UK	b	Kolb (1984)
MCP	9 F,3f	most night	5 mo	103 ± 50 (31–233)		Edinburgh, UK	b	Kolb (1986)
MCP	9 M	night	21 mo	52	E,L	Bristol, UK	c	Woollard and Harris (1990)
MCP	2 M,1 F	most night	?	90 ± 36 (60–130)		Bendigo, Australia		Coman et al. (1991)
MCP	3 M	night	15 mo	33.9 ± 3.9	L(3)	Bristol, UK	c	Saunders et al. (1993)
MCP	3 F	night	15 mo	25.9 ± 1.5		Bristol, UK		Saunders et al. (1993)
MCP	4 (2 M,2 F)	both	5.3 mo	258 ± 139 (147–460)		Newport News Park, USA		Rountree (2004)
MCP	11 (3 M,6 F,1 m,1f)	evening	3–5 mo	27 ± 12 (5.5–46)		Melbourne, Australia		Marks and Bloomfield (2006)
MCP	9 (6 M,3 F)	day = night	8 mo	44.6 ± 13.2 (19.2–152.6)		Melbourne, Australia	d	White et al. (2006)
MCP	8 (4 M,2 F,2f)	active	10 mo	36 ± 16 (17–70)		Bristol, UK		White et al. (2006)
MCP	6 M,6 F	night	3 d	32.3 ± 19.1		Bristol, UK	e	Arnold et al. (2011)
MCP	5 M,6 F	night	3 d	20.8 ± 8.6		Bristol, UK	e	Arnold et al. (2011)
MCP	17 (3 M,3 F,6 m,5f)	both		76.6 ± 44.1	L(8)	Starnberg, Germany	f	Janko et al. (2012)
95% harmonic mean	9 (6 M,3 F)	day = night	8 mo	23.9 ± 5.7 (11.6–63.5)		Melbourne	d	White et al. (2006)
KDE (Ranges)	10 (5 M,5 F)	night	~12 mo	325 ± 207 (114–718)	L(9)	Toronto, Canada	g	Rosatte and Allan (2009)
KDE (Ranges)	18 (6 m,12f)	night	~12 mo	165 ± 176 (21–541)	E	Toronto, Canada	g	Rosatte and Allan (2009)
95% KDE	17	both	6.5 mo	139 ± 86	L(8)	Starnberg, Germany	f	Janko et al. (2012)
GPS								
95% KDE	17	both	2 y	198 ± 142 (76–623)		Sunshine Coast, Australia	h	O'Connor et al. (2021)
95% KDE	6 F	both		237 (82–623)		Sunshine Coast	h	O'Connor et al. (2021)
95% KDE	5 M	both		189 (84–415)		Sunshine Coast, Australia	h	O'Connor et al. (2021)
95% KDE	13 (7 M,6 F)	both	54 d	14.2 ± 3.26	L(1)	Briton/Hove, UK		Tolhurst et al. (2020)
95% AKDE$_c$	5 (2 M,3 F)	both	102 d	1,626 ± 3,150 (92–7,257)		Perth, Australia		(this study)

€ 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' (i.e. movements beyond the animal's normal home range – usually identified by the authors of each study by visually screening their data), excluded in estimating home range area

‡ Same: data for potentially the same animals reported in different publications (or same animals but different measure recorded)

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).

Capture and collaring of red foxes

Perth is Australia's fourth-most-populous city, with a population of c. 2.0 million people. It is a metropolitan area sprawling 120 km north-south along the coastline. The urban matrix has been significantly cleared for housing development, most substantially over the last three decades (MacLachlan et al. 2017), with only around 10% of native vegetation remaining within this urban footprint distributed across at least 1,000 isolated bushland reserves (Bryant et al. 2017). We selected potential trapping sites based on previous reported sightings of foxes across some of the oldest and most built-up residential areas in the centre of the Perth metropolitan area.

Capture and collaring of red foxes occurred between December 2015 and July 2016. We began with a three-week trial period using cage traps to capture foxes to address animal ethics concerns, which resulted in no captures. We then moved to leg hold trapping using Victor Softcatch® #1.5 padded jaw leg hold traps (Woodstream Corporation, USA) which proved more successful. Leghold traps were buried just below ground level and positioned where animals would be funnelled through a small space (e.g., along trails in vegetated areas, along fences, around gaps in fences, adjacent to road underpasses) or in areas reported to be frequented by foxes based on local knowledge or sightings. We incorporated a scent (e.g., fox anal glands, urine) or visual (e.g., bird feathers, mammal fur) lure to entice foxes to traps. Traps were checked once every 12 h (i.e., within 3 h of sunrise and late afternoon), and additionally re-checked mid-morning on days forecast to be over 30 °C, to reduce the likelihood that animals were re-trapped after traps had already been cleared in the morning.

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 intramuscularly 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 and to estimate age.

During recumbency, body temperature, respiration and heart rate were monitored. ATS W500 Wildlink GPS (Global Positioning System) tracking collars (Advanced Telemetry

Solutions Australia, Queensland, Australia; Fig. 1, suitable for animals > 4 kg body mass) were fitted. The fox was then 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 locations every 24 h, with a focus of greater location frequency during nocturnal times to capture fox roaming activity in more detail: 30 min location interval between 18:00–08:00 h (28 locations daily), 60 min location interval between 08:00–09:00 h and between 17:00–18:00 h (2 locations daily), and 120 min location interval between 09:00–17:00 h (3 locations daily).

Location data were downloaded from GPS collars remotely by tracking collared foxes via VHF (Very High Frequency) signal to within approximately 200 m of their current den or rest site, before establishing a UHF (Ultra High Frequency) connection to a portable base station, which downloaded location data from the collar. The metropolitan landscape resulted in significant interference to receiving and establishing both VHF and UHF signals; consequently remote download of location data from collars in the field was possible on only a few occasions. Location data for three animals were also downloaded when the collars were recovered (#1.FJ and #3.HX were culled as part of ongoing City Council pest management operations, #2.ES was found dead). We collared six adult foxes, but one fox died later on the day of capture due to trapping complications (re-trapped in a trap that had already been checked). Our data analysis was therefore carried out for five foxes.

Statistical analyses

Habitat selection

To examine whether foxes showed significant habitat selection, all GPS locations were compared in ArcGIS 10.5 with available geospatial databases at the scale of 1:100k. These included (1) landuse category: parkland (parkland and water bodies), residential, transport corridors, and other (industrial, commercial, hospital/medical facilities, education facilities) (Geoscience and Australia 2018). We extracted (2) the Euclidean distance (m) to the nearest road (Main Roads Department of Western Australia, 2018) in ArcGIS 10.5. Each location was classified according to (3) vegetation presence ('veg_raw': classifies pixels into either 1 = green growing vegetation, or 0 = everything else; Caccetta et al. 2012), (4) vegetation height ('vht_all': height in m of vegetation pixels relative to the ground) and (5) presence of

Fig. 1 Attaching a collar to a red fox (*Vulpes vulpes*) in Perth, Western Australia

grass ('grs_all': 1 = vegetation below 0.5 m in height present, 0 = everything else; Caccetta et al. 2012).

To statistically analyse habitat preference, we used Pearson's χ^2 analyses to compare the proportion of fox GPS locations within each land use category with available land use calculated as the proportion of these categories within 1 and 3 km radius buffers centred about the geometric median point (the location that minimises overall Euclidean distance to all data points, equivalent to the centre of activity, ESRI, 2018) of the animal's home range. For Fox #1.FJ, who exploited a thin coastal reserve between more expansive southern and northern areas (Fig. 2), we calculated available land use categories for four sections along the north-south length of his home range for comparison with the observed data.

To test whether habitat type influenced behaviour of foxes, we compared estimated movement speeds with landuse categories. We estimated minimal speed of movement (m/h) from consecutive fixes (i.e., every 30 min overnight, every 2 h during daylight), calculating the distance between consecutive locations for each fox by trigonometry in Excel,

and accounting for differences in the fix schedules or missed data. We carried out generalised linear regression analyses using the *glm* function in the 'lme4' package (Bates et al. 2012) in R 4.1.1 (Core Team 2018) 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 category (grouped into (1) parkland as the reference type, including native bushland and water bodies, (2) residential, (3) transport corridors, and (4) 'other' including industrial, commercial, hospital/medical facilities, and education facilities), distance to nearest road, whether the site was on a road reserve (i.e., distance to road = 0), vegetation presence, vegetation height, and grass presence as predictor variables. Predictor variables were mean-standardised, allowing direct comparison of standardised β values. Model assumptions were checked and final models were validated by examining the residuals using the 'DHARMa' R package (Hartig 2020). 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' R package
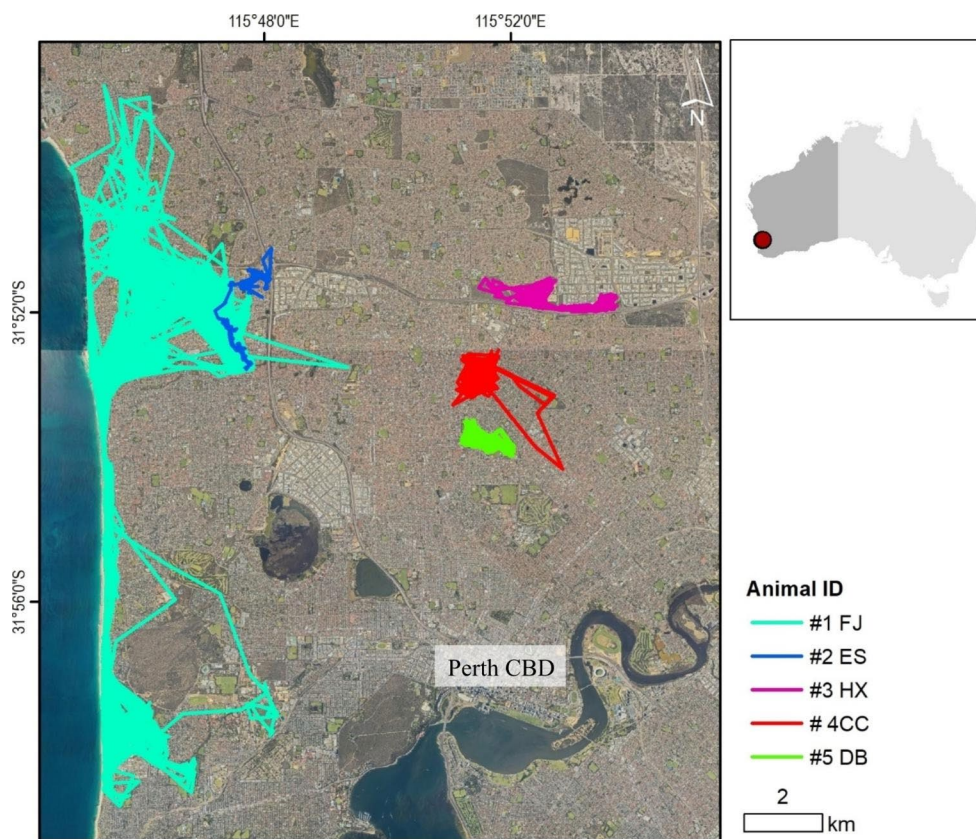
Fig. 2 Map of movements of five foxes in suburban Perth, Western Australia. Base map source: Google Earth

(Barton and Barton 2015). We compared models using Akaike Information Criterion (AIC) (Burnham & Anderson, 2002) and calculated model weights (w_i) for each of the top models (ΔAIC < 2). To visualise the effects of individual variables, we used the *ggpredict* function in 'ggeffects' R package (Lüdecke 2019) to plot predicted values of significant variables (raw unscaled data) where each other factor was held constant at its mean or median value. Values are presented as means ± 1SD.

Home range estimation

All data were included in home range analysis as all HDOP (horizontal dilution of precision) values were ≤3, suggesting 'good' quality data (Isik et al. 2020). As home range analysis assumes range residence, each fox dataset was tested for the presence of multiple home ranges due to temporal range shifts (i.e., relocations to a new home range area) in the 'segclust2d' R package (Patin et al. 2018), using the home range mode as recommended by C. Fleming (pers comm 2021). Area-corrected autocorrelated Kernel Density Estimation (AKDE$_C$) was then used to calculate home range estimates for each individual using the 'CTMM' R package (Calabrese et al. 2016; Fleming et al. 2015), including error

estimation derived from the raw HDOP values (Fleming et al. 2020).

The AKDEc method was used in preference to traditional kernel density estimators as, unlike those estimators, it considers autocorrelation associated with high-resolution GPS data and can be used with irregular sampling. Data were tested for periodicity using periodograms, and autocorrelation structure and model fit using variograms. Home ranges were then calculated using the Ornstein-Uhlenbeck F (OUF) model in the 'CTMM' R package (Calabrese et al. 2016), which considers auto-correlation for both position and velocity and provides a bandwidth by correcting for area estimate bias (Fleming and Calabrese 2017).

To provide biologically meaningful comparison of our data with previous studies reporting fox home ranges, and to determine whether results are robust to the choice of home range estimator (Signer and Fieberg 2021), we included multiple home range estimators in our analyses. We used the 'amt' (Animal Movement Tools) R package (Signer et al. 2019) for managing tracking data and conducting home range area analyses to calculate 50% and 95% estimates using minimum convex polygon (MCP), kernel density estimates (KDE), local convex hulls (LoCoH), AKDE, and AKDE$_c$ with the 2D User Equivalent Range Error (UERE; estimate 29.6 range 22.8–36.4 m) calculated from ES's

collar after it became stationary. We also included Time Local Convex Hull (T-LoCoH) using the k and the a methods (Lyons et al. 2013), thereby integrating time with space in hull construction. These methods are suitable for autocorrelated GPS data, and provide a time-associated geometric home range method to compare against the probabilistic models derived using $AKDE_c$.

Values are presented as means ± 1 standard deviation, unless indicated otherwise.

Results

We collared and collected data for five red foxes. These foxes were tracked for an average of 102 ± 81 (range 25–226) days (Table 2). The GPS devices we used required proximity to UHF remotely download data; we were successful only three times for #1.FJ and only once each for the other four animals. Location data for #1.FJ, #2.ES and #3.HX were also downloaded when the collars were recovered. 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 (Fig. 2).

Habitat selection

Compared with the land use categories present in a 1 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 (Fig. 3). Bushland reserves, golf courses, and water reserves were especially preferred locations. Four golf courses were used by two individuals, where their activities were focussed around the native vegetation between the greens (Fig. 4). Waterbodies were also preferred sites.

A summary of the predictors that were retained in the top models ($\Delta AIC < 2$) 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 (shown for one individual, #1.FJ, in Fig. 6a). The inclusion of collar temperature for all individuals improved model fit, which was likely to be incidental to the temporal rhythm of this primarily nocturnal animal. All foxes moved slower through vegetated areas (this was statistically significant for #1.FJ and #5.DB) and four of the foxes (except #5.DB) were also slower where there was grass. There were few data for land use that was not parkland, and therefore the effects of landuse on speed of movement were weaker than might be expected. Relative to parkland, Fox #1.FJ was slower

when moving through residential areas, and faster around transport corridors and other areas (industrial, commercial, hospital/medical facilities, education facilities). Relative to parkland, #5.DB was faster around residential and other areas. Four foxes moved relatively faster (i.e. commuting) when in close proximity to roads and slowest (i.e. foraging) when further from roads; this effect was statistically significant for #1.FJ and #4.CC. Data for #1.FJ and #3.HX also showed a *time of day x distance to road* interaction term, indicating that speed varied at night but not during the day time (Fig. 6b).

Home range estimation

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. The animal that did not show site fidelity, juvenile 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. Juvenile Male #1.FJ was tracked for the longest period and across the greatest distance. He showed a distinct range shift from a southern to a northern home range, making extensive use of a narrow coastal reserve to repeatedly move north-south (Fig. 2) during the tracking period. He frequently moved between locations, remaining around core patches for days or weeks before moving again. These movements do not fit the definition of dispersal movements because he regularly retraced his tracks. Instead, they conform to the definition of shifts (sensu Cavallini 1996), where the animal moved to a new activity centre for a period of time. 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 (camera trapping implemented by the local government after 13 swans had been found beheaded; Jo Taylor, City of Stirling pers. comm.) 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.

Autocorrelated-corrected home ranges indicated that the three females had a core home range (50% $AKDE_c$) averaging 37 ± 20 ha (range 22–60 ha) or a 95% $AKDE_c$ averaging 208 ± 196 ha (range 85–434 ha) (Table 2). Male #3.HX had a core home range of 95 ha or a 95% $AKDE_c$ covering 349 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 ~ 20 times this: having a core home range of 371 ha or 95% $AKDE_c$ of 7,368 ha. This animal travelled a minimum of 2,500 km in the 7.5 months it was tracked. There were strong correlations (Pearson's r > 0.997)

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	Body mass, age	Dates	Days	2016 D J F M A M J J A	# independent points	Bandwidth (DOF-H)	Distance moved Total (km)	Average (km/day)	AKDE$_c$ Home range area (range); ha 50%	95%
#1.FJM	5.2 kg J	20/12/15–2/8/16	226		7,499	366	2,504	11.08	1,598 (1,323–1,897)	7,368 (5,995–8,873)
#3.HXM	7.1 kg A	26/2/16–15/7/16	140		569	46	62	0.44	95 (64–132)	349 (227–497)
#2.ESF	5.0 kg J?	15/1/16–15/3/16	60		1,650	12	54	0.89	60 (29–100)	434 (120–947)
#4.CCF	5.5 kg A	4/6/16–2/8/16	59		897	654	157	2.66	30 (26–33)	104 (91–117)
#5.DBF	4.85 kg A	8/7/16–2/8/16	25		559	268	74	2.96	22 (18–26)	85 (68–104)

Age categories based on (1) comparison of body mass [95%CI] with ~ 10-month-old dispersing (5.22 kg [5.07–5.36] n = 138) and adult (6.53 kg [6.38–6.68] n = 114) male foxes, or ~ 10-month-old dispersing (4.39 kg [4.27–4.50] n = 138) and adult (5.45 kg [5.32–5.59] n = 91) female red foxes (Forbes-Harper et al. 2017), and (2) month of capture – most cubs are born in August and September in Australia and the majority of dispersal occurs in late summer(January to March) (Saunders et al. 1995)

Bandwidth DOF-H – is the number of datapoints to statistical independence (when home range area reaches an asymptote in the variogram of these data) equivalent to effective sample size
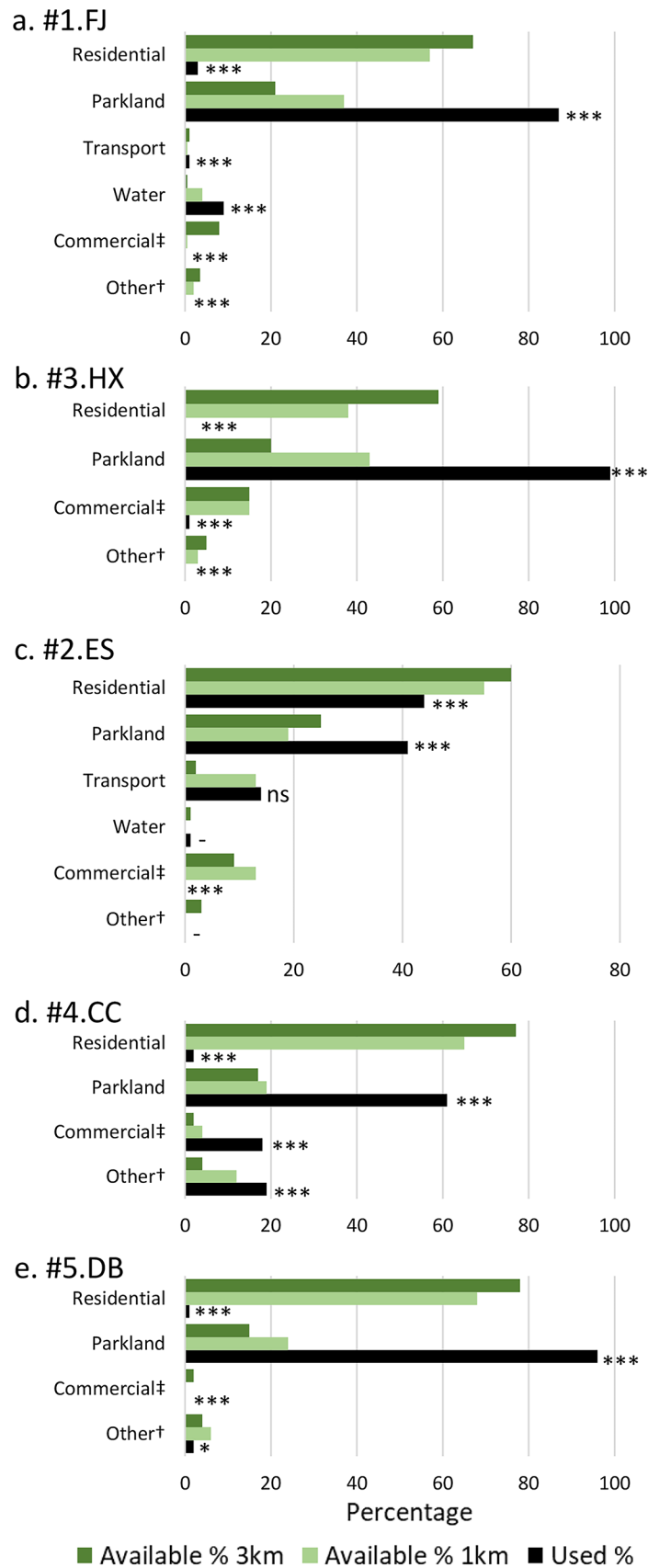
Fig. 3 Habitat selection by five red foxes across Perth, Western Australia. 'Available' data are the percentage of area available to each fox by landuse category within a 1 and 3 km radius centred about the geometric median point of each individual's home range. 'Used' data are the percentage of location datapoints. Statistical significance for χ^2 tests comparing available with used: - insufficient data for statistical analysis, ns not statistically significant, * $p < 0.05$, *** $P < 0.001$. Data were summed across four locations across total home range for #1.FJ. † Hospital/Medical, Education, and Other landuse categories pooled for this figure, ‡ Commercial and Industrial landuse categories pooled for this figure
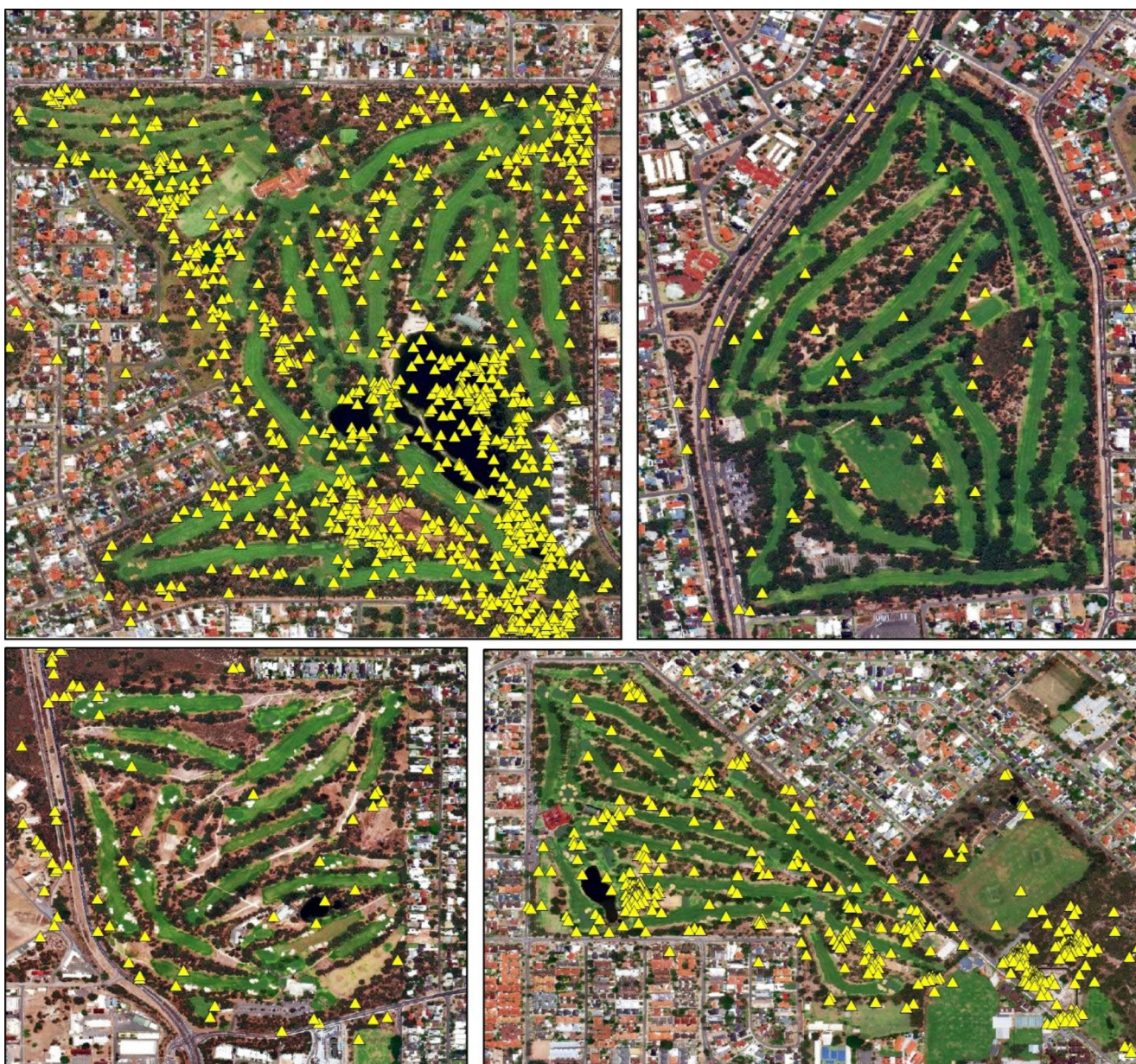
Fig. 4 Three golf courses used by one male (#1.FJ) and one used by a female (#5.DB) (bottom right) red fox (*Vulpes vulpes*) in Perth, Western Australia showing GPS locations (yellow triangles) situated within the bushland between the fairways. Imagery sources: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

amongst home range area values derived using the different home range estimators. Overall, LoCoH yielded the smallest home range area estimates while AKDE estimates were comparable with MCP estimates (Fig. 7; **Table S1**).

Discussion

Habitat preference

Although previous published studies from other cities across the globe indicate that urban red foxes make substantial use of anthropogenic resources for cover and food, foxes in suburban Perth showed significant avoidance of residential areas. These Perth foxes instead showed strong preference for urban parkland (native bushland and water bodies), indicating that they were selectively using natural
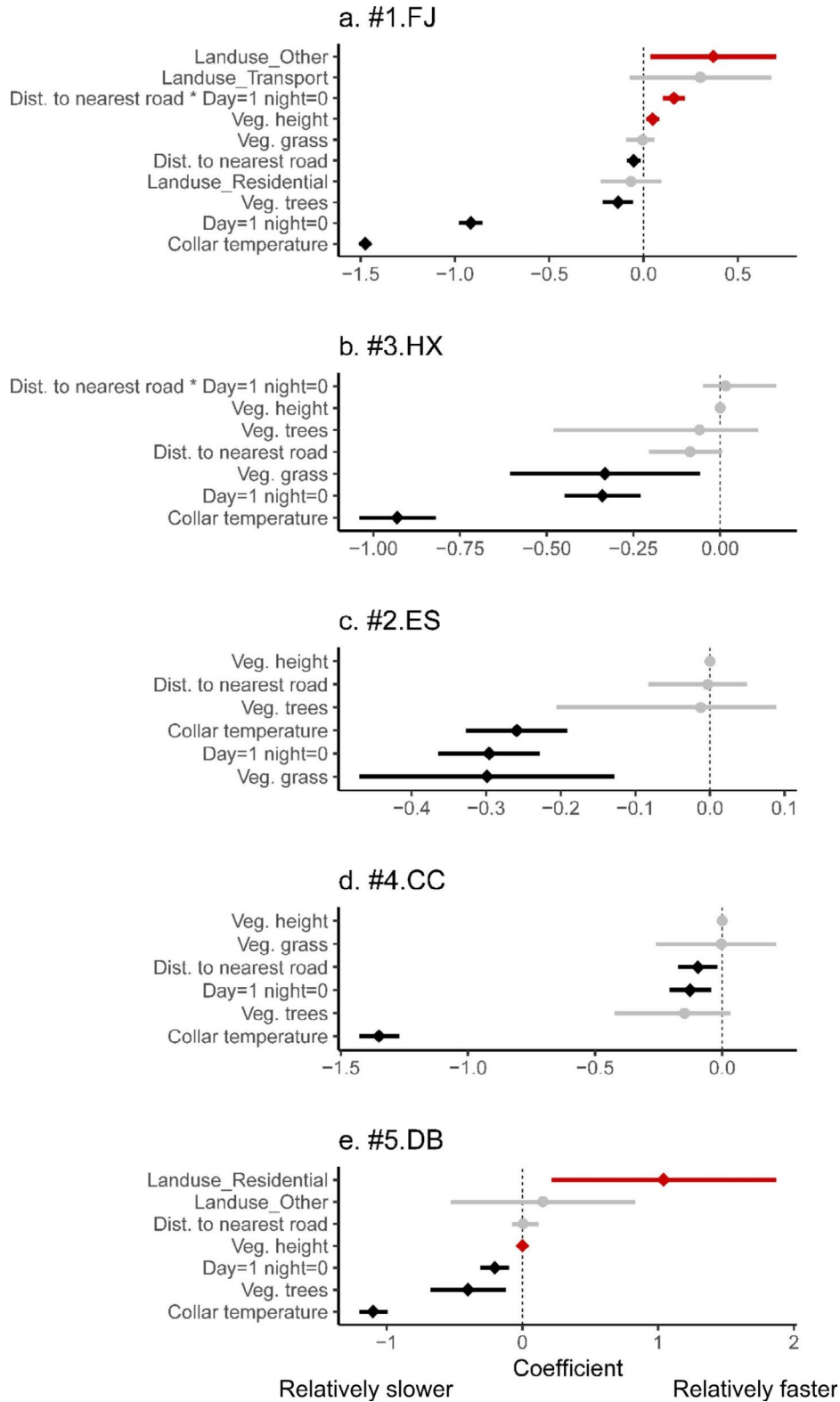
Fig. 5 Beta estimates ± 95% confidence intervals for predictor variables that were retained in the top modelset (AICc/t-AIC < 2) describing their speed of movements (minimum displacement distance for half-hour intervals at night, and 1- or 2-hour intervals during day) for each of five red fox (*Vulpes 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. 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
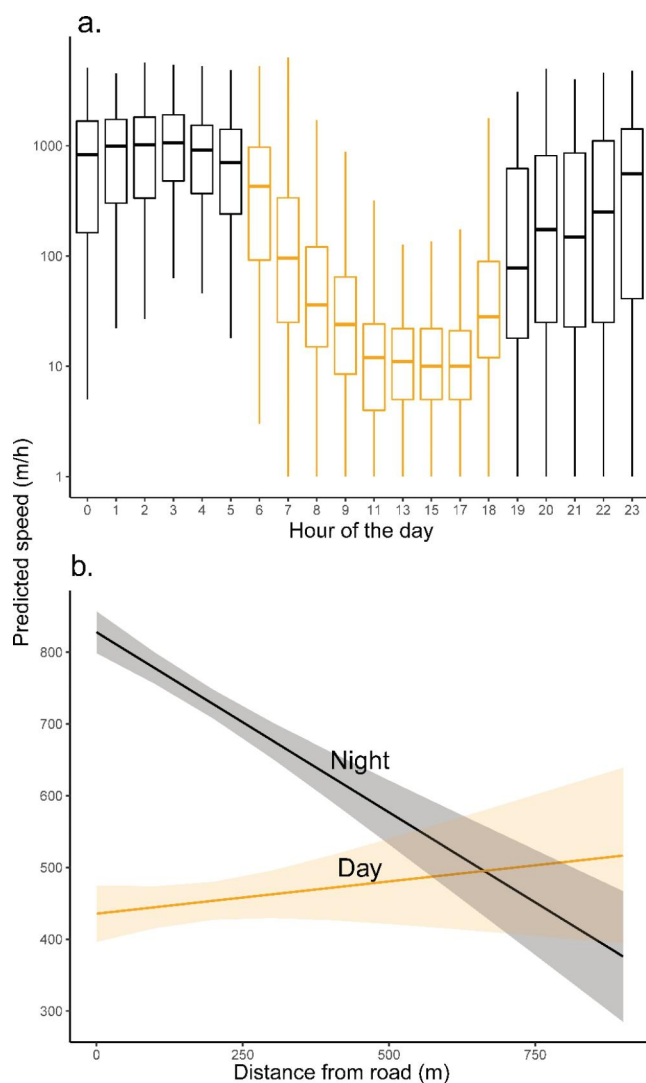
Fig. 6 Comparison of minimum speed and predictor variables for Fox #1.FJ. (a) Average speed was significantly correlated with time of day (fastest speeds were during the early morning hours, especially pre-dawn – presumably on return to diurnal rest sites – while there was limited mobility during the middle of the day). (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

resources across the suburban matrix. We also found evidence that foxes modified their behaviour according to land-use category, with individuals moving faster when they were in proximity to roads. Such evidence of habitat preference is valuable in being able to better identify where the greatest threat to native wildlife species or potential disease transmission is likely to occur (native bushland and water bodies). Tracking information can also guide effective population control by predicting where foxes are likely to rest and which urban corridors are effective at funnelling their activity.

## Foxes show preference for parkland over built-up suburban spaces

Perth foxes preferentially used native bushland 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 or prohibited (e.g. schools, cemeteries, industrial and commercial lands, fenced parks, sporting clubs). 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. Such 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. Rosatte and Allan (2009) also 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, exploiting 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. 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 are more likely to visit gardens where they are 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 vegetation cover, but in North America where they co-exist with larger-bodied 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.
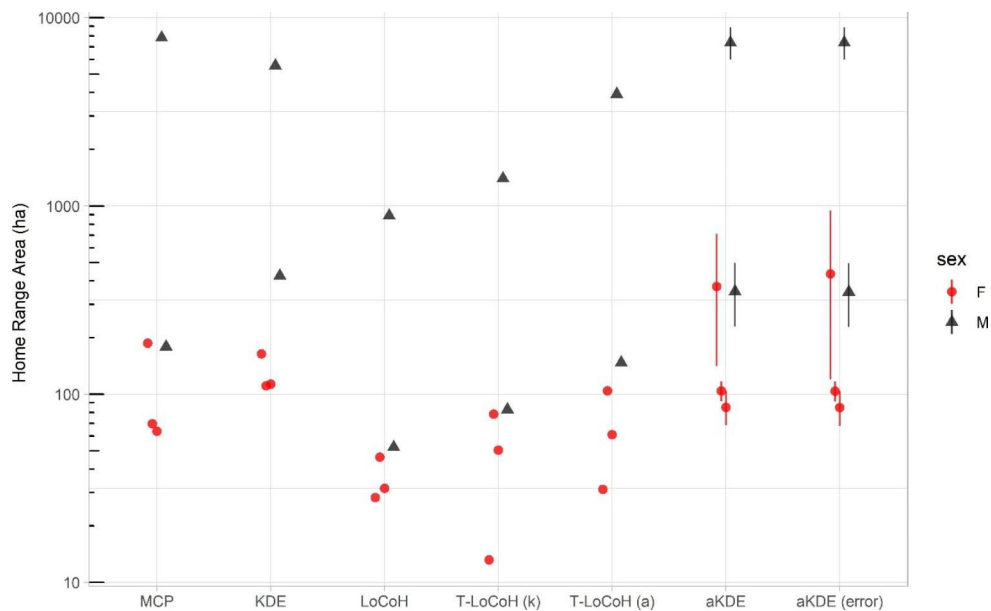
Fig. 7 Summary of Perth red fox (*Vulpes vulpes*) home range area estimates using seven methods of calculation

Four of the foxes sped up when they were in proximity to roads. Road reserves might channel linear movements that would be reflected in apparently faster speeds for our low temporal-resolution data, in contrast with more open places where animals are more likely to backtrack. Visual inspection of GPS data also suggested 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. 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. 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) appear to funnel fox activity and could therefore be important focal points for targeting management action.

Comparison of home range estimates with published urban fox studies

Home range estimates for four tracked individuals were reasonably consistent with some of the larger published values for red foxes (Table 1), but one of the animals we tracked

(#1.FJ) covered an enormous area (7,257 [6,011–8,618] ha or 72 km^2), far greater than previous estimates of urban fox home ranges. This result is partly due to the shape of its home range, with #1.FJ using a narrow 25 km-long north-south coastal reserve. However, all the home range estimators applied in this study yielded large home range area values for this animal (Fig. 7), indicating that the result was not simply an artefact of the estimator used.

The most conservative estimator was LoCoH, while time-corrected measures (t-LoCoH(k) and t-LoCoH(a)) resulted in larger estimates. The autocorrelated-corrected measures (AKDE$_c$) resulted in large estimates that were comparable with MCP or KDE estimates, likely representing that AKDE$_c$ captured backtracking over frequently-used corridors. For reasonably coarse temporal resolution data, such as we have used here (minimum 30 min intervals), and for movements that are constrained by heterogeneous land uses within the urban matrix, the value of autocorrelated-corrected methods (Calabrese et al. 2016; Fleming et al. 2015), which assume equal likelihood of movement in all directions, were not an improvement on MCP or KDE methods that assume each datapoint is independent (Signer and Fieberg 2021) (an assumption rarely correct for high resolution GPS data). The three LoCoH area estimators, which are sensitive to animals whose movements are constrained by hard borders, such as roads or defined green spaces, are likely better representative of true home range sizes in this species as they exclude areas that are not used (such areas are included using MCP and KDE methods), thereby deriving smaller estimated HR areas for all foxes in this study.

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, especially in rural locations. For example, 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) being larger than 10 km^2 (90% LoCoH(k), n = 44). By contrast, all bar one fox home ranges in their northern study area were larger than 10 km^2 (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 shifted home range twice and did not settle down, resulting in an annual range of 18,285 ha (182.9 km^2) (the authors note that these data were excluded from their calculation of average home range analysis).

Burt (1943) defined an animal's home range as *"that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range"*. Such 'excursions', i.e. movements 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 have also been 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) recognised a fraction of the red fox population acting as 'transient', 'nomadic' or 'floating', and identified that few authors report information about these animals because they were too difficult to follow and study (Lovari et al. 1994; Zabel and Taggart 1989; Zimen 1984). Home range estimates based only on residents are therefore likely to underestimate the true distances that can be covered by red foxes.

Published home range and space use calculations derived from VHF tracking are also highly likely to have underestimated fox home ranges due to lost signals. 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 most likely to reflect times when the animal moved beyond 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

movement 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 VHF receiver range or excluded 'excursions' in estimating average ranges (Table 1) while the description of methods for the remaining studies do not indicate how excursions or lost signals were handled. As for only handling data for residents, home range estimates based only on easy-to-track animals will similarly underestimate the true distances that can be covered by red foxes.

A study comparing the home ranges of 10 VHF- and 3 GPS-tracked red foxes indicated that 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 difficulties of tracking animals across private property in suburban landscapes has been particularly challenging and therefore improvements in tracking technology have a great deal of value in revealing how urban wildlife exploits these landscapes. 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 substantial 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. High resolution GPS tracking data, coupled with improved models that account for spatial and temporal autocorrelation as well as hard barriers and unused habitat, will be important

in developing accurate and repeatable analyses of urban wildlife.

Conclusions and management implications of this study

Concentrated introduced fox control efforts for wildlife conservation and disease transmission would be more effective with improved understanding of how these animals use the urban matrix. Understanding the habitat preferences and movement patterns of foxes can help inform questions such as where to proceed with control activities and who needs to be undertaking such control. Tracking information can help with informing such decisions.

Data Availability data available from movebank.org. <- *data will be made available upon acceptance of this manuscript*.

Code Availability Finalised R code will be made available upon acceptance of this manuscript.

Declarations

Conflict of interest None.

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).

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