Adaptations of the red fox (*Vulpes vulpes*) to urban environments in Sydney, Australia

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Abstract

With urban encroachment on wild landscapes accelerating globally, there is an urgent need to understand how wildlife is adapting to anthropogenic change. We compared the behaviour of the invasive red fox (*Vulpes vulpes*) at eight urban and eight peri-urban areas of Sydney, Australia. We observed fox behaviour around a lure and compared fox activity patterns to those of potential prey and to two domestic predators (dogs—*Canis lupus familiaris* and cats—*Felis catus*). We assessed the influence of site type, vegetation cover, and distance from habitation on fox behaviour, and compared the temporal activity patterns of urban and peri-urban red foxes. Urban red foxes were marginally more nocturnal than those in peri-urban areas (88% activity overlap). There was greater overlap of red fox activity patterns with introduced mammalian prey in urban areas compared with peri-urban areas (90% urban vs 84% peri-urban). Red fox temporal activity overlapped 78% with cats, but only 20% with dogs, across both site types. The high degree of overlap with cats and introduced mammalian prey is most likely explained by the nocturnal behaviour of these species, while pet dogs are generally kept in yards or indoors at night. The behavioural differences we documented by urban red foxes suggest they may adapt to human modifications and presence, by being more nocturnal and/or more confident in urban areas.

Key words: red fox, urban predator, invasive species, Canidae, urban ecology

Introduction

Cities are highly modified landscapes but can still support biodiversity (van Heezik and Seddon 2018). For example, urban areas can harbour substantially more threatened species per unit of area than non-urban sites (Ives et al. 2016). But, urban wildlife may display behavioural or life-history adaptations relating to movement, diet, reproduction, density, disease and survival (Ditchkoff, Saalfeld, and Gibson 2006). Understanding these responses provides insights into how animals evolve to persist in a rapidly changing world.

Of the species that thrive in urban areas, predators can be especially influential community members (McNeill et al. 2016). The most successful urban predators have generalist diets (i.e. they are not hypercarnivores), are of medium body size (average 4.60 kg) and display highly adaptable behaviour (Bateman and Fleming 2012). In Japan, some of the most successful mammal predators in urban environments include mid-sized species such as the masked palm civet (*Paguma larvata*), raccoon dog (*Nyctereutes procyonoides*) and domestic cat (*Felis catus*), each of which have high annual reproductive capacities and flexible

diets (Saito and Koike 2015). Similarly, coyotes (*Canis latrans*) in North America are successful urban dwellers in part due to their behavioural and dietary plasticity (Bateman and Fleming 2012).

Introduced predators also occur in cities, and there they can impact native biodiversity (Doherty et al. 2016). In Australia, for instance, the introduced red fox (*Vulpes vulpes*) has moved into cities (Marks and Bloomfield 1999; Johnson, Isaac, and Fisher 2007). The red fox has been strongly implicated in declines and extinctions of Australian native terrestrial fauna (Kinnear et al. 2002; Woinarski, Burbidge, and Harrison 2015). They are also a known vector of diseases and parasites, including hydatids, and may pose a potential host for rabies if the latter is accidentally introduced into Australia (Marks and Bloomfield 1999). To effectively mitigate the potential negative impacts of red fox presence in urban areas, we need to understand more about their ecology within the urban environment and how they have adapted to it.

To understand the negative impacts of an introduced predator, it is essential to study their interactions with native species (Carthey and Banks 2014; Díaz-Ruiz et al. 2016). Both response and vulnerability to red fox predation depend on the species, and individual species may vary in their responses to individual threat factors at different sites or times (Woinarski, Burbidge, and Harrison 2015). Native species, those that weigh between 35 and 5500 g, defined as the 'critical weight range', are known to be particularly at risk from red fox predation (Burbidge and McKenzie 1989). However, for urban red foxes, there are also non-native potential prey species such as mice (*Mus musculus*), rats (*Rattus rattus* and *Rattus norvegicus*), rabbits (*Oryctolagus cuniculus*), birds and invertebrates (Davis et al. 2015).

Interspecific interactions between mammalian wild predators have been fairly well studied, nevertheless, little is known about wild predator interactions with domestic predators (Krauze-Gryz et al. 2012). The interactions between domestic and wild carnivores can be agonistic, to the extent that one predator may eat the other (Harrison et al. 2011; Plumer et al. 2014). For example, red foxes are known to kill domestic cats in urban areas (Plumer et al. 2014). Conversely, domestic dogs (*Canis lupus familiaris*) may have important effects on red foxes (Harris 1981). All types of domestic dogs, from feral to fully domestic, can interact with wildlife and severely impact biodiversity (Doherty et al. 2017). The presence of domestic dogs can induce temporal displacements in the activity of mammalian carnivores, such as bobcats and coyotes (George and Crooks 2006). In their native range, the distribution of urban red foxes is negatively correlated with the distribution of stray dogs, especially where the latter have high abundance (Harris 1981). Dogs impact the behaviour of carnivores directly by chasing, barking and attacking, and indirectly through fear effects, mediated by scent marking via urine and scats (George and Crooks 2006). Within an urban setting, domestic dog presence may therefore be expected to represent a danger to red foxes.

In urban areas worldwide, red foxes often rely on plentiful anthropogenic food sources, enabling greater population densities than in peri-urban or more rural areas, and resulting in decreased home range sizes (Contesse et al. 2004; Bino et al. 2010; Bateman and Fleming 2012). One consequence is that urbanisation may select for behavioural traits that confer competitive advantages not seen in natural environments. For example, in domestic cats, the orange coat colour allele is linked to aggressive behaviour in males and is found at higher frequencies in rural areas (Mendl and Harcourt 2000). In these habitats, aggressive behaviour confers an advantage where males must defend territories. However, in urban environments, ginger males

spend more time fighting and less time securing mates. Females also avoid mating with these hyper-aggressive male cats, making this trait less common in urban areas (Pontier, Rioux, and Heizmann 1995; Mendl and Harcourt 2000). Across vertebrates, individuals from urban areas tend to be bolder than their rural counterparts. For example, urban *Anolis sagrei* lizards are bolder and more explorative than those in natural areas (Lapiedra, Chejanovski, and Kolbe 2017). Similarly, urban fox squirrels (*Sciurus niger*) show reduced vigilance and anti-predator responses (McCleery 2009), whereas birds in urban areas approach objects made from human litter more rapidly than do rural birds (Greggor et al. 2016).

It is difficult to tease out the effects of urbanisation itself from the effects of increased food resources and altered predation risk in urban environments. However, we expect that these facets of the urban habitat will result in urban foxes that show differences in behaviours related to exploration, boldness and nocturnality, by comparison with their peri-urban counterparts (Thompson et al. 2018; Breck et al. 2019; Uchida et al. 2019). Although some articles have reviewed the differences between foxes in urban and rural areas (Trewhella et al. 1991; Arnold, Soulsbury, and Harris 2011; Bateman and Fleming 2012; Šálek, Drahníková, and Tkadlec 2015), to our knowledge, no study has yet investigated the effects of urbanisation on red fox behaviour and ecology across an urban to peri-urban land use gradient.

Here we used inactivated, non-toxic-baited canid pest ejectors (hereafter: lures) as attractants to assess behavioural differences between red foxes in urban and peri-urban areas of Sydney. These lures can attract animals because of the smell of the bait, but the bait itself can also be taken. The latter offers an assessment of how bold or curious an individual is, because shy individuals should be less likely to take the bait. We specifically aimed to investigate how red foxes respond to cover, moonlight, distance to human habitation and the presence of domestic dogs and feral cats, at urban and peri-urban sites. We also compared the temporal activity patterns of red foxes in urban and peri-urban areas, as well as the overlap of these temporal activity patterns with prey groups and domestic predators as an indicator of the potential for red foxes to interact with or avoid these species.

Our hypotheses were:

1. That red foxes in urban areas would display more confident behaviour than red foxes in peri-urban areas, and that this behaviour would also relate to environmental variables such as cover and distance from human habitation.
2. That urban red foxes would be more nocturnal than red foxes in peri-urban areas.
3. That urban red fox activity patterns would show a higher overlap with mammalian prey, because of their nocturnal activity, than with bird prey, which are mainly diurnal. The overlap with mammalian prey could be stronger in cities if the activity of red foxes is more nocturnal. Thus, the activity overlap with birds could be higher in peri-urban areas where red foxes may be more active during the day.
4. That red fox temporal activity patterns would overlap more with domestic cats than with domestic dogs.

Methods

Study sites

The Greater Sydney Region, New South Wales, Australia, is highly diverse, extending from densely urbanised city areas and coastal waterways through to rural lands and extensive World

Heritage wilderness areas (Kinnear et al. 2002). This region has a total population of 5.1 million people. We selected 16 sites across the Greater Sydney Region. Eight of our sites were within urban areas and eight sites within peri-urban areas (Fig. 1). We selected our sites based on their proximity to obvious housing nuclei, from their appearance in Google Earth. Housing density was measured by dividing the number of houses to $78.54\,km^2$. Sites with housing densities exceeding 900 habitations/km^2 were considered urban, and those with < 900 habitations/km^2 were considered peri-urban. All sites were at least $5\,km$ apart from each other to ensure site independence, based on recent fox home range calculations for Sydney (J. Martin, unpublished data). Half of our sites had strict dog access restrictions, enforced by fencing and signage, whereas the other half did not.

Sampling design

At each of the 16 sites, we erected five sampling stations. Each sampling station consisted of one lure and one camera trap (HC600 Reconyx® remote-sensing trail cameras, http://www.reconyx.com.au). The sites were active over two separate periods: 3–27 April 2018 and 1–25 May 2018. We randomly allocated sites to time periods to ensure that all site types were sampled evenly across each time period (i.e. number of urban and peri-urban sites, and those with or without dog restrictions). The lures deployed in this study were not activated (i.e. their springs were not depressed) and did not contain any toxic component (they did not have any poison capsule inside the bait head). The bait heads of the lures consisted of dried beef liver treats (Black dog®) blended and mixed with PVA glue. After lure installation, we drizzled $50\,ml$ of fish oil (Wilson Fish Attractant®) within a radius of $30\,cm$ around the lure. The bait heads were refreshed once per week. For the second period of sampling in May, we also secured the lures with fishing line to prevent their removal.

At each station, the camera faced the lure from a distance of $2\,m$, $\sim 60\,cm$ above the ground. The cameras were programmed to take 10 consecutive photos in the hyperfire mode, without delay between activations. Sampling stations were placed at increasing distance intervals of $50\,m$ from the nearest human habitation (Fig. 2). However, these distances varied slightly depending on the terrain ($\pm 20\,m$), or the need to place cameras discreetly to avoid vandalism or theft. Stations were located strategically to maximise the probability of detecting foxes (i.e. in close proximity to trails, dens or sandy soil).

Data Analyses

Behaviour of urban versus peri-urban red foxes

Camera images were tagged with the software DigiKam (https://www.digikam.org) and processed with the CamtrapR package in R (Niedballa et al. 2016; R Core Team 2017). We conservatively defined visits as being independent if they were separated by at least 24 h. We then divided behaviours into two categories: 'timid' or 'confident'. The 'timid' behaviour included a camera-shy response: a slow and cautious approach to the camera, usually in a crouching position, or a cautious posture towards the lure (Fig. 3a). 'Confident' behaviours included pulling the lure, digging and removing the lure, or marking the lure area, either by spraying or rolling (Fig. 3b). In a single visit, a red fox could display one or more of these behaviours, but we only recorded each behavioural category only once per visit. At some stations, lures were removed before the end of the sampling period by foxes, dogs or humans. We therefore conservatively included only independent records (i.e. records separated by at least 24 h at each station) obtained while the lure was present in the area.

Data on fox visitations to stations were analysed using a generalised linear mixed model fit by maximum likelihood, with the Laplace Approximation in the package *lme4* package for R (Bates et al. 2015). We used the binomial family with the
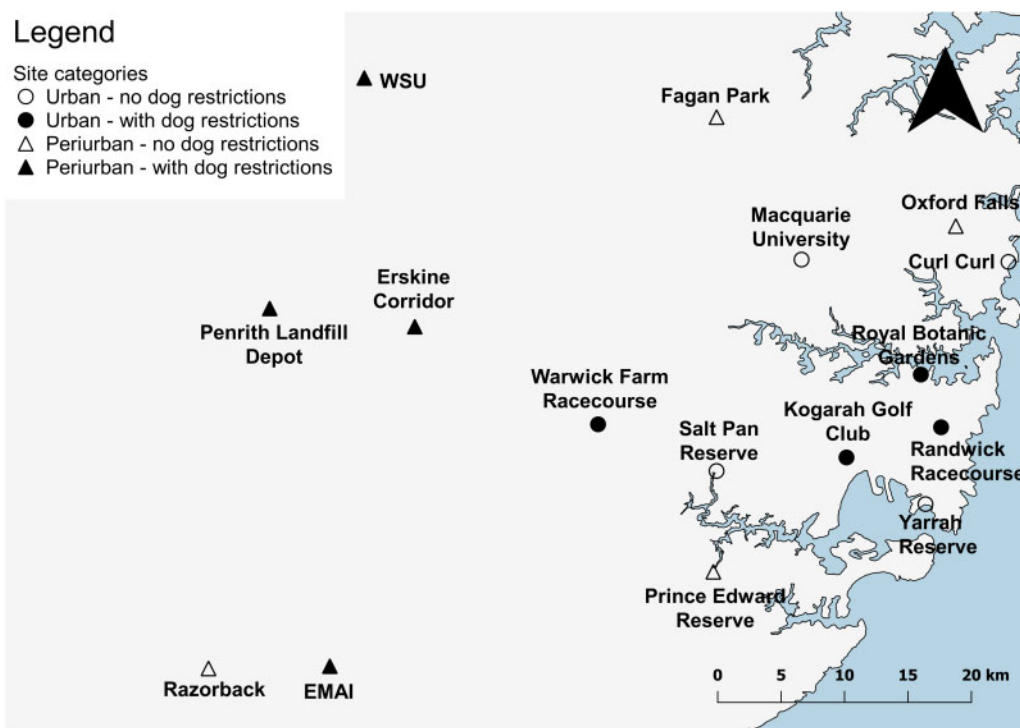

Figure 1: Study sites for the assessment of the behaviour and ecology of the red fox in urban and peri-urban areas in Sydney, NSW, Australia.

Figure 2: Sampling stations design to assess the behaviour and ecology of red foxes in Sydney, Australia. At each site, we located five sampling stations (**A**). Each station was composed of: (**B**) Reconyx HC600, one camera was allocated per station, (**C**) canid pest ejector installed into the ground, with only the bait head on the surface, (**D**) tuna oil spread around the canid pest ejector.

Figure 3: Examples of red fox behaviours classified as timid (**A**) or confident (**B**); (**A**) the fox approached the lure, but its posture was tense, it kept its hind legs away and kept its body close to the ground, (**B**) fox pulling up the lure. See Supplementary Appendix S1 for a detailed description of each behaviour.

logit link function. Our response variable was binomial, and it was the number of red foxes displaying *timid* versus the number of foxes displaying *confident* behaviours. The explanatory variables were: (i) site type (urban or peri-urban) and (ii) vegetation cover (measured immediately above the lure at each station, using wide-angle photographs taken with a GoPro Hero4 Silver® camera). Images were processed with Gap Light Analyzer software, which determines the percentage of vegetation openness by dividing pixel intensities into sky and non-sky classes (https://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla) and (iii) distance from habitation (sampling stations ranged from 50 to 250 m distance from human habitation, so we divided the distance in two categories <150 and >150 m, to reflect distance restrictions of the current Pest Control Order). In all cases, the site, which refers to the locations, was used as a random factor among the independent variables.

All possible additive combinations of variables into models were analysed and compared with the *MuMIn* package in R (Barton 2018). The best models were chosen based on the Akaike Information Criteria (AICc) for small samples, because the number of observations was <40 times the number of explanatory variables in the models (Anderson et al. 2001). The best models were considered to be those with the lowest AICc and a ΔAIC of less than two (Bozdogan 1987). It must be highlighted that *MuMIn* delivers the results for averaged models and allows us to select the highest weight models.

Temporal activity patterns

To compare temporal activity patterns, we used the package *overlap* in R, which determines the overlap between two activity patterns based on kernel density estimates. For these analyses we used all of the records for each species. We used the estimate Dhat4, which is the most suitable for samples with >50 observations per species. The mean overlap and confidence

intervals were obtained from 500 bootstrap iterations (Ridout and Linkie 2009). We compared temporal activity patterns of (i) red foxes in urban and peri-urban areas, (ii) foxes and their potential bird and mammalian prey (both introduced and native) between urban and peri-urban sites (see Supplementary Appendix S2 for the list of species in each group) and (iii) red foxes, cats and dogs, across all sites, and among site types.

Results

Lure stations were active for a total of 1659 camera trap nights. However, at some of the stations, lures were removed by foxes, dogs or humans. We only considered sampling effort when the lure was present, leaving 1472 camera trap nights across all sites. On average, each station was active for 19.2 camera trap nights (SD = 4.10). We recorded 409 independent fox visits (separated by at least 24 h) to 72 of 80 sampling stations. Red fox visitation rates varied greatly among study sites (Fig. 4). Warwick Farm Racecourse had the highest number of independent visits, with 49 independent visits in 75 trap nights, and an average of 0.68 visits per night across all five stations (SD = 0.25).

Behavioural responses of urban versus peri-urban foxes

Across all sites, red foxes showed 178 incidences of confident behaviour and 174 incidences of timid behaviour (behavioural categories detailed in Supplementary Appendix S1). The best
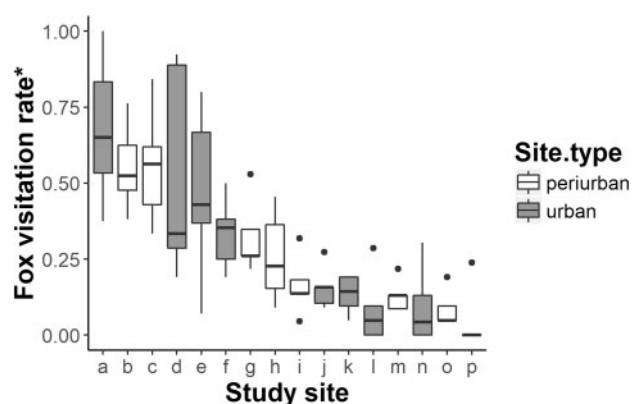
Figure 4: Red fox visitation rates at each study site in Sydney, NSW, Australia. Sites: a = Warwick Farm Racecourse, b = Erskine Biodiversity Corridor, c = Fagan Park, d = Yarrah Reserve, e = Kogarah Golf Club, f = Royal Botanic Gardens, g = Prince Edward Reserve, h = Razorback, i = Elizabeth Macarthur Agricultural Institute, j = Salt Pan Reserve, k = Randwick Racecourse, l = Curl Curl Beach, m = Oxford Falls, n = Macquarie University, o = Western Sydney University (Hawkesbury campus), p = Penrith Landfill Depot. *Fox visitation rate is the proportion of nights with foxes sighted, divided by the total nights of sampling on each station when the lure was present.

Table 1: Best models to explain confident versus timid behaviour of foxes in Sydney, NSW, Australia

Models	AICc	df	ΔAICc
Fox behaviour: cover + site type	165.1	4	0
Fox behaviour: cover + dog restrictions + site type	165.8	5	0.7
Fox behaviour: cover + distance + site type	166.9	5	1.9

In all models, site type was included as a random factor. Lower AICc values indicate better support for the model. Models with differences in AICc (ΔAICc) < 2 are well supported.

model (lowest AICc) for predicting confident behaviour included vegetation cover and site type as fixed effects, and site (location) as a random factor. However, two other models were also acceptable (ΔAICc < 2; Table 1). Red foxes were more confident in urban than peri-urban sites (Fig. 5, $F < 0.01$) and were increasingly confident with increasing vegetation cover in both site types [but this relationship was stronger in urban than peri-urban sites (Fig. 5, $F < 0.001$, grey *cf.* black line)]. In urban sites, the probability of red foxes displaying confident behaviour was 62% (95% CI = 9–80), whereas in peri-urban areas this probability was 50% (95% CI = 41–60).

Temporal activity patterns of red foxes in urban and peri-urban areas

Red fox temporal activity patterns in urban and peri-urban areas showed a mean temporal overlap of 0.88 (95% CI = 0.83–0.94, on a scale from 0 to 1). Peri-urban red foxes tended towards greater morning activity, with some activity extending until midday (Fig. 6a, grey line), whereas urban red foxes tended towards greater night-time activity, with all activity ceasing before 9 am (Fig. 6a, black line).

Temporal activity patterns of red foxes and their potential prey

Red fox and mammalian prey activity patterns had a mean temporal overlap of 0.93 (95% CI = 0.90–0.96, Fig. 6b). Temporal activity patterns of introduced mammals had a slightly higher overlap with red foxes (mean 0.93, 95% CI = 0.90–0.96), than did native mammals (mean 0.90, 95% CI = 0.85–0.94). This contrasts with both native and introduced bird species, which are mainly diurnal (mean overlap 0.14, 95% CI = 0.12–0.17, Fig. 6c).

Comparing between site types, red fox activity patterns overlapped more with that of introduced mammalian prey in urban (mean overlap 0.90, 95% CI = 0.86–0.96) than peri-urban sites (mean overlap 0.84, 95% CI = 0.77–0.91), and was similar to that of native mammalian prey in both site types (peri-urban mean overlap 0.85, 95% CI = 0.78–0.91; urban mean overlap 0.86, 95% CI = 0.78–0.93). Finally, red fox activity patterns overlapped slightly more with birds in peri-urban (0.19, 95% CI = 0.13–0.24) than in urban sites (0.14, 95% CI = 0.10–0.17). Few introduced
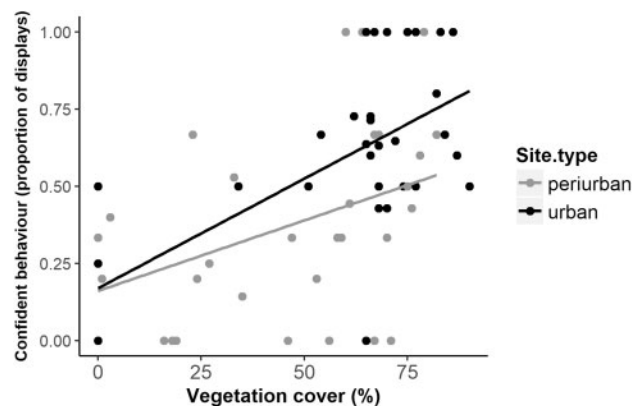
Figure 5: Proportion of confident displays (proportion of confident behaviours scored per camera station, across the total sampling period) in relation to the percentage of vegetation cover and site type. Sydney, NSW, Australia. Each dot on the graph represents a sampling station. The lines represent linear regressions, but these are not related to our statistical analyses, these are only to show the tendency in the data.
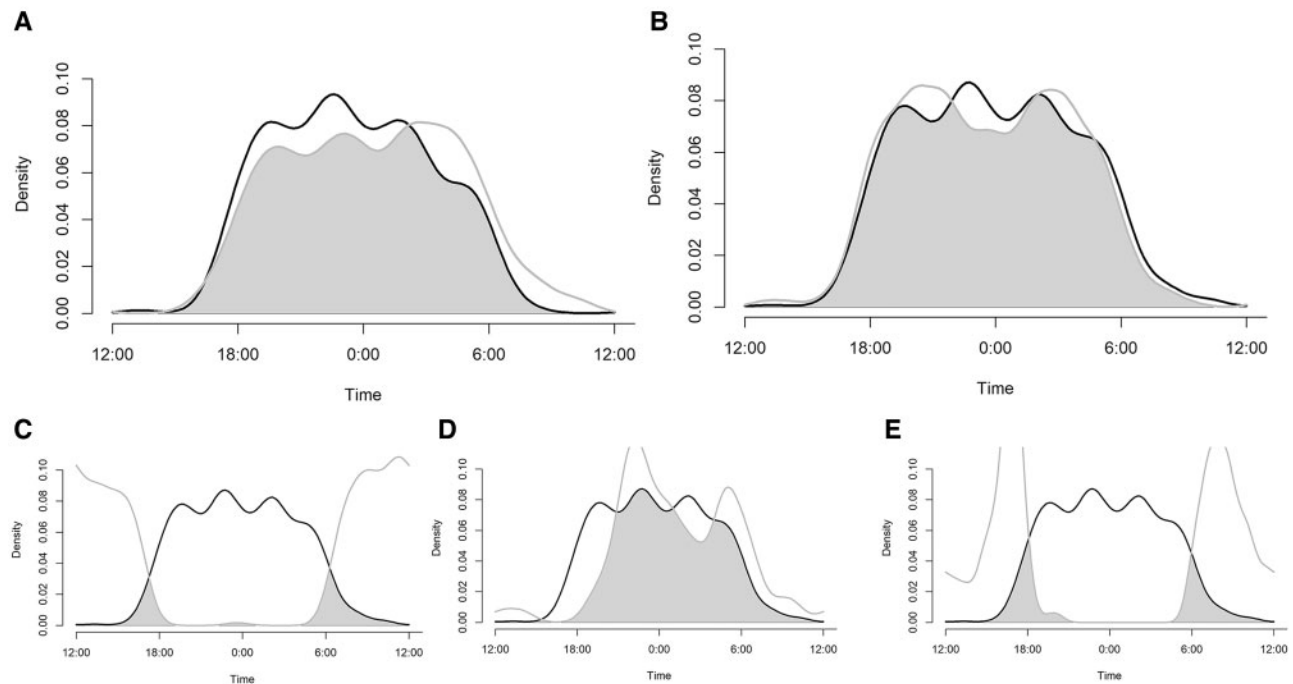
Figure 6: Activity overlaps of the red fox: (**A**) between individuals in urban (black line) and peri-urban areas (grey line), (**B**) the red fox (black line) and mammal prey species (grey line), (**C**) the red fox (black line) and bird prey species (grey line), (**D**) the red fox (black line) and domestic cat (*Felis catus*, grey line), (**E**) the red fox (black line) and domestic dog (*Canis lupus familiaris*, grey line). The shaded areas represent the overlaps. Sydney, NSW, Australia.

birds were recorded in peri-urban areas, so we do not discuss activity patterns of introduced and native birds separately.

Temporal activity patterns of red foxes, cats and dogs

Across both site types, fox activity patterns overlapped much more closely with those of cats (mean overlap 0.78, 95% CI = 0.70–0.87, Fig. 6d) than with dogs (mean overlap 0.20, 95% CI = 0.17–0.24, Fig. 6e). There was little difference in the overlap between red fox and cat activity among site types (mean peri-urban overlap 0.74, 95% CI = 0.61–0.87; mean urban overlap 0.75, 95% CI = 0.65–0.85). Similarly, there was little evidence of a difference in degree of activity pattern overlap between foxes and dogs in peri-urban (mean overlap 0.21, 95% CI = 0.16–0.27) and urban sites (mean overlap 0.23, 95% CI = 0.17–0.29).

Discussion

Our results suggest that urban red foxes in Sydney are more nocturnal and behave more boldly than their peri-urban counterparts (especially when under high vegetation cover). The red fox has been shown to exhibit behavioural plasticity in activity patterns in its native range, which allows it to adapt to environmental changes and prey activity (Díaz-Ruiz et al. 2016). Human (and domestic dog) activity is mostly concentrated in daylight hours, potentially making daytime activity risky for red foxes, particularly in urban areas where humans live in higher densities.

Urban red foxes in this study were significantly more confident than peri-urban red foxes. They were also more confident when protected by dense vegetation cover, with this effect stronger in urban than peri-urban areas. Humans (and dogs) are likely the red foxes' greatest threat in urban areas. Thus, it makes sense that cover should be particularly valued in more densely human/dog populated areas. Similar behavioural

differences have been found in another urban-adapted carnivore, the spotted hyaena (*Crocuta crocuta*), with juveniles living in high-disturbance areas found to be significantly less neophobic and more exploratory than individuals living in low-disturbance areas (Greenberg and Holekamp 2017). Studies from Europe have shown that whilst red foxes may move through areas with or without vegetation cover, they show a clear preference for dense vegetation when denning and resting (Janko et al. 2012; Drygala and Zoller 2013). Together these findings indicate that highly generalist species adjust their activity levels and behaviour in different habitats, including in urban areas (Trewhella and Harris 1988).

Activity patterns are shaped by evolution, but additionally fine-tuned by flexible responses to the environment (Monterroso, Alves, and Ferreras 2013). Shifts towards crepuscular or nocturnal activity have been observed in a range of urban species, including hedgehogs (*Erinaceus europaeus*), coyotes (*C. latrans*), dingoes (*Canis dingo*) and bobcats (*Lynx rufus*; Grinder and Krausman 2001; Ditchkoff, Saalfeld, and Gibson 2006; George and Crooks 2006; Dowding et al. 2010; McNeill et al. 2016). The red fox is primarily nocturnal (Travaini et al. 1993; Lariviere and Pasitschniak-Arts 1996). However, red foxes can benefit from diurnal activity by gaining access to a wider range of prey, and it has been reported mainly for dense habitat with low human activity (Díaz-Ruiz et al. 2016). Therefore, where humans live in lower densities (i.e. peri-urban areas), it makes sense for foxes to extend their active hours into daylight, as we have seen here (Plumer et al. 2014).

At the temporal level, there is a constant and dynamic relation between predator and prey, where the prey attempts to reduce predation risk by decreasing activity overlap with predators, while the latter track down prey by trying to synchronise their activity with them (Lima 2002). Our observed overlaps in temporal activity patterns between red foxes and potential prey were markedly higher than those reported in other red

fox studies. We observed an overlap of 0.90 between red foxes and potential mammalian prey, whereas the largest overlap between mammalian prey and predators reported in another study was 0.60 (Foster et al. 2013). One study reported an overlap of 0.4 between red foxes and rabbits (Díaz-Ruiz et al. 2016), while we observed an activity pattern overlap of 0.95 between red foxes and introduced prey, including rabbits. This suggests high overlap and potential for predatory interactions with introduced mammals in urban and peri-urban areas.

Humans can affect carnivores in both spatial and temporal dimensions via the chance of human encounter and alterations related to urban development (Moll et al. 2018). Thus, in urban areas, both predators and prey could become more nocturnal in order to avoid human activity, suggesting that the prey perceive humans as an equal or bigger threat than their natural predators (Parsons et al. 2016). In urban areas, trophic dynamics have been hypothesised to change due to modifications in biodiversity composition. In these places, there is a remarkable decrease in top predators, which releases mesopredator populations and promotes the invasion of non-native omnivores (El-Sabaawi 2018). Thus, there are undeniable interaction shifts in some species. For example, the cougar (*Puma concolor*), changes its diet from near complete specialisation on native herbivores in wildlands to greater use of exotic and invasive species in urban areas in Colorado, USA (Moss et al. 2016).

Understanding the overlap in red fox and potential prey, temporal activity patterns could indicate the degree to which both species are active at the same time, indicating the potential for predation. In some cases, predators adjust their activity to match that of their main prey, so as to reduce foraging energy expenditure (Foster et al. 2013). The red fox has been shown to exhibit behavioural plasticity in activity patterns in its native range, which allows it to adapt to environmental changes and prey activity (Díaz-Ruiz et al. 2016). Seasonal fluctuation in the diet of red foxes has been shown in natural pine-wood Mediterranean forests, with the activity of red foxes highly dependent on the activity of prey during the warm season (Lovari, Valier, and Lucchi 1994).

There is very recent research conducted in our study city, Sydney, that shows that the urban environment favours an increase in size in red foxes so that individuals are now larger than their non-urban counterparts (Stepkovitch et al. 2019). Given that both native and non-native prey are potentially available to red foxes in cities, it would be useful to understand the degree to which each prey type is potentially vulnerable to fox predation. Still, further research on diet and prey selection is required to ascertain whether bigger red foxes impact a broader range of native species in urban environments (Stepkovitch et al. 2019).

The temporal sympatry of a predator and its potential prey species does not always mean that the predator controls prey numbers. For example, city rats can persist in high densities, even in the presence of domestic cats, just by altering their space-use (Parsons et al. 2018). Furthermore, shifts in food web dynamics are likely to be common in urban ecosystems (Faeth et al. 2005; El-Sabaawi 2018). Urbanisation can alter trophic dynamics by reducing top-down control through multiple mechanisms and by increasing bottom-up forcing through the greater availability of anthropogenic food (Fischer et al. 2012).

In urban areas, anthropogenic resources, when available, have been reported to be the main component of the diet of red foxes. These resources could include pet food, kitchen waste, wrappers and other indigestible items, and remains of processed food such as pasta or cheese (Contesse et al. 2004; Panek and Budny 2017). It has been shown that where there is an abundant supply of human subsidies, red foxes consume less wild prey (Reshamwala et al. 2018). If red foxes are largely satiated by anthropogenic food resources, it may reduce the role of the red fox as a pest controller as well as a threat to native species, or conversely it could support higher populations than would otherwise be present without anthropogenic foods.

Little is known about the interactions between wild and domestic predators (Krauze-Gryz et al. 2012). The interactions reported so far include spatial avoidance of dogs (George and Crooks 2006; Vanak and Gompper 2010), lethal interactions for domestic cats (Plumer et al. 2014) and evidence of disease transmission (Mackenstedt, Jenkins, and Romig 2015). We observed a high overlap in red fox and cat activity, while the overlap was much lower for red foxes and domestic dogs. The higher overlap with cats is likely due to their nocturnal activity patterns. Although foxes are generally known to fear dogs as apex predators (Krauze-Gryz et al. 2012), we do not propose that the low degree of overlap here is suggestive of an avoidance or fear of dog predation. Rather, dogs in cities are generally kept in yards or indoors at night, and their diurnal activity is related to that of humans—e.g. through dog-walking. In our records, some of the dogs were clearly accompanied by humans, but most of them were not. We cannot discard the presence of the owners given that most of the individuals wore collars, we interpreted this as indicating ownership and hence domesticity. The red foxes in this study might therefore have avoided human activity, more so than they avoided dog activity (George and Crooks 2006). Further research on urban red fox anti-predator behaviour in response to dogs would resolve this possibility.

Conclusions

Our results suggest that red foxes are more confident in urban than in peri-urban areas, which is likely related to the range of novel habitats and anthropogenic resources to which foxes are exposed in cities. Boldness may better enable urban red foxes to profit from anthropogenic resources. This shows how flexible red foxes can be, learning the times or places to avoid and the resources to exploit, in order to thrive within a growing city. Nevertheless, even though red foxes appear well-adapted to urban environments, they still avoid human activity in both urban and peri-urban areas. Although urban foxes are currently cryptic and barely noticed by human urban residents, repeated human exposure in urban environments may lead to continued increases in boldness and habituation, with the potential to result in a greater number of fox–human interactions.

The flexibility of red foxes is potentially leading to burgeoning urban populations in Australia, which does not bode well for urban native wildlife. Foxes and their prey show modified activity and behaviour in cities. We conclude that red foxes have overcome many of the challenges posed by the life in the city, thanks to their behavioural plasticity. We must have a deeper understanding of how red foxes are interacting with urban species, whether native, domestic or introduced, in order to be aware of their direct and indirect impacts on these species.

Supplementary data

Supplementary data are available at *JUECOL* online.

Acknowledgements

Data availability

The data produced in this study are available upon reasonable request for the purposes of verification or further analyses.

Ethics statement

This study was approved by the Animal Ethics Committee of Macquarie University, under the Ethics Reference Number 5201800006. Also, we worked under the Scientific licence number SL102038.

Conflict of interest statement. None declared.

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