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I. Castañeda, C. Bellard, I. Jarić, B. Pisanu, J.-L Chapuis, et al.. Trophic patterns and home-range size of two generalist urban carnivores: a review. Journal of Zoology, 2018, 307 (2), pp.79-92. 10.1111/jzo.12623 . hal-02179251

HAL Id: hal-02179251

https://hal.sorbonne-universite.fr/hal-02179251

Submitted on 10 Jul 2019

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Trophic patterns and home-range size of two generalist urban carnivores: a review

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Keywords
diet; home range; red fox; domestic cat; anthropogenic habitats; trophic pattern; urban carnivores; predation.

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Abstract

Foxes and cats are the most abundant medium-sized urban carnivores. To date, however, there has been a lack of effort to synthesize data on the spatial and trophic resources used by these two carnivores, despite the importance of this information for assessing their similarity and roles in urban food webs. In this paper, we first synthesize all available information on the trophic patterns and home-range size of these two predators based on a total of 91 studies. Second, we conduct statistical analyses to test the influence of environmental and biological variables such as regional differences, habitat characteristics, age, and sexual status on their home-range size and diet patterns within urban habitats, and then evaluate the methods used to investigate these components. Our findings highlight the lack of studies that simultaneously monitor the diet and home-range size of both predators within urban habitats. To the best of our knowledge, this is the first study to compare fox and cat home-range size and diet. Foxes exhibited larger ranges than cats, while intact cats showed larger home ranges than desexed cats. Diet diversity obtained for both predators confirmed their trophic plasticity within urban habitats. Both predators consumed fewer mammals and invertebrates in highly disturbed habitats compared to medium ones. We also found that the procedure of data acquisition significantly influenced fox and cat home-range sizes. In terms of diet, the type of recovered samples had a significant effect on the diet composition of both predators. To improve our understanding of the relative impact of these two urban carnivores on urban wildlife, we recommend simultaneously studying both species in future studies. Moreover, methodological standards for both diet and home-range size studies are needed to allow comparisons.

Introduction

Among medium-sized (<5 kg) carnivore species, red foxes (*Vulpes vulpes*) and domestic cats (*Felis silvestris catus*) (hereafter foxes and cats, respectively) are the most abundant species associated with human settlements (Flockhart, Norris & Coe, 2016; Lombardi *et al.*, 2017). Foxes are one of the most widespread carnivores; while they originated from the Middle East (Statham *et al.*, 2014), today they are present in all continents with the exception of Antarctica. Specifically, British foxes derived from Central European populations (Edwards *et al.*, 2012), North American foxes differ from their European counterparts (Sacks *et al.*, 2011; Leite *et al.*, 2015), while Australian foxes were introduced by humans from Europe (Macdonald & Reynolds, 2004). Cats were probably domesticated in the early Neolithic period (i.e. 9000 years ago; Driscoll *et al.*, 2007), becoming ubiquitous residents of human settlements. The habitat use (Gehring & Swihart, 2003; Saito & Koike, 2015) and foraging behavior (Mirmovitch, 1995; Contesse *et al.*, 2004) of these two species allow them to establish urban populations (Bateman & Fleming, 2012), as they make use of a wide range of wild and anthropogenic resources through fragmented urban landscapes (Meckstroth, Miles & Chandra, 2007; Krauze-Gryz, Żmihorski & Gryz, 2017).

In human-altered habitats, home-range sizes have been studied for over 50 years for foxes (Storm, 1965) and over 30 years for cats (Panaman, 1981). The home-range size of urban foxes (Gloor, 2002; Gosselink *et al.*, 2003) is usually greater than that of cats (Mirmovitch, 1995; Barratt, 1997; Schmidt, Lopez & Collier, 2007). Adult foxes use larger areas than juveniles do (Rosatte & Allan, 2009), while the opposite has been recorded for urban cats (Morgan *et al.*, 2009). Males display larger home-ranges than females for both foxes (White, Saunders & Harris, 1996) and cats (Liberg *et al.*, 2000). Although the sexual status of cats may heavily influence home-range size within urban areas (Baker *et al.*, 2010), previous findings did not show any difference between intact and desexed individuals (Guttilla & Stapp, 2010; Hall *et al.*, 2016). However, current home-range sizes are inferred using a wide range of calculation methods, making it difficult to disentangle the role of habitats and species specificities to explain variations (Laver & Kelly, 2008).

The diet of generalist predators such as foxes and cats depends on prey abundance that may vary temporally and spatially (Paltridge, 2002; Krauze-Gryz *et al.*, 2017). Birds and small rodents are usually found in fox and cat diets within urban and suburban habitats (Meckstroth *et al.*, 2007; Krauze-Gryz *et al.*, 2017). The diet of urban or suburban foxes and cats is also characterized by the use of anthropogenic refuse as a food resource (Mirmovitch, 1995; Contesse *et al.*, 2004). However, diet analyses may be affected by the method used to infer prey composition and abundance (e.g. carried home vs. eaten *in situ*; Krauze-Gryz *et al.*, 2017).

Comparisons between fox and cat home-range size or diet are needed in order to determine the similarities and differences regarding these two key ecological features. This knowledge would help us to understand and quantify the impact of these predators, which could exert synergic predation on the same prey populations. Simultaneous monitoring of fox and cat home-range size or diet has been conducted in wild habitats, showing high similarities between the two species (Catling, 1988; Molsher, 1999; Risbey, Calver & Short, 1999; Krauze-Gryz *et al.*, 2012). Recently, it was demonstrated that in such habitats (foreshores of Lake Burrendong), fox removal results in a decrease in cat home-range size and an increase in cat consumption of invertebrates and carrion (Molsher *et al.*, 2017). Within human-altered habitats, the abundance and impact of these predators can strongly vary, meaning that ecological information is required to improve management and/or control measures.

In this paper, we conducted an extensive literature review to compare fox and cat home-range size and diet patterns in urban and suburban habitats. Our aims were first to summarize available knowledge on these two key ecological components for both species, which are currently understudied in comparative studies despite their similar role as predators in urban ecosystems, and examine the possible competition between the two species. Based on current knowledge, we expected that foxes and cats would exhibit similar home-range size and diets, with species-specific biological features and habitat properties influencing home-range size. Second, we aimed to test how the distinct methodologies used to analyze diet or space use would consistently alter the biological inferences in comparative studies. Finally, we aimed to discriminate the environmental variables (i.e. level of disturbance) that could explain differences in home-range size and diet for both predators.

Materials and methods

Sample selection criteria

First, we conducted a complete literature review using the online bibliographic database ISI Web of Knowledge to search for studies monitoring foxes and cats in urban and suburban habitats (Fig. 1). Specifically, we used the following keywords for foxes ('*Vulpes vulpes*' OR 'fox'), cats ('*Felis silvestris catus*' OR '*Felis catus*' OR 'cat'), and urban and suburban habitats ('urban' OR 'suburban' OR 'exurban' OR 'city' OR 'metropolitan' OR 'municipal' OR 'non-rural' OR 'peri-urban'). The keywords were combined as follows: one predator species AND one urban synonym. We then refined results by selecting the following categories from the Web of Science: zoology, ecology, biodiversity and conservation, multidisciplinary sciences, biology, evolutionary biology and development biology. We also explored references in the literature of the selected papers. We automatically screened the abstract and title of each relevant publication using R programming language (version 1.1.423) with functions from the 'tm' package. First, we removed punctuation, whitespaces, and link words to analyze the words within the titles and abstracts. Second, we used the 'grepl' function to search the words related to diet and home-range size (i.e. 'diet', 'intake', 'nutrition', 'food', 'menu', 'aliment', and 'comestible' for diet, and 'spatial use', 'home range', 'movement pattern', 'territory' and 'utilization distribution' for home range size). Finally, publications containing these words were screened manually. We retained studies that: (1) focused on foxes and/or cats; (2) were conducted in urban or suburban areas; and (3) described home-range size and/or (4) quantified diet. This resulted in a total of 91 studies. For each study, we reported the region (Africa, Asia, Europe, North America, or Oceania), location of the study site, home-range size, as well as diet information.

Home-range size

Home-range size can be calculated using different methods that are listed in Table 1. Each method can be assessed using a predetermined percentage of independent fixes. For each study, we recorded the number of independent fixes used to calculate home-range size, the temporal interval of these fixes, and the data acquisition procedure (i.e. triangulation or automatic localization). We also reported the weight of the collars used and the animals studied. The age (juvenile or adult), sex and sexual status (intact or desexed) were taken into account as biological characteristics of the studied individuals.

Diet patterns

Diet in the selected studies was based on the analysis of scats, stomachs and prey items brought to the owner's home. For each study, we recorded the sample types, sample sizes and

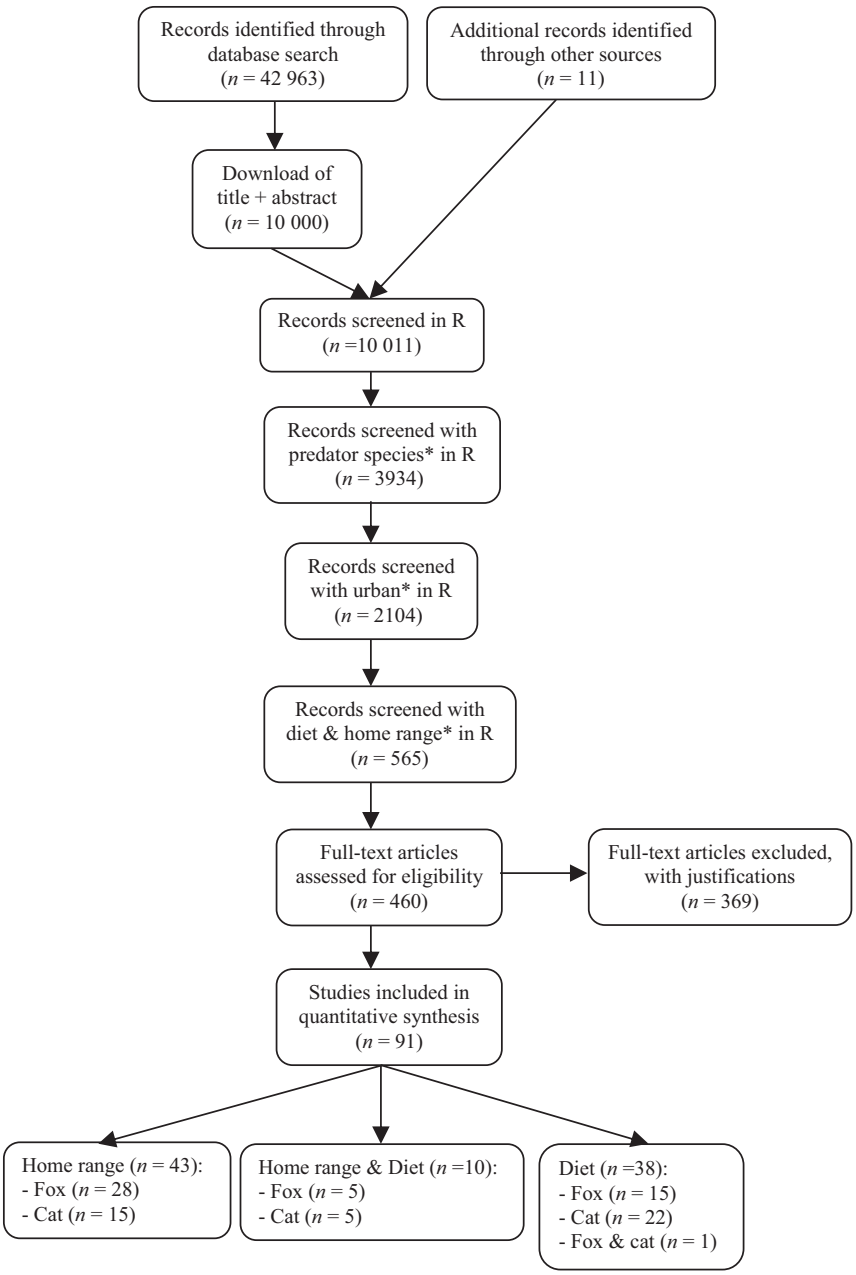


Figure 1 PRISMA diagram flow. * and synonyms.

number of prey categories. We considered eight main prey categories: mammal, bird, reptile, amphibian, invertebrate, fish, fruit and anthropogenic refuse. Then, we calculated the percentage of relative frequency of occurrence (% RFO) as the number of occurrences of each prey category multiplied by 100 and divided by the total number of occurrences of all prey categories in all samples. We also determined diet diversity using Levin's standardized index (B_A) (Krebs, 1989) with the following formula:

where n is the number of prey categories and P is the proportion of records for each prey category (i). The standardized form of the formula is thus:

where B is Levin's index of niche breadth and B_{max} is the total number of prey categories. B_A ranges from 0 to 1. For a complete generalist individual $B_A = 1$, while the value decreases with greater specialization.

Additional variables

Although the selected studies were conducted in urban and suburban areas, in order to quantify the degree of anthropogenic habitat pressure, we used the Anthropogenic Biomes of the World spatial layer, Version 2: 1900–2000 (Ellis *et al.*, 2010). This database represents a global spatial dataset of the

Table 1 Description of the variables used in statistical data analysis

Group of variables	Factor	Levels	Global home-range size (ha)	Fox home-range size (ha)	Cat home-range size (ha)	Diet diversity (BA)	RFO prey$_i$
Methodological variables	Calculation methods	Fixed Kernel (95%) (FK 95%)	✓				
		Kernel Density (50%) (KDE 50%)					
		Kernel Density (90%) (KDE 90%)	✓				
		Kernel Density (95%) (KDE 95%)	✓				
		Minimum Convex Polygon (100%) (MCP 100%)	✓				
		Minimum Convex Polygon (75%) (MCP 75%)	✓				
		Minimum Convex Polygon (95%) (MNP 95%)	✓				
	Procedure of data acquisition	Automatic localization	✓	✓	✓		
		Triangulation	✓	✓	✓		
	Type of sample	Scat				✓	✓
		Stomach				✓	✓
		Prey items				✓	✓
	RFO prey$_i$						✓
Environmental variables	Habitat	Low anthropogenic pressure (LAP)	✓	✓	✓		
		Medium anthropogenic pressure (MAP)	✓	✓	✓	✓	✓
	Region	Europe	✓	✓	✓	✓	✓
		North America	✓	✓	✓	✓	✓
		Oceania	✓	✓	✓	✓	✓
Biological variables	Predator	Red fox (*Vulpes vulpes*)	✓			✓	✓
		Domestic cat (*Felis silvestris catus*)	✓			✓	✓
	Age	Adult		✓			
		Juvenile		✓			
	Sexual status	Intact			✓		
		Desexed			✓		

anthropogenic transformation of the biosphere through direct human interaction with ecosystems for the period 1900–2000, including agriculture and urbanization. Anthropogenic transformation within each biome is estimated using population density, agricultural intensity (cropland and pastureland) and urbanization. The biomes are divided into 19 subclasses and grouped in six main classes: dense settlements (urban and other dense settlements), villages (dense agricultural settlements), croplands (land used mainly for annual crops), rangelands (land used mainly for livestock grazing and pasture), semi-natural lands (inhabited land with minor use for permanent agriculture and settlements) and wild lands (land without human populations or substantial land use). We excluded the classes of semi-natural and wild lands, because this study focuses on urban and suburban habitats. We then reclassified the four remaining classes into two categories given the low number of studies found in each category: high anthropogenic pressure (HAP) (dense settlements and villages) and medium anthropogenic pressure (MAP) (croplands and rangelands). The degree of anthropogenic pressure was determined using a buffer (based on mean home range in each study) around the central point of the study location. We plotted the localizations in R Studio (R Core Team, 2016) using raster (Hijmans *et al.*, 2017), sp (Hijmans *et al.*, 2018), rgdal (Bivand *et al.*, 2018a), and rgeos (Bivand *et al.*, 2018b) packages.

Statistical analysis

For each dataset (53, 33 and 20 studies for the global, fox, and cat home-range size models, respectively), we first calculated variance inflation factors to detect collinearity. A cut-off value of 3 can be used to remove collinear variables (Zuur *et al.* 2009). Home range estimates as the dependent variable were log-transformed prior to analyses to ensure normality and homogeneous variances. Because observations were not independent (i.e. multiple observations within the same study), we used linear mixed models to fit the statistical models. First, we constructed a full model with all likely influencing variables (calculation method, procedure of data acquisition, region, habitat and predator species) for the home-range size (Table S1). We included study.ID and animal.ID (individuals or group of individuals within studies) as random factors in order to take into account variations between and within studies. Then, we selected by a stepwise backward elimination procedure of the least significant terms ($P > .05$) to determine the best adequate minimal model (i.e. the best-performing model had the best trade-off between goodness of fit and model simplicity). We analyzed two full additional models, one for each predator species (Table S1). In these models, in addition to study.ID and animal.ID, we included the calculation method as the random factor because of its significant influence on home-range size estimations.

Diet data was described using the diet diversity index and % RFO of prey categories. As not all eight prey categories were reported in the studies, only the prey categories with at least 10 observations > 0% RFO were used to fit the models. Diet diversity was sine-transformed before analysis, and the % RFO of the main reported prey categories (mammals, birds and invertebrates) were square-root transformed before analysis to ensure normality and homogeneous variance. Because observations were not independent (i.e. multiple observations within the same study), we also used linear mixed models with the study.ID as random variables to analyze diet diversity and variation in the % RFO (Table S1). The Kenward-Rogers method was used to generate the approximate denominator degrees of freedom. Post-hoc multiple comparisons of means were conducted using the Bonferroni test. All analyses were performed in R studio. We used the lmer functions from the 'lme4' package (Bates *et al.*, 2007), the step function from the 'lmerTest' package (Kuznetsova, Brockhoff & Christensen, 2016), corvif from the 'lsmeans' package (Lenth, 2016), and glht from the 'multcomp' package (Hothorn *et al.*, 2007, 2010).

Results

We obtained a total of 91 studies dating from 1934 to 2016, of which 43 studies exclusively reported home range (28 for foxes and 15 for cats), 10 studies involved both home-range size and diet (five for foxes and five for cats) and 38 studies addressed diet (15 for foxes, 22 for cats and 1 for both foxes and cats) (Table S2 for home range and S3 for diet studies). Overall, 62 studies were carried out in MAP habitats, while 28 studies were conducted in HAP habitats. Regarding regions, 38 studies were carried out in Europe, 30 in North America, 15 in Oceania, six in Asia, and only one in Africa. By consequence, studies from Asia and Africa were not included in the statistical models.

Home-range size

The best models to predict home-range size of red foxes and cats within urban habitats are shown in Table S1 in Supporting Information. A synthesis of the analyzed studies on home-range size is available in Table S2 in Supporting Information.

A positive trend was observed in publication output on home-range size for different home-range calculation methods used (Figure S1a). However, publishing rate was relatively low, when compared with the general publishing rate within the Web of Science (Figures S1b and S2).

Among the 53 home-range size studies analyzed, home-range sizes were generally monitored for both males and females in 45 of the analyzed studies (85%), with the number of studied individuals ranging from one (4%) (i.e. Macdonald, 1980) to 55 (Haspel & Calhoon, 1987). Thirty-eight studies (72%) only monitored adult home-range size. Thirty-three studies (64%) reported the number of independent fixes, ranging from 20 (Hough 1980) to 24 202 (Woollard & Harris, 1990). The most frequent method for data acquisition was triangulation (85%), followed by automatic localization (13%). The majority of studies (76%) used only a single method to calculate home-range size, while 23% used at least two methods. Only a single study (Gehrt *et al.*, 2013) calculated home-range size using three different methods (MCP, fixed kernel, and local convex hull). The two most frequently used calculation

methods were MCP 100% and kernel density estimation 95%. MAP habitats were more represented in the dataset (68%) compared to HAP habitats (32%). Most home-range studies were conducted in Europe (40%), followed by North America (32%), Oceania (19%), Asia (8%) and Africa (2%).

Within predator species, foxes exhibited significantly larger home ranges than cats (118.00 ± 30.81 ha and 77.40 ± 27.27 ha, respectively) (Table 2, Fig. 2b).

With respect to the factors that might separately be able to influence the home-range size of each species, fox home-range size was significantly affected by the life stage of individuals ($F_{1,2}$ = 6.84, P = .0096). Juvenile foxes exhibited significantly smaller home-range sizes compared to adults (102.46 ± 32.06 ha and 176.88 ± 38.94 ha, respectively) (Table 2; Fig. 2c). Cat home-range size was affected by the sexual status of the individual ($F_{1,2}$ = 24.56, P = 2.015e-06), with larger values observed for intact cats compared to desexed cats (77.64 ± 30.45 ha and 2.33 ± 1.29 ha, respectively) (Table 2; Fig. 2d).

Home-range size of both predators was significantly affected by the calculation methods ($F_{5,6}$ = 47.67, P < 2.2e-16), procedure of data acquisition ($F_{1,2}$ = 9.38, P = .0033), and predator species ($F_{1,2}$ = 17.04, P = .0003). Although calculation method is one of the significant factors influencing home-range size, this is only due to the different percentage of fixes among the methods; by contrast, the home-range sizes obtained using the same percentage of fixes (e.g. Fixed Kernel 95% vs. MCP 95%) were not significantly different (Table 2). Data acquisition using triangulation produced significantly larger home ranges than the automatic localization of individuals (107.50 ± 24.86 ha and 57.42 ± 28.79 ha, respectively) (Table 2; Fig. 2a).

Diet patterns

The best models to predict diet patterns of red foxes and cats within urban habitats are shown in Table S1 in Supporting Information. A synthesis of the analyzed studies on diet is available in Table S3 Supporting Information.

Table 2 Mixed linear model with log home-range size (ha) of both predator species (global model), red foxes (fox model), and domestic cats (cat model) as dependent variables, and the method of calculation, procedure of data acquisition, predator species, age and sexual status as explanatory variables. Monitored animal groups (nested within studies) and study ID were used as random variables, and in the fox and cat models, calculation methods were also used as random variables. Test statistics are given for the final model achieved by a stepwise backward elimination procedure of the least significant terms from a global model based on the predicted relationship and likely interactions. Only levels of explanatory variables with at least 10 observations were included in models to avoid powerless analysis

	Global model			Fox model			Cat model		
	B	CI	*P*	*B*	CI	*P*	*B*	CI	*P*
Fixed parts									
(Intercept)	0.04	−0.51 to 0.59	0.881	1.72	1.38 to 2.07	**<0.001**	−0.02	−0.050 to 0.46	0.938
KDE 50%	−0.73	−1.00 to −0.46	**<0.001**						
KDE 90%	−0.31	−0.55 to −0.08	**0.010**						
KDE 95%	−0.09	−0.36 to 0.18	0.503						
MCP 100%	0.16	−0.04 to 0.36	0.110						
MCP 75%	−0.85	−1.14 to −0.57	**<0.001**						
MCP 95%	−0.30	−0.51 to −0.09	**0.006**						
Triangulation	0.81	0.29 to 1.33	**0.003**						
Fox	1.01	0.53 to 1.49	**<0.001**						
Juvenile				−0.19	−0.32 to −0.05	**0.010**			
Intact							0.74	0.45 to 1.04	**<0.001**
Random parts									
σ^2		0.080			0.067			0.094	
$\tau_{00,\ Animal.ID:Study.ID}$		0.192			0.059			0.304	
$\tau_{00,\ Study.ID}$		0.535			0.248			0.289	
$\tau_{00,\ method}$					0.058			0.166	
$N_{Animal.ID:Study.ID}$		405			183			166	
$N_{Study.ID}$		41			19			18	
N_{method}					4			5	
$ICC_{Animal.ID:Study.ID}$		0.238			0.136			0.356	
$ICC_{Study.ID}$		0.662			0.575			0.339	
ICC_{method}					0.135			0.195	
Observations		678			247			359	
$R^2/\Omega_0{}^2$		0.969/0.968			0.902/0.894			0.933/0.931	

Levels of explanatory variables – Method of calculation: Fixed Kernel 95% (FK 95%), Kernel Density 50% (KDE 50%), Kernel Density 90% (KDE 90%), Kernel Density 95% (KDE 95%), Minimum Convex Polygon 100% (MCP 100%), Minimum Convex Polygon 95% (MCP 95%), and Minimum Convex Polygon 75% (MCP 75%). Procedure of data acquisition: automatic localization and triangulation. Predator species: cat and fox. Age: adults and juveniles. Sexual status: intact and desexed. Bold values indicate significant results.

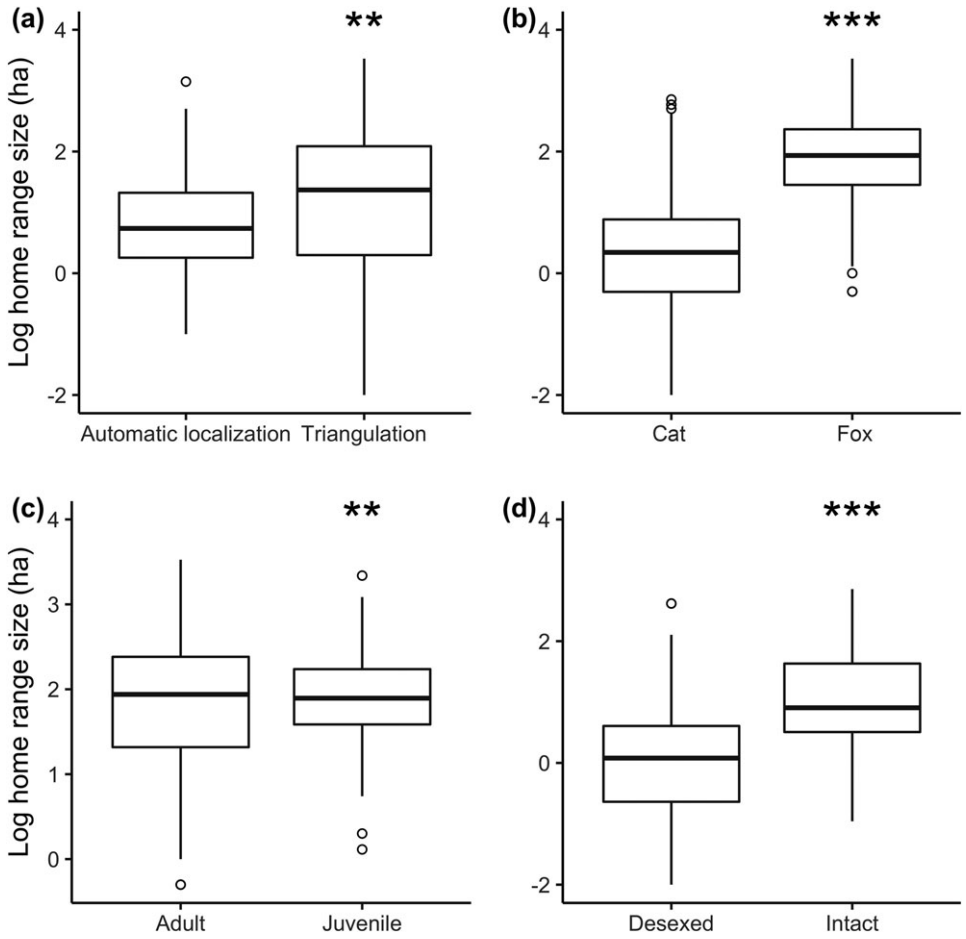


Figure 2 Estimated home-range size (ha) (log-transformed; means ± SE based on: (a) procedure of data acquisition, (b) predator species, (c) fox home-range size based on individual age, and (d) cat home-range size based on sexual status. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

As with studies on home-range size, there was a weak positive trend in publication output on fox and cat diet for different diet samples used (Figure S1b), but the publishing rate was considerably lower than the general growth rate of scientific publication (Figure S2).

Among the 48 diet studies analyzed, 20 analyzed fox diet (42%), 27 cat diet (56%) and one both predator diets (Meckstroth *et al.*, 2007). The most frequently reported type of diet samples for cats were items brought to the owners' house (42%), whereas scats were the most frequent sample type for foxes (44%). Sample sizes ranged from 25 (Cavallini, 1992) to 14 370 (Woods *et al.*, 2003). The number of prey categories ranged from one to seven, with a mean of four categories per study. MAP habitats (77%) were more frequent than HAP habitats (27%) among diet studies, which were mostly conducted in Europe (44%), followed by North America (31%), Oceania (17%) and Asia (8%). No diet studies were carried out in Africa.

We calculated diet diversity based on the % RFO of prey categories contained in diet studies, showing that foxes had a similar diet diversity (0.44 ± 0.05) to cats (0.39 ± 0.03). The principal prey category in fox and cat diet studies were mammals (48 and 71%, respectively). The secondary prey category in fox studies was anthropogenic refuse (19%) and in cat studies was invertebrates (4%) and anthropogenic refuse (4%) as well. Mean diet diversity was slightly higher in HAP habitats (0.49 ± 0.06) than MAP habitats (0.38 ± 0.03). Across regions, diet diversity was slightly higher in Asia (0.47 ± 0.16) compared to the other regions (Europe: 0.44 ± 0.05; N. America: 0.39 ± 0.04, and Oceania: 0.37 ± 0.04). Nevertheless, diet diversity was not significantly influenced by region, degree of anthropogenic habitat pressure, type of samples, or predator species (Table 3).

The % RFO of invertebrates was significantly affected only by the % RFO of the two other main prey categories of mammals ($F_{1,1}$ = 48.35, P = 1.35e-09) and birds ($F_{1,1}$ = 14.19, P = .0003), as well as the type of habitat ($F_{1,2}$ = 4.31, P = .0419). When the % RFO of birds and mammals increased, the % RFO of invertebrates decreased (Fig. 3a,b, respectively). Diet comprised a lower % RFO of invertebrates in HAP compared to MAP habitats (Fig. 3c). The % RFO of mammals was also significantly affected by the type of habitat

($F_{1,2}$ = 9.26, P = .0032). We found that both predators fed significantly less on mammals in HAP compared to MAP habitats (Table 3; Fig. 3d). The % RFO of birds was significantly affected by the type of samples ($F_{2,3}$ = 29.39, P = 2.316e-10) and predator species ($F_{1,2}$ = 10.22, P = .0024). The % RFO of birds was significantly lower in scats and stomachs than prey items. Moreover, foxes consumed significantly more birds than cats did (Table 3; Fig. 3d).

Discussion

Home-range size

To our knowledge, this is the first study to compare fox and cat home-range size within urban and suburban habitats based on the published literature. We found that foxes exhibit larger home ranges than cats in human-altered habitats (118.00 ± 30.81 ha and 77.40 ± 27.27 ha, respectively). This result suggests that the degree of these predators' relation with humans likely explains their home-range size. Because foxes are wild carnivores, they must find their own food resources and shelter sites, while cats rely on humans to obtain these resources (Moodie, 1995). In wild land habitats, such as open forests in New South Wales, Molsher (1999) found fox and cat home-range sizes to be similar, thus supporting our hypothesis that the respective wild and domestic character of foxes and cats may explain the larger home ranges of foxes in the selected studies. Compared with other urban carnivores, the home-range sizes found for foxes and cats in this study are smaller than those of jackals in farmlands near the town of Dinsho in southern Ethiopia (Admasu *et al.*, 2004), similar to those of urban dingoes in peri-urban areas of Queensland (Allen *et al.*, 2013) – probably due to the smaller body size of jackals compared to dingoes – and larger than those of free-roaming domesticated male dogs in the city of Puerto Natales (Chile) (Perez *et al.*, 2018) – probably due to the dogs' high site fidelity to their owner's home as described by the authors.

The lack of significant influence of environmental variables (habitat and region) on fox and cat home-range size suggests that the predators' spatial behavior is similar at these scales. Our findings showed that juvenile foxes were characterized by smaller home ranges than adults (102.46 ± 32.06 ha and 176.88 ± 38.94 ha, respectively), which is consistent with previous studies conducted in similar habitats (i.e. Frafjord, 2004; Rosatte & Allan, 2009) and with juvenile philopatry (Baker *et al.*, 1998; Robertson, Baker & Harris, 2000).

Regarding cats, only sexual status affected their home-range size. Specifically, intact cats displayed larger home ranges than their desexed counterparts (77.64 ± 30.45 ha and 2.33 ± 1.29 ha, respectively), which might indicate the behavioral effects of sterilization. This result contrasts with the available data for feral cats (Guttilla & Stapp, 2010) as well as pet and farm cats (Hall *et al.*, 2016) in which desexing did not reduce home-range size. Thus, while cat sterilization may reduce home-range size, its impact could be more concentrated (not lower). Future studies should delimit the extent of these biological features on cat home-range size in order to better understand the spatial ecology of cats.

Table 3 Mixed liner model with the sine-transformed B_A (diet diversity), square root of % RFO of mammals, birds, and invertebrate as dependent variables, and habitat, predator species, type of samples, and % RFO of invertebrates, mammals, and birds as explanatory variables. Study ID was used as a random variable. Test statistics are given for the final model achieved by a stepwise backward elimination procedure of the least significant terms from a global model based on the predicted relationship and likely interactions. Only levels of explanatory variables with at least 10 observations were included in models to avoid powerless analysis

	BA model			RFO mammal			RFO bird			RFO invertebrate		
	B	CI	*P*	*B*	CI	*P*	*B*	CI	*P*	*B*	CI	*P*
Fixed parts												
(Intercept)	0.40	0.35 to 0.45	**<0.001**	7.88	7.31 to 8.45	**<0.001**	29.28	22.89 to 35.66	**<0.001**	5.84	4.84 to 6.84	**<0.001**
RFO invertebrate				−0.08	−0.10 to −0.05	**<0.001**						
HAP				−1.32	−2.17 to −0.47	**0.003**				−0.90	−1.74 to −0.05	**<0.042**
Scats							−20.36	−26.28 to −14.43	**<0.001**			
Stomachs							−20.77	−26.83 to −14.71	**<0.001**			
RFO mammal							−0.08	−0.17 to 0.01	0.104	−0.05	−0.06 to −0.04	**<0.001**
Fox							9.59	3.71 to 15.46	**0.002**			
RFO bird										−0.05	−0.07 to −0.02	**<0.001**
Random parts												
$N_{Study.ID}$	44			44			44			44		
$ICC_{Study.ID}$	0.505			0.713			0.497			0.569		
Observations	89			89			89			89		

Levels of explanatory variables – Habitat: HAP = high anthropogenic pressure and MAP = medium anthropogenic pressure. Type of samples: scats, stomachs, and prey items. Predator species: cat and fox. Bold values indicate significant results.

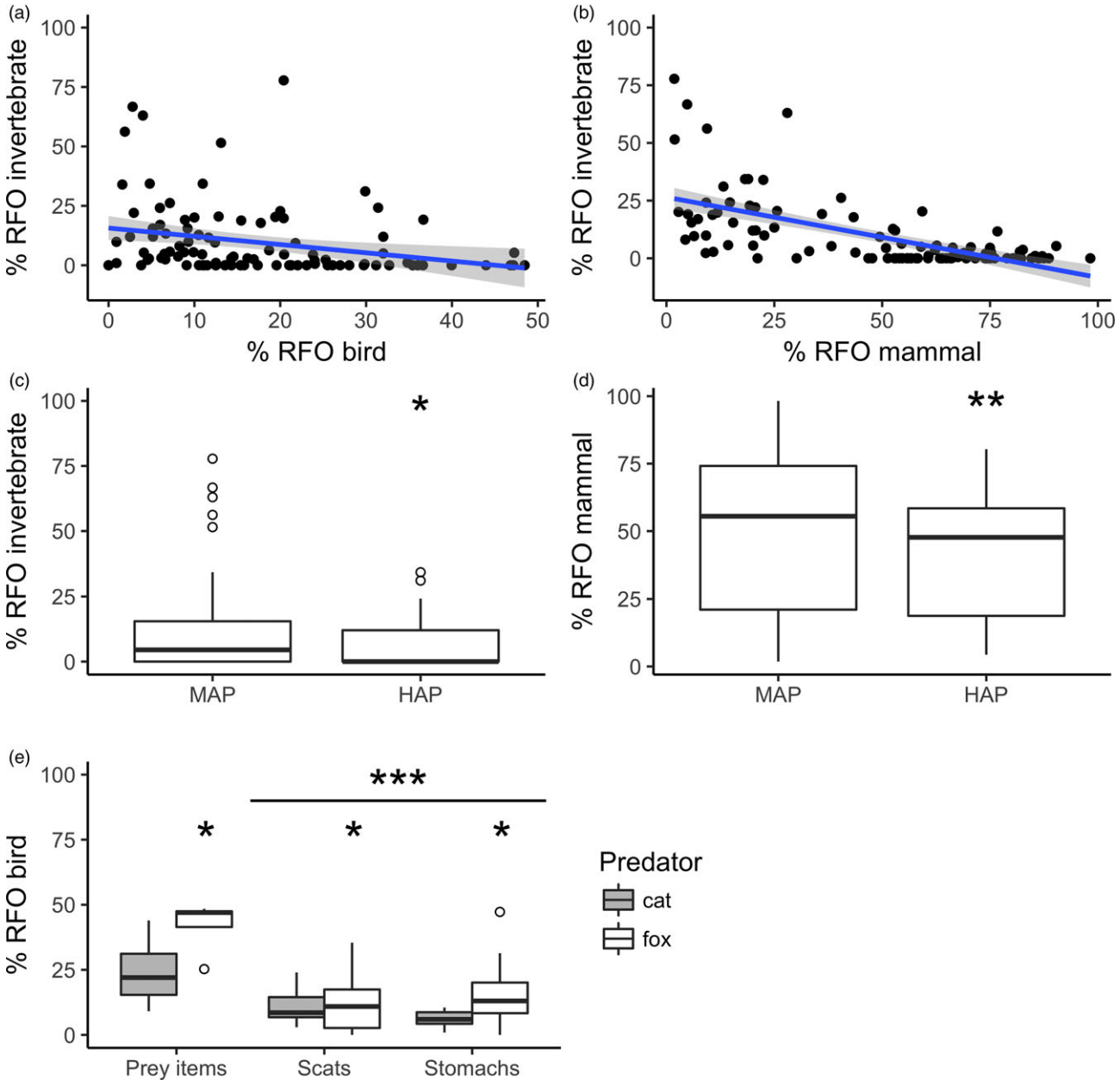


Figure 3 Predators' diet composition: (a) percentage of relative frequency of occurrence (% RFO) of invertebrate versus % RFO bird; (b) % RFO of invertebrate versus % RFO mammal; (c) % RFO invertebrate by habitat; MAP = medium anthropogenic pressure and HAP = high anthropogenic pressure; (d) % RFO mammal by habitat; (e) % RFO bird by predator species and sample types. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com].

Our results showed that the home-range size of both predators obtained using the same percentage of fixes did not differ, thus supporting the reliability of assessed home-range sizes as determined with different calculation methods but the same percentage of fixes. Home-range sizes estimated with triangulation were 50% larger than those estimated with automatic localizations, which led to overestimating the activity areas of monitored individuals and consequently the spatial delimitation of their different activities (i.e. reproduction, rest, feeding). This difference in home-range size obtained using the triangulation or automatic localization of individuals may be due to the lower accuracy of the former method (Springer, 1979; White & Garrott, 1986). Although the greater use of triangulation (80%) is probably due to the low costs of the equipment, we recommend using more accurate procedures such as the automatic localization of individuals, which, despite being

more expensive, are much less time-consuming and currently better adapted to respond accurately to the spatial ecological questions.

Diet patterns

Our results show that fox and cat diet diversity was similar. To the best of our knowledge, this is the first study in which fox and cat diet diversity and composition have been compared within urban and suburban habitats. The lack of significance between fox and cat diet diversity contrasts with the results of Molsher (1999) and Risbey *et al.* (1999) who respectively found fox diet diversity to be significantly higher and lower than cat diet diversity. Mammals were the principal prey category in the reviewed fox and cat diet studies, while anthropogenic refuse (for foxes) and both anthropogenic refuse and invertebrates (for cats) were the secondary prey categories. Mammals were also the principal prey category in the studies conducted by Meckstroth *et al.* (2007) and Krauze-Gryz *et al.* (2017) in human-altered habitats. In addition, the use of anthropogenic refuse by the urban populations of foxes and cats has been highlighted by other authors (i.e. Mirmovitch, 1995; Contesse *et al.*, 2004) in urbanized areas.

Compared with other urban carnivores, mammals were also the principal prey category of coyotes in the Denver urban area (Poessel, Mock & Breck, 2017), golden jackals in Serbia (Ćirović *et al.*, 2014) and dingoes in peri-urban habitats of Queensland (Allen *et al.*, 2016).

We showed that the consumption of the main reported prey categories (mammals, birds, and invertebrates) varied depending on the different factors considered: prey category, predator species, habitat, and type of recovered samples. There was a significant negative relationship between the consumption of invertebrates and vertebrates by both predators. This negative relation might be due to the nutrient composition of each prey category and/or the metabolism of the predators. For instance, the metabolic energy provided to free-ranging cats from invertebrate prey items is higher than those provided by birds or mammals (Plantinga, Bosch & Hendriks, 2011). We also found that both invertebrates and mammals were consumed at a lower rate in highly disturbed habitats. This result may reflect the influence of two non-exclusive effects: the high availability of anthropogenic food refuse, synanthropic birds and mammals, and ornamental fruits in more urbanized habitats (McKinney, 2008) and/or the negative effect of urbanization on prey invertebrate and mammal populations, which are more abundant in highly disturbed habitats (Gentili, Sigura & Bonesi, 2014).

Even so, among the vertebrates consumed by foxes, birds represent a higher % RFO compared to those consumed by cats. This consumption preference of foxes highlights the need to specifically study the trophic behavior of generalist carnivore species, as it may have a contrasting impact in urban trophic webs. However, this result should be considered with caution, as the % RFO of birds highly depends on the type of sample recovered.

Foxes and cats may directly impact the abundance of urban prey (through predation) or indirectly by consuming anthropogenic food refuse (interference). This *top-down effect* of predators on prey species abundance has been described by Fischer *et al.* (2012) but it is rarely studied (cf. this review) in urban and suburban habitats, where two types of food resources may be found: natural and commensal. Thus, these two predators can have contrasting effects, as they can (i) negatively impact depleted populations of natural prey and/or (ii) control through predation the spatial and/or temporal boosting abundance of commensal prey.

Future directions

In a context of global change, widespread and potentially overabundant predators such as foxes and cats need further attention, as changes in their population dynamics may significantly disrupt ecosystem structure, function, and services.

We identified intra- and interspecific differences in the home-range sizes and diets of foxes and cats. The highly flexible spatial and trophic behaviors of foxes and cats demonstrated in this review will influence predator impacts on prey population dynamics, that will deserve further investigations and considerations to optimize management strategies in these human-altered habitats.

Although foxes and cats are two common predators, the future increase in urbanized areas will not have the same effect on these predator populations. While fox populations will lose their natural habitats, this species is able to efficiently use urban habitats to maintain or even increase their populations. It is also likely that the number of cats will continue to increase within urban areas, while the number of prey killed by cats will probably be higher than at present (i.e. Loss & Marra, 2017; Woinarski *et al.*, 2017). Thus, management policies based on their ecological features such as home-range size and diet patterns should be applied. We thus strongly advocate for more studies to investigate the home-range size and diet of these two generalist species in urban and suburban habitats following our recommendations regarding the design of such monitoring. Indeed, we detected a significant effect of methodology when investigating home-range size and diet of both predators. We also clearly detected the effects of biological and local environmental variables (degree of anthropogenic habitat pressure). Therefore, and not surprisingly, our findings suggest that future studies dealing with home ranges should be conducted with as many individuals as possible, a more even distribution of sexes, different age classes (i.e. juveniles and adults), and different sexual statuses (intact and desexed) when applicable.

Regarding diet studies, the types of samples recovered may influence the evaluation of diet composition, since they contain different proportions and types of prey. As highlighted in MAP habitats, cat diets are commonly studied through the analysis of scats and stomachs (Pearre & Maass, 1998; Turner & Bateson, 2000), whereas in HAP habitats, prey items brought to the owner's house are more commonly assessed (Kays & Dewan, 2004; Baker *et al.*, 2005; Flux, 2007). We thus recommend encouraging cat owners to recover cat scats to allow for study comparisons. We also suggest indicating major taxonomic prey

categories (mammalian, avian, etc.) as well as more precisely identifying the lower taxonomic categories (up to the level of species, when possible). Moreover, the % RFO is often an insufficient descriptor of predator diet (Medina *et al.*, 2008). Other suitable descriptors such as the minimum number of prey items contained in scats and ingested biomass are required to calculate different trophic indexes that will help to decipher predator diet, the consequences for prey populations, and predator-prey interactions more generally. Finally, we recommend simultaneously monitoring prey densities or using prey density data to provide more complete data on predation pressure and impact on prey populations.

Acknowledgments

We acknowledge Ecology Population and Community group members for their pertinent comments at the beginning of the study. We are grateful to the editor and two anonymous reviewers who helped to improve our paper. We also thank B. Castagneyrol for helping with the statistical analyses. We are grateful to D. Zarzoso-Lacoste for the useful discussions. This work was supported by a Region Ile-de-France Ph.D. scholarship for IC.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Table S1. Best models to predict home-range size and diet patterns of red foxes and cats within urban habitats

Table S2. Synthesis of analyzed home-range studies with details on publication (first author and year of publication), environmental features (habitat (HAP = high anthropogenic pressure; MAP = medium anthropogenic pressure) and region), predator species and methodologies (mean number of independent fixes, interval of fixes, home-range calculation, collecting data (triangulation/automatic location), collar and animal weight, number, age (A = adult; J = juvenile; A&J = Adult & Juvenile), sex (Male = male; F = Female; M&F = male and female) and sexual status (I = Intact; D = Desexed; I&D = Intact and Desexed) of studied individuals)

Table S3. Synthesis of analyzed diet studies with details on publication (first author and year of publication), environmental features (habitat (HAP = high anthropogenic pressure; MAP = medium anthropogenic pressure) and region), predator species, sample types (stomachs, scats or prey items), sample size, number of prey categories, percentage of relative frequency of occurrence for nine main prey categories (mammal, bird, reptile, amphibian, invertebrate, fish, fruit, anthropogenic, unidentified)

Figure S1. Cummulative publication output during 1975–2015 on home-range size (a) and diet (b) of red foxes and domestic cats in urban habitats, for different home-range calculation methods and diet samples used

Figure S2. Relative increase (%) in the number of studies on home-range size and diet of red foxes and domestic cats in urban habitats during 1981–2015 (1981 was standardized to 100% for each dataset); relative increase in the number of publications in the entire Web of Science (WoS) is shown for comparison.