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Authors: Kauhala, Kaarina, Talvitie, Kati, and Vuorisalo, Timo

Source: Folia Zoologica, 64(1) : 45-55

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v64.i1.a6.2015

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Folia Zool. – 64 (1): 45–55 (2015)

Free-ranging house cats in urban and rural areas in the north: useful rodent killers or harmful bird predators?

Kaarina KAUHALA[1]*, Kati TALVITIE[2] and Timo VUORISALO[2]

[1] *Natural Resources Institute Finland, Itäinen Pitkäkatu 3A, 20520 Turku, Finland; e-mail: kaarina.kauhala@luke.fi*
[2] *Department of Biology, University of Turku, 20014 Turku, Finland; e-mail: timo.vuorisalo@utu.fi*

Received 9 December 2014; Accepted 30 March 2015

Abstract. The prey of 66 free-ranging urban and rural house cats *Felis catus* was studied in a mainland area in SW Finland. The data included 1624 home-brought prey animals, of which 92 % could be identified at least to the class level. The mean number of prey brought home was 4.1 per cat per month (excluding winter). Rodents were the most common prey (72 %), 18 % of prey being birds, 5.4 % insectivores, and the rest other mammals (hares, least weasels, pine martens, and a bat), reptiles or amphibians. Six "super predator" cats accounted for 40 % of all prey items captured. There were no differences between the sexes in the number or diversity of prey brought home. The prey of young cats was more diverse than that of older, more experienced cats. Especially old cats in rural areas benefit humans by killing many rodents. The proportion of birds captured was 24 % in urban areas where cats represent a possible threat to native birds: probably > 1 million prey animals are monthly killed by free-ranging cats in Finland, at least 144000 of these being birds. "Super predator" cats should thus be kept in the house, especially in urban areas, to prevent predation on birds.

Key words: birds, domestic cat, *Felis catus*, predation, rodents

Introduction

The domestic cat *Felis catus* is the most widespread and probably also the most abundant mammalian carnivore inhabiting almost all terrestrial ecosystems of the world (Ebenhard 1988). It has been introduced in the wild by man, accidentally or deliberately to control pest animals, into all continents except the mainland Antarctica (e.g. Ebenhard 1988, Pearre & Maass 1998, Courchamp et al. 2003, Baker et al. 2010). Domestic cat is considered as one of the 100 worst invasive alien species in the world (Lowe et al. 2004), and according to Ebenhard (1988) it is the most dangerous predator ever introduced by man. Feral cats can have a great influence on native animal populations, especially on seabirds on oceanic islands (e.g. Kirkpatrick & Rauzon 1986, Ebenhard 1988, Pontier et al. 2002, Courchamp et al. 2003, Faulquier et al. 2009, Bonnaud et al. 2011).

Due to human assistance the population density of domestic cats is usually not limited by disease, food availability or lack of shelter, and therefore their numbers are usually high, especially in urban areas and villages (Baker et al. 2005, Silva-Rodrigues & Sieving 2011, Tschanz et al. 2011). Together with other medium-sizes carnivores, they belong to the carnivore guild in mainland rural areas (Kauhala & Holmala 2006, Kauhala et al. 2006, Holmala & Kauhala 2009). Free-ranging house cats may be the most abundant and dominant predators, especially in fragmented urban habitats where they can kill a large number of native animals (Baker et al. 2005, Sims et al. 2008, van Heezik et al. 2010, Tschanz et al. 2011). The fact that most house cats are fed by their owners is no obstacle to outdoor predation by free-ranging cats (Meek 1998, Woods et al. 2003, Tschanz et al. 2011).

Felids are obligate carnivores, and feline cats are physiologically adapted to several small meals per day (MacDonald et al. 1984, Bradshaw et al. 1996). The domestic cat is an opportunistic hunter and has a more varied diet than any other cat species (Kitchener 1991, Baker et al. 2010). It is a skillful solitary hunter that preys on mammals, birds and to a lesser extent on other prey, even insects (e.g. Pearre & Maass 1998, Faulquier et al. 2009, Bonnaud et al. 2011). Cats are also known to scavenge (Konecny 1987, Pontier et al.

* *Corresponding Author*

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2002). Cats switch between their main prey animals according to their availability (Liberg 1984, Pontier et al. 2002, Kays & DeWan 2004). Birds may be the preferred prey, especially on islands, but when their numbers decline cats may shift their attention to rodents (Bloomer & Bester 1990). Domestic cats can be considered beneficial when they prey on rodents but more often they are considered detrimental to native fauna, such as seabirds (e.g. Bloomer & Bester 1990, Fitzgerald et al. 1991, Pearre & Maass 1998, Peck et al. 2008, Faulquier et al. 2009).

On mainland areas rodents, rabbits *Oryctolagus cuniculus* and, in Australia, reptiles are usually the main prey of cats (Liberg 1984, Woods et al. 2003, Tschanz et al. 2011, Yip et al. 2014). Habitat composition within the cat's feeding territory probably influences the selection of prey of a generalist predator and, thus, predation habits between urban and rural cats may differ. Cats living in villages and urban areas may prey more often on birds than those living in the surrounding countryside (Churcher & Lawton 1987, Barratt 1997a, Woods et al. 2003, Baker et al. 2005). Season may also affect the predation rate of cats: as juveniles are easier to catch than older animals, the number of prey killed may be greatest in the breeding season of wildlife (Baker et al. 2005).

The predation rate of individual cats may vary according to age, sex or personal characters, some cats being "super predators" (e.g. Tschanz et al. 2011). Due to their experience older cats may be more effective predators than young individuals. Physical condition of the cat may also affect its success as a predator. As birds are in general more difficult to catch than ground-dwelling mammals, young and very old cats probably are less successful bird hunters than experienced middle-aged cats in a good physical condition (Woods et al. 2003).

Most studies of the prey of domestic cats have been carried out on island ecosystems (e.g. Karl & Best 1982, Nogales & Medina 1996, Peck et al. 2008, Bonnaud et al. 2011) and in Australia (e.g. Jones & Coman 1981, Catling 1988, Paltridge et al. 1997, Kutt 2011). Fewer studies exist from mainland ecosystems in Europe (Liberg 1982, 1984, Woods et al. 2003, Tschanz et al. 2011, Krauze-Gryz et al. 2012). We investigated the effects of the environment (urban *versus* rural) and season, as well as the age and sex of cats on the composition and diversity of the prey brought home by free-ranging house cats at a high latitude mainland area in SW Finland. To our knowledge this is the northernmost area where the prey of domestic cats has been investigated. The aim was also to estimate the possible benefits or threats of free-ranging house cats to native fauna in urban and rural areas. Specifically, we predicted, based on the above mentioned studies that (1) there are "super predators" among cats which kill the majority of prey, (2) on mainland areas, urban cats bring home more birds than their rural conspecifics and, (3) the prey of inexperienced young cats is more diverse, and young cats bring home fewer birds than older cats.

Material and Methods

An inquiry of the prey brought home by free-ranging house cats was carried out from July to November 2009 and from March to December 2010. Cat owners were recruited by us to participate in the research project by leaving announcements in the notice-boards of shops and local newspapers. Forty-two cat owners with 66 cats which brought some prey home participated in the project. The cat owners lived in or around the city of Turku, SW Finland (60°27′ N, 22°16′ E, Fig. 1). The cats were classified as urban or rural on the basis of their owners' address (in a population centre or not). A population centre is a group of buildings with at least 200 inhabitants and where the distance between houses is usually less than 200 m (Statistics Finland 2014a). Most cat owners in Turku live in row or detached houses. People residing in blocks of flats do not usually let their cats roam out freely.

Cat owners were asked to report the age and sex of their cats, and their address. Thirty-four cats were rural and were 32 urban (Table 1). Ten cats were 0-2 years old ("young"), 22 were 3-6 years old ("middle-aged") and

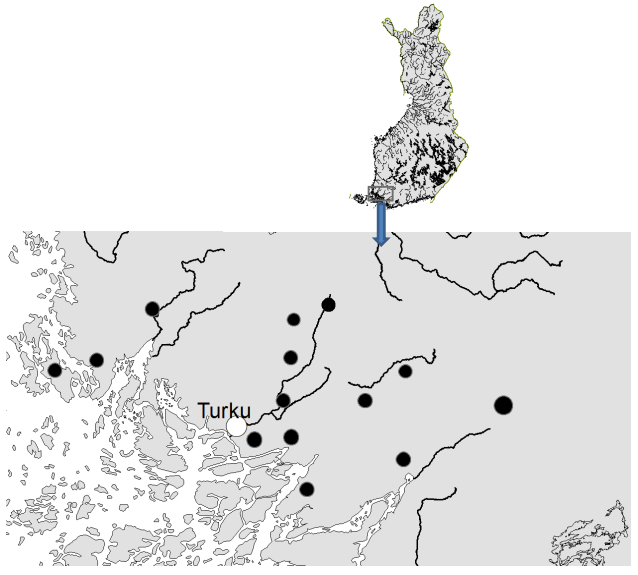


Fig. 1. The city of Turku and rural places in SW Finland from where cat owners sent the reports of the prey their cats brought home.

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Table 1. Cat data with known sex and age (females + males). Breeding season of prey animals: March-July, Autumn: August-December. Young: 0-2 years, middle-aged: 3-6 years, old: > 3 years.

Area	Females	Males	Young	Middle-aged	Old	Unknown age	Total
Rural							
Breeding season	18	15	0 + 4	5 + 3	12 + 8	1 + 0	33
Autumn	18	14	0 + 4	6 + 2	11 + 8	1 + 0	32
Urban							
Breeding season	15	7	1 + 5	9 + 2	3 + 0	2 + 0	22
Autumn	19	10	1 + 5	11 + 3	5 + 2	2 + 0	29

28 were 7-18 years old ("old"). Classification to age groups was done according to Tschanz et al. (2011). The number of females was 39 and that of males 25. The information of age and sex was missing for some cats. There were more old cats in rural than in urban areas ($\chi^2 = 8.5$, df = 2, P = 0.014). The sex ratio of cats did not differ between areas ($\chi^2 = 0.4$, df = 1, P = 0.511). Most (67 %) cat owners gave us information on whether the cats were neutered or not. Ninety-five percent of their cats were neutered, only two females were intact.

Cat owners reported the date, place and description of prey animals brought home by their cats. The owners were asked to take a photograph of the prey, if they were not able to identify it. To help the identification, instructions for identifying typical prey animals were sent to the cat owners. Unfortunately not all owners were even then able to identify the prey species but recorded only the class of the animal (e.g. mammal or bird). Some prey animals could not be identified due to their poor condition or because there were only some internal organs left.

The mean number of months when the prey of the cats was monitored by a household was 5.8 (range 1-12 months). The data for January and February were excluded because the mean temperatures were the lowest in this period (Finnish Meteorological Institute 2014), and cats were practically inactive due to coldness and the thick snow cover (George 1974, oral information by cat-owners). A radio-tracking study done simultaneously with diet data collection in Turku area also showed that cats did not move outdoors when the temperature fell below +5 °C (K. Talvitie, unpublished data).

The identified prey animals were classified into six groups: insectivores (*Sorex* spp. and *Talpa europaea*), rodents, lagomorphs, other mammals, birds and reptiles (this category included amphibians). Reptiles and amphibians are ectotherms usually available as prey only in the warm season. The unidentified prey animals (if not even the class was known) were excluded from the analyses (but were included in the numbers of prey brought home). The prey animals were also classified into those killed in the breeding season of wildlife (March-July, "breeding season") and into those brought home in late summer or autumn (August-December, "autumn").

The frequency of occurrence (FO) of each prey category for each cat was calculated according to the formula: FO = 100* the number of the prey item/ total number of prey items the cat brought home. FO was calculated when the cat brought home > 14 prey animals because, when the sample size is very small, FO is not reliable. The variables affecting the FO of different prey categories were analysed with ANOVA. Independent variables were the sex and age group of cats (young, middle-aged or old) and area (rural or urban). A stepwise procedure was done and variables with P > 0.10 were excluded starting from the one with the highest P-value. The normality of distributions was tested from residuals with a Kolmogorov-Smirnov test. Relationship between the exact age of the cat and the FO of each prey item was tested with the Spearman rank correlation analysis. Because almost all cats in the two seasons were the same individuals, the sign test was used when comparing the effect of season on the FO of different prey items. Differences in the prey numbers between the cat groups or seasons were tested with the Kruskal-Wallis analysis of variance.

The Shannon-Wiener diversity index (H) for prey of different cat groups (urban *vs.* rural, sex and age groups) was calculated using the formula: $H = -\sum p_i (\ln p_i)$ where p_i is the proportion of each prey type (FO/100).

Overlap indices were also calculated to find out the possibility of competition for prey between cat groups (male *vs.* female, age groups) according to the formula (Southwood 1978): $1 - 0.5 \sum I p_1 - p_2 I$ where p_1 is the proportion of each food item (FO/100) for cat group one and p_2 the proportion of each food item for cat group 2.

Another inquiry was also carried out to inhabitants of areas with row and detached houses in the city of

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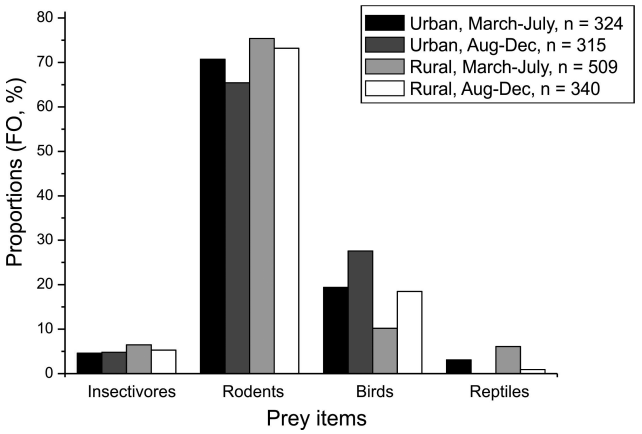


Fig. 2. The proportions (FO, %) of different prey brought home by domestic cats in urban and rural areas in different seasons in SW Finland (the city of Turku and surrounding rural areas). N gives the number of prey items. Reptiles include amphibians.

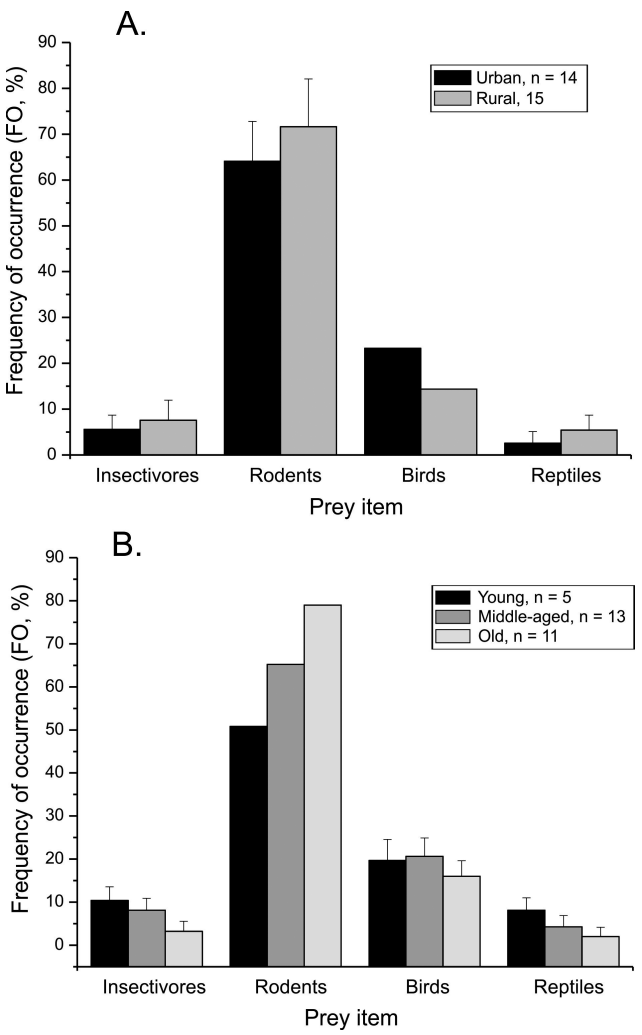


Fig. 3. Predicted values of FO (frequency of occurrence; mean, SD) for each prey category of rural and urban cats (A), and of cats of different age groups (B). Cats which brought home > 14 prey animals were included. N gives the number of cats.

Turku. People were asked to report, whether they had a cat or not, whether their cat was let out to range free

Table 2. Different mammal and bird species among the prey brought home by domestic cats in the city of Turku and in rural places in SW Finland.

Mammals
Rodents
striped field mouse *Apodemus agrarius*
yellow-necked mouse *Apodemus flavicollis*
water vole *Arvicola amphibious*
harvest mouse *Micromys minutus*
field vole *Microtus agrestis*
house mouse *Mus musculus*
bank vole *Myodes glareolus*
Siberian flying squirrel *Pteromys volans*
brown rat *Rattus norvegicus*
red squirrel *Sciurus vulgaris*
Insectivores
common shrew *Sorex araneus*
Eurasian least shrew *Sorex minutissimus*
Eurasian pygmy shrew *Sorex minutus*
mole *Talpa europaea*
Other mammals
European hare *Lepus europaeus*
rabbit *Oryctolagus cuniculus*
bat Chiroptera sp.
least weasel *Mustela nivalis*
pine marten *Martes martes*
Birds
Passerines
tree pipit *Anthus trivialis*
Bohemian waxwing *Bombycilla garrulus*
European greenfinch *Carduelis chloris*
Eurasian siskin *Carduelis spinus*
hawfinch *Coccothraustes coccothraustes*
domestic pigeon *Columba livia domestica*
hooded crow *Corvus corone*
yellow hammer *Emberiza citrinella*
European robin *Erithacus rubecula*
European pied flycatcher *Ficedula hypoleuca*
common chaffinch *Fringilla coelebs*
Eurasian jay *Garrulus glandarius*
white wagtail *Motacilla alba*
coal tit *Parus ater*
blue tit *Parus caeruleus*
great tit *Parus major*
house sparrow *Passer domesticus*
Eurasian tree sparrow *Passer montanus*
common redstart *Phoenicurus phoenicurus*
willow warbler *Phylloscopus trochilus*
magpie *Pica pica*
dunnock *Prunella modularis*
Eurasian bullfinch *Pyrrhula pyrrhula*
goldcrest *Regulus regulus*
redwing *Turdus iliacus*
song thrush *Turdus philomelos*
fieldfare *Turdus pilaris*
Other birds
common swift *Apus apus*
common pheasant *Phasianus colchicus*

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Table 3. Results of ANOVA (Stepwise procedure). Dependent variables were the FOs (frequency of occurrence) of different prey categories. Independent variables were sex, age group (young, middle-aged, old) and area (urban, rural). Test results with P < 0.05 are included. Reptiles include amphibians. Normality of distributions was tested with a Kolmogorov-Smirnov test, and only the tests with P > 0.05 are presented in the table. Sample sizes were too small to study the interactions between area and age group.

Independet variable	Dependent variable	F	df	P
Insectivores	Age group	5.2	2, 25	0.013
	Area	5.0	1, 25	0.034
Rodents	Age group	7.0	2, 25	0.004
Birds	Area	4.9	1, 32	0.034
Reptiles	Age group	3.8	2, 25	0.037
	Area	5.2	1, 25	0.031

Table 4. Correlations (Spearman rank correlation) between the FO (frequency of occurrence) of different prey items and the exact age of the cat, and between the FO of different prey items. Results with P < 0.05 (r_s > I0.36I) are included.

Correlations between FO of prey and the cats' age		
	r_s	n
All cats		29
Age*insectivores	–0.48	
Age*rodents	0.65	
Age*birds	–0.38	
Rural cats		15
Age*insectivores	–0.53	
Age*rodents	0.64	
Age*reptiles	–0.42	
Urban cats		14
Age*insectivores	–0.41	
Age*rodents	0.58	
Age*birds	–0.44	
Correlations between FO of prey items (all cats)		
Rodents*insectivores	–0.41	
Rodents*birds	–0.75	
Mammals total*birds	–0.89	
Mammals total*reptiles	–0.43	

and whether the free-ranging cats brought prey home. In this way the total number of free-ranging cats that bring home prey in the Turku area was estimated. Answers from 168 inhabitants in the city of Turku were received.

Results

According to the answers from cat owners, their cats brought home altogether 1624 prey animals. Eighteen cats (27 % of cats) brought home > four prey animals per month (altogether 1055 animals, 65 % of prey animals), and six cats (9 %) brought home at least eight animals per month (655 animals, 40 %). Two of these "super predators" were 10-year-old males, one was an 8-year-old female, and two were middle-aged females. These five cats were neutered. The age and information of neutering of one female was unknown. Four "super predators" were rural cats, one was urban and one spent time both in the town and countryside.

The mean number of prey brought home was 4.1 per cat per month (range 1-18). The mean values were 4.4 for rural and 3.5 for urban cats, 3.5 for young, 3.8 for middle-aged and 4.4 for old cats, and 4.0 for females and 4.4 for males. The mean number of prey brought home during the breeding season of wildlife was 5.0 and during autumn 3.8 per cat per month. None of the differences in the number of prey between the cat groups were, however, significant (P > 0.05, Kruskal-Wallis analysis of variance).

The total number of identified prey animals was 1488 (Fig. 2). Most prey animals were mammals (n = 1178, 79.2 % of all identified prey items), mainly rodents (n = 1070, 71.8 %) but also insectivores (n = 81, 5.4 %; Table 2). Other mammals included European hares *Lepus europaeus*, (n = 22, 1.5 %), one rabbit, a couple of least weasels *Mustela nivalis*, pine martens *Martes martes* and a bat. Eighteen percent of prey items were birds (n = 265). About 50 % of all birds and 99 % of identified birds were Passeriformes (Table 2). Cats also killed some reptiles (vipers *Vipera berus*, common lizards *Zootoca vivipara*, a slow worm *Anguis fragilis*) and amphibians *Rana* sp. (n = 45, 3 %). Cats did not bring home invertebrates but five cats were seen to catch them (one spider, four dragonflies, and two moths). One owner described that his cat had eaten carrion.

The diversity index for the prey of urban cats was slightly greater than that for the prey of rural cats (H_{urban} = 0.90, H_{rural} = 0.85). The diversity index for the prey of young cats was greater than that for the prey

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of old cats (H_{young} = 1.12, $H_{middle\text{-}aged}$ = 1.01 and H_{old} = 0.73). The diversity index was almost similar for the prey of both sexes (H_{males} = 0.91 and $H_{females}$ = 0.88). Overlap between the prey brought home by males and females was almost complete (index = 0.99). The overlap index between the prey of young and middle-aged cats was high (0.94), that between the prey of middle-aged and old cats was slightly lower (0.86), and that between the prey of young and old cats was the lowest (0.77).

Results of ANOVA indicated that age group and area affected the FO of different prey items brought home by cats (Fig. 3, Table 3). Sex had no effect on the FO of any of the prey categories. Young cats brought home insectivores and reptiles (including amphibians) more often than old cats (young cats: insectivores FO = 10.4 %, reptiles 8.1 %; old cats: insectivores 3.2 %, reptiles 2.0 %). Old cats brought home rodents more often (79 %) than younger ones (61 %). FO for insectivores and reptiles was higher in rural than in urban areas (rural: insectivores 7.6 %, reptiles 5.4 %; urban: insectivores 5.6 %, reptiles 2.6 %), whereas FO for birds was higher in urban (23.6 %) than in rural (13.7 %) areas. Correlations between the exact age of cats and the FO of prey items indicated a positive relationship between the cats' age and the FO of rodents (rural and urban cats), and a negative relationship between the cats' age and the FO of insectivores (rural and urban cats), birds (urban cats) and reptiles (rural cats, Table 4). The FO of rodents correlated negatively with that of insectivores and birds, and the FO of mammals total correlated negatively with that of birds and reptiles.

The prey composition of 54 cats was monitored in both seasons. The results of the sign test indicated that the FO of reptiles was higher in the breeding season of wildlife than in autumn (P = 0.001). The FO of birds tended to be higher in autumn than in the breeding season (P = 0.055). No differences between the seasons existed in the FO of other prey items.

According to the other inquiry, 42 % of the households in row and detached houses in the city of Turku reported that they had at least one cat, and 41 % of the cats were roaming free. Thus, 17 % of households had at least one cat roaming free, and 79 % of these brought prey home, i.e. 14 % of all households had a cat which brought prey home.

Discussion

Sources of error in a questionnaire study

There are some well-known sources of error in the prey-brought-home method (e.g. Krauze-Gryz et al. 2012). Cat owners may leave some of the home-brought prey undocumented, and cats do not bring home all of their prey (Kays & DeWan 2004, Loyd et al. 2013). The total numbers of killed prey animals may thus be higher than the numbers reported by cat owners (Tschanz et al. 2011). However, Kays & DeWan (2004) reported that the observed kill rate of cats was 5.5 prey animals per cat per month in summer in Albany, USA. In the present study, cats brought home five prey animals per month in the breeding season, which is close to the value given by Kays & DeWan (2004).

Furthermore, the cat owners' ability to identify prey correctly is limited, which may lead to errors in the estimated prey composition. As the analyses in the present study were based on main animal categories, this source of error was probably small. The proportion of prey brought home may also vary between prey species: rodents and birds are probably eaten more often than shrews and amphibians which are usually brought home (Krauze-Gryz et al. 2012). Krauze-Gryz et al. (2012) found, however, that an analysis based on prey brought home provided similar results of the percentages of mammals (total) as did an analysis based on scat and gut contents. Identification problems in the present study probably did not concern some unusual but easily identified prey species such as the common viper, the slow worm, pheasant (*Phasianus colchucus*), European hare and magpie (*Pica pica*).

Numbers of prey

The cats brought home about four prey animals per cat per month (except the winter months which were excluded from the data). The number was higher than that in a rural village in Switzerland in spring (2.29, Tschanz et al. 2011). However, unlike the study by Tschanz et al. (2011) results in the present study concerned cats which brought home at least one prey animal. In the inquiry about cat densities, cat owners reported that 79 % of cats which were allowed to roam free brought some prey home. The value for all free-ranging house cats in Turku area would thus be 3.2 prey animals per cat per month, and 4.0 for the breeding season, i.e. almost twice as much as that for the Swiss cats (Tschanz et al. 2011). Differences between habitats and prey densities likely affect the numbers of prey brought home by cats.

The prey numbers per cat were not evenly distributed: as predicted, a small number of cats brought home the majority of prey. "Super predators" indeed exist among house cats (Churcher & Lawton 1987, Gillies & Clout 2003, Tschanz et al. 2011). In the present study, these cats were old or middle-aged cats, both males and females. The most effective predators are

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sometimes young cats (Churcher & Lawton 1987, Gillies & Clout 2003, Woods et al. 2003, Morgan et al. 2009, van Heezik et al. 2010, Loyd et al. 2013), whereas sometimes no correlation between age and predation efficiency has been observed (Calver et al. 2007, Tschanz et al. 2011). Besides experience, inherited individual characters and neutering may determine the predation efficiency (Robertson 1998). Cats may also differ in their willingness to bring prey home: van Heezik et al. (2010) reported that one third of cats never brought prey home.

In the city of Turku there are about 25000 households in detached and row houses (Statistics Finland 2014b). According to our inquiry, 14 % of these households (3500) have a cat which brings prey home. This may be an overestimate, if there was a tendency of cat-owners to answer the questionnaire more often than those who did not own a cat. Based on the 14 % estimate, the number of prey animals brought home would be about 14000 (4*3500) each month (excluding winter months). The total number of prey brought home by house cats in Finland can also be roughly estimated. There are about 1400000 households in detached or row houses in the whole country (Statistics Finland 2014b), and if 14 % of these households (196000) have a free-ranging cat which brings prey home, the whole cat population would bring home about 800000 (4*196000) prey animals each month. The total number of animals killed by house cats is even higher because not all prey killed by house cats are brought home. The number of truly feral cats in Finland is unknown but certainly there are some, at least in southern Finland (Kauhala et al. 2006). Adding predation by these cats to the figures above would most likely give a figure of > 1000000 prey animals killed by cats each month. According to Liberg (1984), feral cats kill 4-5 times more prey animals than house cats do.

Prey composition and diversity

Although cats are opportunistic predators, the bulk of the prey brought home by them was mammals, especially rodents (72 % of prey). During the study period vole populations were at the low phase in southern Finland (H. Henttonen, pers. comm.). It is probable that during vole peak years the share of rodents would be even higher, especially in rural areas. We must remember, however, that in the present study there were more old cats in rural than in urban areas, and old cats preferred rodents as their prey. The different age structures of urban and rural cats may thus partly explain the different prey in rural and urban areas. Probably many cats in urban areas are killed by traffic and therefore their life span is shorter than that of rural cats.

In spite of the northern location of our study area the distribution of prey was fairly similar to some other mainland areas, rodents being the most frequent prey of house cats. For instance, the proportion of rodents was 72 % in an urban area of Virginia, USA (Mitchell & Beck 1992), 76 % in a rural village in Switzerland (Tschanz et al. 2011), and 65 % in rural and suburban areas in Poland (Krauze-Gryz et al. 2012). The total number of rodents brought home by the house cats in the city of Turku would be about 9000 each month and about 550000 in the whole country.

Insectivores constituted a minor fraction (5.4 %) of prey brought home in the present study, and the proportion was higher in rural than in urban areas, probably due to different habitats, i.e. greater numbers of shrews and other insectivores available in rural areas. Inexperienced young cats brought insectivores home more often than old cats. Insectivores probably are not the favourite prey of cats, and cats learn by age that shrews are distasteful and usually inedible prey (Krauze-Gryz et al. 2012). The total number of insectivores killed by cats is probably close to the number brought home, i.e. about 800 each month in the city of Turku and 54000 in the whole country.

The category of other prey mammals included especially young hares (*Lepus* sp.). Young lagomorphs seem to be particularly favoured by feral cats, even more so than rodents in many areas (Liberg 1984, Carss 1995, Woods et al. 2003). Flux (2007) reported that while his cat's predation activity generally declined with age, it continued to catch rabbits by the stalk to the end of its life. Feral and house cats in rural southern Sweden preyed predominantly on rabbits (Liberg 1982, 1984). The Turku area is farther north, between the hemi-boreal and boreal vegetation zones, and lacks a permanent rabbit population (there are only few escaped pet rabbits), which explains the lack of rabbits (only one) in the present data.

The proportion of birds was 18 % of all prey animals brought home, and it was higher in urban (23.6 %) than in rural (13.7 %) areas, as predicted. Gardens with flower-visiting insects, berries and fruits in suburban and urban areas are particularly important for many small birds (Mead 2000, Lepczyk et al. 2004). Birds may also gather to gardens because winter-feeding of birds is popular in Finland. In the city of Turku the density of breeding birds is highest (on average 638.5 pairs per km^2) in small house areas where gardens are abundant (Vuorisalo & Tiainen 1993). As the

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density of gardens is higher in suburban areas than in the countryside, it is likely that the number of birds available for cats is also higher there. Also Liberg (1984) reported that birds were less important prey than mammals for cats in the countryside. According to our questionnaires, numbers of birds brought home each month would be > 3200 in Turku, and at least 150000 in the whole country. The land area within 10 km from the centre of Turku is 277 km^2 (Kauhala et al., unpublished manuscript). About 22 % (61 km^2) of it consists of areas with row and detached houses. If there are about 640 bird pairs/km^2 in these areas (above), the total breeding bird population would be about 78000 adult birds. If the total bird population during summer and autumn were about twice the size of the adult population, cats would take about 2 % of the bird population each month. This figure includes only the birds brought home by cats, and the total number of birds killed by cats may be much higher because not all prey are brought home.

Reptiles and amphibians were brought home mainly in the breeding season. When the weather gets cold in autumn, no reptiles or amphibians are available for cats. Young cats brought home reptiles and amphibians more often than did old cats, probably because young cats try to catch several prey items which old cats avoid or do not bother to catch. The number of reptiles and amphibians brought home by cats is > 350 per month in Turku and 33000 in the whole country.

As predicted, the diversity index for the prey of young cats was indeed higher than that of older ones, i.e. old cats are more selective in their prey choice. Old cats prey more on rodents, whereas younger ones prey also on shrews, reptiles and amphibians. This fact may reduce competition between cats of different ages. Contrary to our prediction, age of the cat did not explain the proportion of birds among the cat's prey.

There were no significant differences in the prey composition between males and females, and the composition of their prey overlapped almost totally. This does not necessarily imply between-sex competition for prey, as prey animals may be abundant in the study area. However, individual differences in the character of cats may affect their favourite prey, as noticed by other authors, too (Churcher & Lawton 1987, Barratt 1997a, Baker et al. 2005, Nelson et al. 2005, Morgan et al. 2009, Tschanz et al. 2011).

Benefits and threats to native fauna

The present study indicated that in northern latitudes on mainland areas the most common prey animals of cats were rodents. Cats can thus provide economic benefit by killing rats, voles and mice. In fact, cats were domesticated about 9000 years ago probably because of their tendency to kill rodents in grain stores (Driscoll et al. 2007, Baker et al. 2010). Old cats brought home more rodents than younger ones: old cats may control the most productive predation localities in the area and may therefore be successful predators of rodents (Barratt 1997b). Furthermore, there were no young cats among the "super predators". Since old cats are more efficient predators and prey more often on rodents than younger ones, they may be especially beneficial by removing pest animals from the yards and grain stores. Also middle-aged female cats may bring many rodents and other mammals to their kittens (Crowell-Davis et al. 2004). Predation on rodents, especially rats *Rattus* spp., may be beneficial also to bird populations, because rats kill birds, especially juveniles ("the mesopredator release effect", Courchamp et al. 2003).

However, cats also prey on birds. Woods et al. (2003) estimated that in Britain cats brought home 27 million birds in April-August, i.e. 5.4 million per month. These birds included at least 44 species of wild birds. The real number of prey individuals killed by cats has been estimated as 2-3 times higher than the number of prey brought home (George 1974, Kays & DeWan 2004). Some urban bird populations may even be threatened due to predation by cats, i.e. cat predation is, at least partly, additive to other causes of mortality (van Heezik et al. 2010). House cat densities are not regulated by prey populations but are more dependent on human density (Sims et al. 2008), and cats can continue predating on native birds even when the prey population density declines (Baker et al. 2005). In British cities, a negative correlation was found between cat densities and the number of bird species breeding in the area (Sims et al. 2008). Furthermore, together with city foxes (*Vulpes vulpes*) which are common in many European cities including Turku (e.g. Harris & Rayner 1986, Gloor et al. 2001, Vuorisalo et al. 2014), cats can form a predator guild which may threaten some native bird populations, such as ground feeding birds (Baker et al. 2010). Contrary to some other studies (van Heezik et al. 2010), there was not a peak in the occurrence of birds in the breeding season but the FO for birds tended to be higher in autumn. This fact may increase the impact of cat predation on bird populations because the reproductive value of juveniles is usually lowest due to their high mortality rate. Reproductive values of individuals are higher in autumn when the young of the year have already survived the most critical phase in their lives.

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Furthermore, mortality rates of prey may be underestimated also because cats often harm their prey by playing with it. The prey may escape but may later fail to reproduce or die due to its wounds (Kays & DeWan 2004). Cats can affect the prey populations also indirectly by disturbing the nesting birds and exerting fear and thus stress in birds (Beckerman et al. 2007, Bonnington et al. 2013).

In conclusion, cats may provide economic benefit by killing numerous rodents especially in rural areas. On the other hand, they may threaten local bird populations in urban areas, particularly birds common in gardens, by killing a moderate proportion of these birds each month. To reduce the impact of cats on birds, one should identify the "super predators" among house cats and limit their freedom to go out at least in vulnerable areas and times. Calver et al. (2011) recommended that cats should be kept indoors as soon as the first signs of active predation have emerged. Fitting free-ranging cats with bells or "pounce protectors" may reduce their success of killing birds (Ruxton et al. 2002, Calver et al. 2007). Barratt (1997a) found that most birds were taken by cats in the morning and mammals in the evening. So, keeping cats indoors in the morning might reduce their impact on bird populations and letting them go out in the evening might increase their predation rate on pest animals, such as mice and rats.

Acknowledgements

We are very grateful to all households who answered our questionnaires. We wish to thank especially the cat owners who reported the prey brought home by their cats.

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