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ORIGINAL PAPER

Hunters and non-hunters: skewed predation rate by domestic cats in a rural village

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Abstract Domestic cats *Felis catus*, as companion animals provided with supplemental food, are not limited by the availability of wild prey and locally occur at extraordinary high densities. There is growing concern about the potential impact of large cat numbers on native prey populations. In the present study, we quantified the minimum number of animals killed in a rural village in Switzerland by asking owners (1) to estimate the predation rate in advance and (2) to record prey animals returned home by their pets. The frequency distribution of the numbers of prey items was markedly skewed: 16% of the cats accounted for 75% of prey, irrespective of sex, age or breed. A large fraction of owners considerably overestimated their cat's predation, indicating that surveying predation rates by means of a questionnaire alone is not sufficient. The observed average rate of predation within 48 days in spring was 2.29 prey items/cat/month (N=32 cats); major prey types were rodents (76.1%) and birds (11.1%). The absolute number of prey items taken per area is striking and indicates that cat predation represents an important factor in ecosystems. Its role may be momentous in intensively fragmented urban habitats, where cat densities are especially high. We thus highlight the need to identify the factors determining predation rates of individual cats. Further extended studies, especially in urbanised areas, are needed to quantify the actual impact of cat predation upon the population dynamics of their prey.

Keywords Predation rate · Prey spectrum · Rural habitat · Birds · Small mammals · Conservation

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Introduction

Domestic cats *Felis catus* have undoubtedly contributed to the decline and endangerment of a number of species worldwide (see for example Dickman 1996; Lowe et al. 2000; Nogales et al. 2004). The consequences of cat predation are especially severe on oceanic islands, where native prey species, such as flightless and breeding seabirds, have little ability to escape (Fitzgerald and Turner 2000; Hughes et al. 2008). In contrast, prey species on continental landmasses have co-evolved with domestic cats over hundreds of generations and have thus been considered little susceptible to this hunter for decades (Churcher and Lawton 1987). However, recent declines in many farmland and garden birds (Beckerman et al. 2007), the importance of gardens as wildlife refuge in fragmented landscapes (Baker et al. 2003; Sattler et al. 2010) and increasing cat populations due to intensified urbanisation (Baker et al. 2005; Baker et al. 2008; Sims et al. 2008) have brought the ecological role of cats on continents into focus of much scientific debate.

Unlike wild predators, domestic cats are provided with supplemental food, medical care, space and shelter by their owners. Cat densities therefore do not directly depend on fluctuations in prey abundance (i.e. they do not show any numeric response) and may substantially surpass the carrying capacity of the environment (Kays and DeWan

2004; Woods et al. 2003). Thus, even though supplemental food probably reduces individual predation rates, domestic cats can maintain their hunting and predatory behaviour (Fitzgerald and Turner 2000), and the collective kill of the entire cat population has to be considered (May 1988).

Despite the fact that large numbers of prey are certainly taken, the actual impact of predation on prey populations remains unclear (Baker et al. 2005; Barratt 1997; Barratt 1998) and depends on the degree to which cat predation is additive or compensatory to other sources of mortality. This lack of information causes controversy between preservationists on the one hand, who accuse cats of the local endangerment of certain prey species, and some cat owners on the other, who are not willing to attribute negative ecological effects to their pet animals. Recent population models however indicate low likelihood of population persistence for some prey species in habitats with cat predation (Van Heezik et al. 2010).

An initial step when investigating the impact of predators on prey populations is to investigate, temporally and/ or spatially, the hunting habits of the predator, such as its prey spectrum, its spatial use and the predation rate. Although such studies have been conducted all over the world (in Australia (e.g. Barratt 1997; Barratt 1998), New Zealand (e.g. Gillies and Clout 2003), North America (Kays and DeWan 2004; Lepczyk et al. 2003), South America (e.g. Campos et al. 2007) and in the UK (e.g. Churcher and Lawton 1987; Woods et al. 2003)), investigations on cat predation in Western Europe are scarce (but see Borkenhagen 1978, Weber and Dailly 1998). This contrasts with the fact that cats have recently been indicted for their negative ecological impact (e.g. Baker et al. 2003). The present study aims to contribute to fill this geographical gap by analysing the hunting habits of cats in a small rural village in Switzerland. With 36 individuals living within approximately 0.25 km^2 (density of 144 cats per km^2), domestic cats do occur at a moderate high density in this study village (for comparison see Liberg et al. 2000), suggesting that susceptible prey species probably are still present in the area.

Taking into account the seasonal aspect, we assume that susceptible species are particularly vulnerable during their reproduction period, i.e. in late spring months. The intensity of cat predation on birds, for example, has been demonstrated to be greatest in this season, probably reflecting the killing of juvenile individuals (Baker et al. 2005; Lepczyk et al. 2003).

Predation rates of domestic house cats have mostly been indirectly quantified by asking cat owners to collect and record the number of prey returned home ("What the cats brought home", e.g. Baker et al. 2005; Barratt 1997; Barratt 1998; Churcher and Lawton 1987; Gillies and Clout 2003; Woods et al. 2003). Assuming that these prey items are a representative fraction of the total and variety of prey cats actually kill, this is a logistically feasible method of investigating cat predation at a large scale (Flux 2007). However, if cat owners can estimate their cats' predation rates with some accuracy, questioning cat owners may serve as an alternative, quicker and easier method. We simultaneously conducted these two indirect approaches to test if questionnaires could provide an accurate estimate of predation rates.

In the present study, we thus investigated the extent of cat predation on prey species in spring time by asking cat owners (1) to estimate the predation rate in advance and (2) to record prey animals returned home by their pets. In particular, our results aim to give an insight into the cats' prey spectrum in a rural habitat and to estimate the average number and variation of prey caught in spring in a characteristic Western European village.

Material and methods

Study site

The study was conducted in the small rural village of Finstersee (70 households, 0.25 km^2, 47°10′ N 8°37′ E), situated in Central Switzerland. Finstersee is surrounded by agricultural farmland and forests and therefore represents a predominantly isolated settlement area.

Cat population

As revealed by a complete survey, 20 households kept at least one individual cat in the study village. This incidence of cat ownership corresponded to the national average of approximately one cat for every three households (public survey MACH Consumer 2009-1, WEMF AG for advertising media research). The total cat population consisted of 40 cats, 36 individuals thereof had access to the outdoors. Fifteen households owning 32 cats (59.4% females) participated in the study. Information on cat sex, age, breed ("physical attributes") and the owners' estimations of hunting activity were obtained by means of a questionnaire. Ten cats were between 0–2 years old, 12 cats, between 3–6 years and 10 cats, between 7–16 years. Most cats were crossbreds, except three "Maine Coon" cats, one "Persian" and one "European Shorthair" breed.

Prey spectrum and predation rate

Predation rates of cats were indirectly quantified by asking cat owners to record and, whenever possible, collect prey brought home by their cats. This method ("What the cats brought home") provides an indication of the minimum

number of animals killed by cats. Cat owners were supplied with plastic bags, in which to place the remains of any prey animal. The date of each kill was recorded, and the collected prey animals were frozen until later identification. All prey remains were determined as precise as possible, except ten innards which could not be attributed to a taxonomic group. In addition, participants were asked to record catch observations without prey remains. Data were collected between April 19 and June 6, 2007 (for 48 days).

The importance of physical attributes for determining the number of prey caught was analysed by a general linear model (GLM; SPSS 11, 2001). Insect prey was excluded from the analyses, since its recording was probably not consistently conducted by cat owners.

Results

Hunting activity

Study cats considerably varied in their hunting activity (Fig. 1). Twenty-one cats (65.6%) returned at least one prey item, and 11 cats (34.4%) did not bring home any prey at all. A minority of the hunting cats was responsible for the majority of prey being returned: Five cats (15.6 %) captured more than six prey items each. They accounted for nearly 75% of the prey recorded. These differences between cat individuals are neither explained by their sex, age nor breed (GLM, all p values>0.20 for mammals and birds, respectively).

In the course of the study period, a total of 117 prey individuals were reported to have been captured and brought home by cats (71 samples, 46 observations). Major prey items were small mammals (rodents, 76.1% and insectivores, 4.3% of prey caught) and birds (11.1%), details are listed in Table 1. Based on this data set, the mean rate of predation in spring time was 2.29 prey items/cat/month. Excluding five prey items, which could not be attributed to a specific cat, the data set revealed an interquartile range from 0.00 to 1.41 for the individual predation rates, with a median of 0.63 prey items/cat/month.

Estimation of cat owners

Prior to commencing data collection, cat owners estimated 16 cats to return prey at least once per week ("frequent hunters", 50.0%), seven cats to return prey at least once per month ("rare hunters", 21.9%) and eight cats to never return prey ("no hunters", 25.0%). For cats being estimated as "rare hunters" or "no hunters", the owners' estimation was in accordance with the number of prey collected. However, the predicted predation rate of the estimated "frequent hunters" exceeded the subsequently observed predation rate (randomised $\chi^2=5.59$, two-tailed $p<0.02$): eleven of 16 cats returned less than one prey item per week.

Discussion

Differences between cat individuals

We found a notedly skewed frequency distribution of the number of prey brought home by the studied cats: 16% of the cats accounted for nearly 75% of prey items returned. This high variation in hunting activity and the fact that only a small fraction of the studied cat population returns the majority of prey are supported by previous investigations

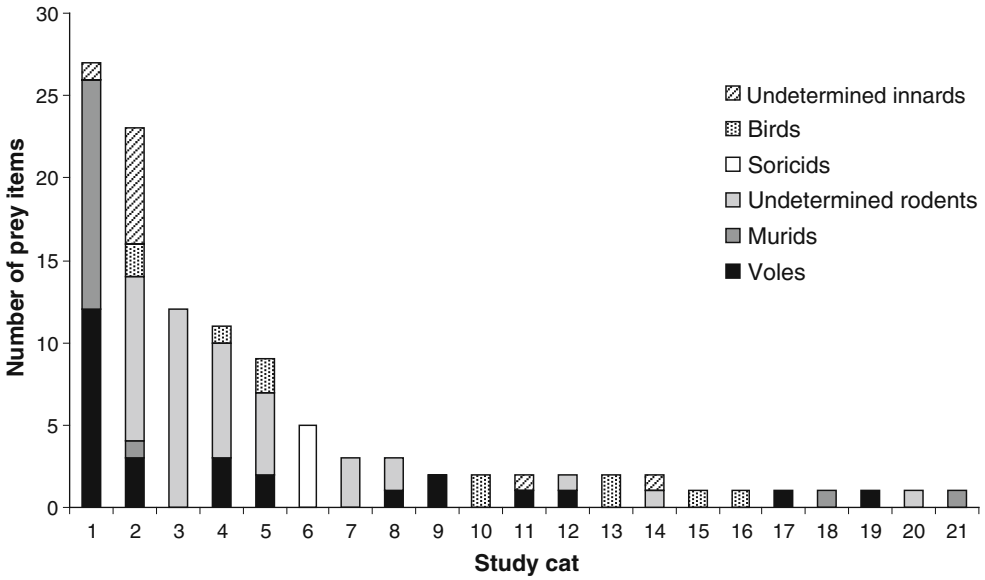

Fig. 1 Numbers and taxonomic groups of prey brought home by 21 free-ranging cats within 48 days (11 cats did not return any prey item)

Table 1 "What the cats brought home": number of prey caught by 32 cats within 48 days in spring, monthly predation rates (referring to 30 days)

	N_{prey}				N_{prey}/cat/month
	Juvenile	Adult	Undetermined	Total	
Rodentia				89	1.74
Murids	2	13	2	17	
Voles:					
Arvicola terrestris	1	11	5	17	
Myodes glareolus	1	10	2	13	
Undetermined rodents			42	42	
Insectivora (Soricids)				5	0.10
Crocidura russula		4		4	
Sorex sp.		1		1	
Aves				13	0.25
Passer domesticus	1	1		2	
Fringilla coelebs		1		1	
Cyanistes caeruleus	1			1	
Delichon urbicum		2		2	
Ficedula hypoleuca		2		2	
Undetermined songbirds	1		4	5	
Undetermined prey				10	0.20
Total[a,b]				117	2.29

[a] Additionally, there were 25 records of insects: Lepidoptera (N =12), Odonata (4), Saltatoria, Diptera and Coleoptera.

[b] Five prey items could not be attributed to an individual cat

(Baker et al. 2005; Barratt 1997; Borkenhagen 1978; Churcher and Lawton 1987; Gillies and Clout 2003; Nelson et al. 2005; Ruxton et al. 2002; Woods et al. 2003). In our study, none of the measured physical attributes (sex, age, and breed) were responsible for the observed variation between cats. Factors determining the hunting strategy of domestic cats are not known. Although the variation might partly be explained by differences in the observational ability and effort of cat owners (Barratt 1998; Gillies and Clout 2003), by different aspects of the cats' domestic lifestyle (e.g. time spent indoors, feeding rate, bell wearing) (Nelson et al. 2005; Woods et al. 2003), by individual-based differences in cat behaviour (e.g. early experiences of juvenile cats) (Fitzgerald and Turner 2000; Woods et al. 2003) or by different rates of "kills-brought-home" (Kays and DeWan 2004), our results highlight a putative key factor for predation: the individual predation behaviour. There is a need to better understand the factors determining variation in hunting activity.

Prey spectrum, hunting area and potential impact of cat predation

The finding that small mammals were the most numerous prey type in our study is in accordance with previous investigations, which have indirectly quantified predation rates of cats in other regions (Baker et al. 2005; Baker et al. 2008; Barratt 1997; Borkenhagen 1978; Churcher and Lawton 1987; Gillies and Clout 2003; Kays and DeWan 2004; Woods et al. 2003). Also in terms of biomass, mammals were identified as most important prey (Carss 1995). Our result corresponds to the view that cats are primarily hunters of small mammals, having evolved well-adapted hunting techniques (Fitzgerald and Turner 2000).

Bank voles *Myodes glareolus*, compromising 11.1% of prey caught in our study, mainly occur in forests and thus indicate that domestic cats do not only hunt in gardens, yards or on agricultural fields, but additionally exploit woodland for hunting. The composition of mammalian prey found in the present study does not contain any endangered species. Water voles *Arvicola terrestris* (14.5% of prey caught), in contrast, are considered agricultural pests in Continental Europe, and their control is an important factor for keeping domestic cats as pets in rural areas. Despite different habitat conditions and different sampling methods, the recorded spectrum of mammal species in a rural village was similar to the one found by faeces analyses conducted in a Swiss mountainous area (Weber and Dailly 1998).

Although birds were reported to be less important prey than mammals, the diet of our study cats contained five different bird species, each represented by just one or two individuals. Interestingly, two adult house martins *Delichon urbicum* have been caught: This species very rarely stays on the ground, except for searching nest material in April/May. Cats thus seem to exploit this behaviour and, according to our data, occasionally capture house martin individuals. This exemplary adaptation to a specific trophic condition supports the findings of several dietary studies,

showing that wildcats (e.g. Malo et al. 2004) and cats (e.g. Weber and Dailly 1998) functionally respond to prey abundance and availability. As opportunistic and generalist predators, cats thus change their predatory behaviour and their diet in relation to prey density (Fitzgerald and Turner 2000).

All bird species recorded in this study are not endangered in Switzerland and were designated as "species of least concern" on the Swiss Red List of breeding birds (Keller et al. 2001). There is thus no indication that domestic cats significantly reduce or destabilise vulnerable bird populations in rural landscapes, where the availability and the diversity of other prey are high (Churcher and Lawton 1987; Fitzgerald and Turner 2000). However, cat predation may be more momentous in artificial habitats, such as e.g. intensively fragmented and limited vegetation areas within cities (Baker et al. 2003; Baker et al. 2005; Baker et al. 2008; Beckerman et al. 2007). Losses in such locations might probably be non-trivial for populations of house martins, which have significantly declined since 1990 (Keller et al. 2009), or for populations of pied flycatchers *Ficedula hypoleuca*, whose estimated abundance in Switzerland is rather low (10,000–20,000 individuals) (Burkhardt and Schmid 2001).

Analysing the results of several investigations conducted in rural habitats, Liberg et al. (2000) found a high variability in mean domestic cats' home range sizes (females, 0.02–1.12 km^2; males, 0.03–2.28 km^2). Compared to the area of our study village (0.25 km^2), these ranges indicate that the hunting area of the study cats probably by far exceeded the village ground and thus included adjacent green areas, such as gardens, yards, agricultural fields, grassland, hedges and forests.

Significance of predation rate

The average predation rate observed in our study approximately lies in the middle of the range of predation rates reported in previous investigations conducted all over the world (range, 0.58 (Baker et al. 2005) to 6.57 prey items/cat/month (Calver et al. 2007)).

Despite the difficulty that predation rates estimates can vary between studies, their comparison and discussion are required, especially as some of these data have been used to valuate national levels of mortality (May 1988; Woods et al. 2003). Being aware of the limitations to extrapolate relatively small data sets into estimates for large areas containing different habitat types and conditions, we attempted to do so in order to obtain an approximated total number of animals killed per area. In August 2009, the permanent resident population in Switzerland reaches 7.8 million inhabitants (Swiss Statistics, Federal Administration), who, by estimation, own a total of 1.38 million cats (public survey, petfood industry 2008). Thereof, a fraction of 72% has access to the outdoors (public survey, petfood industry 2008). A strict extrapolation of the minimum and maximum predation rates (mean ± SE) found in our study to this total national number of cats having access to the outdoors reveals that between 1.2 and 2.4 million mammals and between 0.1 and 0.3 million birds could be captured within an average spring month in Switzerland (i.e. within an inhabited area of 2,790 km^2). These estimates should imperatively be treated with caution. They do not equate to an assessment of the cats' impact on wildlife populations (Baker et al. 2005; Barratt 1997; Barratt 1998; Patronek 1998), notably as most prey species are small, short-lived and have high reproductive rates. However, these figures are undoubtedly striking and indicate that predation by domestic cats is an important factor in ecosystems, possibly contributing to a decline of native species, if only on a local or temporal basis.

Conclusions

A large fraction of owners considerably overestimated cat predation, probably because they are emotionally touched (Barratt 1998). Surveying predation rates by means of a questionnaire alone is therefore not sufficient. We recommend applying the method "What the cats brought home" at a larger scale in time and space, in order to increase its adequacy for assessing the seasonal variation in predation rates, the individual hunting behaviour throughout the year and the actual impact of cat predation on prey populations. Different habitat types, namely urban and suburban areas, should thereby imperatively be considered: despite the view that hunting may play a small role in food acquisition of urban cats (Patronek 1998), cities and suburban areas are places with especially high cat densities and might expose already vulnerable prey populations to an intense predation pressure. The resulting predation rates must then be interpreted in relation to local prey availabilities, prey reproduction rates and other mortality factors, as exemplary conducted by Baker et al. (2008). In addition, studies experimentally exploring factors accounting for a reduced hunting activity are warranted. They could promote the evaluation of conservation strategies minimising the number of wild animals killed by cats (Woods et al. 2003). The public acceptability of such strategies determines their feasibility and should be investigated at an early stage (Lilith et al. 2006).

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