Contributions of wild and provisioned foods to the diets of domestic cats that depredate wild animals

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Abstract.   Predation of wildlife by domestic cats *Felis catus* presents a threat to biodiversity conservation in some ecological contexts. The proportions of wild prey captured and eaten by domestic cats and thus the contributions of wild prey to cat diets are hard to quantify. This limits the understanding of any impacts of cats may have on wild animal populations and confounds analyses of the effects of interventions aimed at reducing wildlife killing. We used stable isotope analyses to quantify the relative contributions of wild and provisioned foods to the diets of domestic cats kept as companion animals and which frequently captured wild prey. We tested the effects of treatments aimed at reducing killing upon stable isotope ratios of cat whiskers and, where treatments had significant effects, we estimated variation in the contributions of wild prey to cats' diets before and during treatment. We evaluated bells, Birdsbesafe collar covers, provision of food in a "puzzle feeder," provision of food in which meat was the principal source of protein, object play, and a control group. As expected, cat diets consisted primarily of provisioned foods, though the contribution of wild animals to the diets of these cats, all of which regularly caught wild animals, was low (cat food ~96%, wild animals ~3–4%). Compared to the pre-treatment period and control group, cats with a Birdsbesafe collar cover exhibited a significant reduction in nitrogen stable isotope ratios in their whiskers and consumed less wild prey, most likely attributable to effective inhibition of hunting, particularly for birds. Fitting cats with a Birdsbesafe collar cover, therefore, reduced both returns of wild birds and consumption of wild prey. While multiple interventions can significantly affect the numbers of wild animals that cats capture and return home, the remarkably small dietary contributions made by wild animal prey mean dietary change is harder to discern. Domestic cats rely almost exclusively on food provided by people, even when they frequently kill wild animals. This suggests that the hunting behavior of domestic cats may be driven by behavioral motivations, or by a need to address micronutrient requirements, but is unlikely to alter macronutrient intake.

Key words: cats; companion animal ecology; diet; domestic cats; mixing model; pet food; predation; stable isotope; wildlife.

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INTRODUCTION

Predation of wild animals by domestic cats *Felis catus,* in combination with their global distribution and abundance, constitutes a hazard for the conservation of biodiversity in a range of ecological contexts. In particular, cats living on islands are often considered to be invasive, non-

native species that are responsible for the decline, extirpation, and, in some cases, extinction, of endemic species (Medina et al. 2011, 2014). In continental areas, while the relative importance of compensatory (Møller and Erritzøe 2000, Baker et al. 2005) and additive (van Heezik et al. 2010) mortality due to predation by cats remains in debate, a growing body of evidence has identified the substantial direct and indirect impacts that owned and unowned free-ranging cats have on populations of some threatened vertebrates (Loss and Marra 2017), and upon the welfare of the animals they capture (Baker et al. 2018).

Domestication of cats has progressed less completely than for other widely domesticated species (Driscoll et al. 2009a,b). Retention of a full behavioral repertoire for hunting (Bradshaw et al. 1999, Bradshaw 2006) means that cats are adaptable to diverse ecosystems and are able to live independently of human care and food provision. Hunger is a key driver in hunting; indeed, hungry cats hunt more than well-fed cats (Kays and DeWan 2004). However, hunger, in a broad sense, is not the only reason for expression of hunting behavior. Some free-ranging cats, kept as companion animals and regularly fed by people, frequently capture wild animals and bring them back, alive and dead, to the human household (Woods et al. 2003, Blancher 2013, Loss et al. 2013, Murphy et al. 2019). Some cats are more proficient and prolific hunters than others (Kays and DeWan 2004, Tschanz et al. 2011), with most domestic cats probably catching few or no prey (Churcher and Lawton 1987, Baker et al. 2005). Even if the individual frequency of killing is low, however, the cumulative impact of locally high densities of cats may be severe (Baker et al. 2005, Sims et al. 2008, Thomas et al. 2012). It has been suggested that the number of animals brought home by cats is not a reliable means of estimating the numbers of animals they kill (Loyd et al. 2013, Seymour et al. 2020), and this remains a key uncertainty in determining rates of predation and the impact of cat predation upon prey populations. Consequently, for studies of predation rates, coupling surveys of prey returns with other methods of dietary analysis has been advocated (Krauze-Gryz et al. 2012). Cat owners rarely appreciate killing of wild animals by their cats (Crowley et al. 2019, 2020), and some owners attempt to reduce their cats' hunting success through collar-mounted devices like bells, collar covers, and bibs (Ruxton et al. 2002, Nelson et al. 2005, Calver et al. 2007). Such devices have been proven to be effective in reducing numbers of animals captured and brought home, but are characterized by low uptake by cat owners for various reasons, ranging from perceiving cat hunting as natural, albeit undesirable, behavior (Crowley et al. 2019, 2020), to safety and welfare concerns linked to wearing a collar (Lord et al. 2010).

The persistence of hunting by domestic cats kept as companion animals that are generally and regularly provisioned with food suggests there may be physiological or behavioral needs that are not completely met in their environment and/or their provisioned diets. Hunting is a multi-faced behavior affected by a series of drivers, including cat evolutionary constraints, idiosyncratic nutritional physiology, and early life behavior (Cecchetti et al. 2021a). Predatory behaviors can be expressed independently from hunger, and even well-fed cats hunt, or engage in pseudo-predatory play with their owners (Hall and Bradshaw 1998, Ellis et al. 2013). Cats have evolved as obligate carnivores with an absolute requirement for high intake of protein, as the source of essential amino acids and nitrogen, many water-soluble B vitamins (e.g., niacin), vitamin A, vitamin D, arginine, taurine, methionine, cysteine, and some essential fatty acids (Macdonald and Rogers 1984, Morris 2001). All such specific requirements would be fulfilled by eating wild prey. Bradshaw et al. (1999) advanced the hypothesis that retention of hunting behavior in cats that are provisioned with food could be linked to some nutritional inadequacy in the diets provided by people, particularly before the advent of commercial pet food manufacturing, and the adherence to standardized, "complete" and "balanced" diets. Modern, manufactured pet foods are also highly palatable and contain various food enhancers (Pekel et al. 2020). While industry bodies (Fédération Européenne de l'Industrie des Aliments pour Animaux Familiers) provide specific guidelines to meet nutritional requirements of cats, some commercial pet foods have been found not to meet all the minimum requirements for some fatty acids, amino acids, and minerals, and for macronutrient composition (Hewson-Hughes et al. 2011,

Davies et al. 2017, Brunetto et al. 2019, Zafalon et al. 2020). Furthermore, the protein in pet foods can be derived from both animal and plant sources. Plant protein sources have lower digestibility (Neirinck et al. 1991, Kanakubo et al. 2015), lower bioavailability (Zafalon et al. 2020), and a less complete profile of amino acids (Donadelli et al. 2019) than animal proteins. Therefore, it is possible that domestic cats that hunt wild prey are attempting to address some nutritional shortfall, though their success in so doing will clearly depend on successfully hunting, killing, and ultimately consuming their prey.

Stable isotope analysis of consumer and prey tissues can offer an effective means of quantifying variation in the composition of predator diets (Crawford et al. 2008). In broad terms, ratios of the abundance of stable isotopes of carbon, $^{13}C/^{12}C$, reported as $\delta^{13}C$, in consumer tissues vary in relation to the relative importance of primary carbon sources and, within terrestrial systems, the relative importance of production stemming from, among other things, differences in photosynthetic metabolism (such as C3 versus C4 plants). The ratios of $^{15}N/^{14}N$, reported as $\delta^{15}N$, are serially enriched by consumers and therefore can broadly reflect the consumer's trophic level. Many manufactured pet foods contain high proportions of maize *Zea mays*, a C4 plant, and its derivatives, resulting in higher (less negative) values of $\delta^{13}C$ (Jahren and Kraft 2008, Newsome et al. 2015). In temperate regions, isotope ratios of provisioned foods are therefore likely to differ from those of wild animals that feed in natural food webs, where producers are predominantly C3 plants (Farquhar et al. 1989). However, it has been shown that cat foods produced in UK have lower (more negative) values of $\delta^{13}C$, compared to the USA (McDonald et al. 2020), suggesting that less maize is used and possibly making it more difficult to discern provisioned from wild foods. Stable isotope analyses of feral cats' diets have identified reliance on high proportions of anthropogenic food items (Cove et al. 2018, Maeda et al. 2019). For cats kept as companion animals, however, a recent study (McDonald et al. 2020) found that stable isotope analysis of cat hair had little power to discern the proportions of cat diets that were comprised of wild prey or pet foods. This was mainly due to high variability in isotope ratios in pet foods, including variation among batches of the same variety, though their study also relied on small numbers of museum specimens of hair and feathers to sample wild foods, rather than locally collected wild animals (McDonald et al. 2020).

Our aim was to improve understanding of the factors that might drive domestic cats that are kept as companion animals and are fed regularly, to hunt wild prey. We sought to understand the importance of wild foods to the diets of cats that regularly captured wild prey and to ask whether this prey likely contributed to the cats' macro- or micro-nutritional needs. We analyzed the diets of domestic cats through stable isotope analysis of cats' whiskers and of samples of wild animal prey and provisioned foods. We worked exclusively on owned cats living as companion animals that frequently captured wild animals and returned them to their households. We were able to discern provisioned commercial pet foods from wild prey and thereby to quantify the cats' relative reliance on food provided by owners and on wild foods obtained by hunting. Finally, we determined whether intervention measures, which we have shown elsewhere (Cecchetti et al. 2021*b*) to affect significantly the numbers of animals killed and brought home, further affect the relative importance of wild prey in cats' diets.

Materials and Methods

Participant recruitment and sample collection

As part of a larger experimental study (Cecchetti et al. 2021*b*), cat owners living throughout southwest England whose cats regularly captured wild animals and brought them back to the house were recruited through social, broadcast, and print media. Participants completed an online questionnaire regarding their cat, comprising details of sex, age, breed, health status, feeding and outdoor access (access outdoors restricted at night or unrestricted), frequency of hunting, and ongoing management strategies adopted for reducing hunting.

More details of the experimental trial of interventions to reduce numbers of animals killed by cats are reported in Cecchetti et al. (2021*b*). Briefly, the trial was conducted from 20 March to 21 June 2019. Participants were required to remove any existing device that potentially

interfered with cat hunting activity before entry to the trial. Before interventions were applied, owners recorded all prey brought home by cats for a pre-treatment period of seven weeks (Period 1: 20 March to 9 May). There followed a transition period of one week (from 10 to 16 May) during which owners introduced their cats to the intervention to which they were assigned. After this, owners applied the intervention for a treatment period of five weeks (Period 2: 17 May to 21 June). All cats in the same household were treated in the same way. The six treatment groups were as follows: Bell, where cats were fitted with a quick-release reflective collar (Kittygo, Wink Brands, UK) with a bell attached; Safe, where the same quick-release collar was fitted with a rainbow-patterned Birdsbesafe (Birdsbesafe LLC, USA) collar cover; Food, where owners provided cats with a grain-free food in which protein was predominantly derived from meat sources (Lily's Kitchen Everyday Favourites paté multipack 8x85g as wet food; and Lily's Kitchen Delicious Chicken as dry food. Lily's Kitchen, UK); Puzzle, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser. PetSafe, USA); Play, in which owners spent at least 5 min per day dedicated time in object play with their cats, with a "fishing" toy (Cat Dangler Pole Bird) and a "mouse" toy (Kong refillables feather mouse toy, with the catnip replaced with bubble wrap, to provide an auditory stimulus. The Kong Company, USA); and Control with no intervention, where owners were required to not make any changes to management of their cats, but were asked to keep completing prey records.

From the experimental sample of 70 cats per treatment group, we selected a subset of 15–20 cats per treatment for detailed analysis of diets, based on owner willingness and household location to facilitate sample collection. We clipped one of the cats' whiskers at the beginning and one at the end of the trial to represent periods before and during treatment. Whiskers were stored in a paper envelope in ambient conditions.

To sample wild prey, cat owners were asked to collect and freeze the prey items brought home by their cats. Prey items were collected by the project team and stored at −80°C. Owners provided cats with a diversity of pet food brands, varieties, and flavors. There is great variability in the isotope ratios of commercial pet foods, both among and within brands and varieties (˜6‰ in both δ^{13}C and δ^{15}N; McDonald et al. 2020). Our aim was to quantify the relative importance to cats of provisioned versus wild foods, and the contributions of individual pet foods were harder to estimate, given within-brand variance. Therefore, our approach was to obtain a representation of the total isotopic space from which the ratios of all brands and varieties of provisioned foods could be sampled in stable isotope mixing models. We did this by determining the isotope ratios of a large sample ($n = 172$) of commercial foods, across brands and varieties. In the first collection, made from June to December 2017, owners of 106 cats specified the brand and variety of the food ($n = 112$) they had given their cats. Dry food samples ($n = 61$) were sent in by post, while wet foods ($n = 51$) were purchased according to the owners' specifications (see McDonald et al. 2020 on UK samples, for more details). In the second collection, made in February 2018, we collected from owners a further 29 samples of wet food and 31 of dry foods ($n = 60$ samples).

Recording of wild animals captured and brought home

Cat owners recorded the animals that were captured and brought home to the household. They regularly uploaded records online, identifying the cat responsible for the capture, where possible, or entering "unknown" in case of uncertainty in a multiple cat household, date of finding the item, animal type (mammal, bird, reptile, amphibian, insect, or unidentified in case of indistinct remains), species (an identification guide was provided for facilitating species identification), whether the animal was alive or dead, and other observations.

Whisker growth rates

Whiskers generally grow continuously and so the basal section of whiskers sampled at the beginning of the study represented diet prior to the intervention, while the basal section of the whisker sampled at the end of the trial represented diet during and toward the end of the trial intervention period. To estimate the growth rate and thereby the approximate time interval

represented by different whisker lengths, the owners of nine domestic cats were recruited for a biomarker feeding experiment. The cats were fed with their usual wet food (or their preferred food, e.g., tuna) mixed with a dose of 25 mg/kg (cat weight) of Rhodamine B, which, after ingestion, is incorporated into keratinous tissues, leaving a distinctive band detected under a fluorescence microscope (Fisher 1999). Dosing was undertaken twice, one week apart. After a minimum of three weeks, one whisker per cat was clipped and examined under a fluorescence microscope. Growth rate (mm per day) was calculated by measuring the distance between the two fluorescent bands, dividing it by the time span between the two doses (seven days). We have assumed a linear whisker growth pattern for domestic cats, as has been found in a variety of mammal species (Ibrahim and Wright 1982, McHuron et al. 2016, but see Mutirwara et al. 2018 for evidence of nonlinear growth in longer whiskers), and as the analyzed sections represent growth over a matter of weeks, slight non-linearity will also be accommodated (Robertson et al. 2013).

Stable isotope analysis

A small section of muscle from all wild prey and a small amount of all provisioned foods was freeze-dried at $-90°$ for 24–48 h and then ground using a pestle and mortar. 0.6–0.8 mg of the resulting powder was weighed out and placed in tin capsules. Cat whiskers were rinsed in distilled water, wiped and placed in an envelope, and freeze-dried at $-90°$ for 24 h. For each whisker, total weight and total length were measured. Each whisker was divided into one or more sections based on its total weight, with the basal section of the whisker representing the most recent period of whisker growth. Each section was cut into pieces of <1 mm using a scalpel and enclosed in tin capsules. The minimum sample weight was 0.35 mg and maximum 0.85 mg.

Masses of the stable isotopes of carbon and nitrogen and ratios of C:N were quantified using elemental analysis isotope ratio mass spectrometry using a Sercon Integra-2 EA-isotope ratio mass spectrometer at University of Exeter and a Thermoquest EA1110 elemental analyzer linked to a Europa Scientific 2020 isotope ratio mass spectrometer at Elemtex Ltd, Cornwall, UK. Stable isotope ratios were expressed as δ values

in ‰ (per mil), the ratio of heavy to light isotopes, relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPBD) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. In both instances, samples were scale-corrected using USGS40 and USGS41 standards, with additional internal standards of bovine liver (University of Exeter and Elemtex Ltd) and alanine (University of Exeter only) for both drift and stretch corrections, while average alanine values were used for shift correction. QA standards were not run alongside samples, but instrument precision and linearity were checked periodically using bovine liver and alanine samples not included in the corrections. Averaging across standards and laboratories, estimated precision was 0.08‰ ± 0.01 (1 SD ± SE) for $\delta^{13}C$ and 0.11‰ ± 0.02 for $\delta^{15}N$.

Handling of lipids

Lipids are depleted in ^{13}C, relative to proteins and carbohydrates (resulting in more negative $\delta^{13}C$), and variation in lipid content among organisms or among tissues introduces considerable bias into analyses of variation in $\delta^{13}C$. Such bias increases with lipid concentration (Post et al. 2007), which for these purposes can be approximated by C:N ratio. Chemical lipid extraction is often considered suboptimal for many reasons, particularly because it can alter $\delta^{15}N$ by washing out nitrogenous compounds (Elliott et al. 2014), thus model-based normalization of $\delta^{13}C$ values is advised (Ehrich et al. 2011). For terrestrial animals showing C:N ratios higher than 4, a mathematical correction is recommended (Post et al. 2007) and we mathematically corrected the $\delta^{13}C$ ratios of wild food sources ($n = 232$, mean C:N = 3.6, SD = 0.2, range = 3.2–4.7) applying the equation:

$$\Delta\delta^{13}C = -3.44 + 1.00 \times C{:}N \text{ ratio}$$

Our initial analyses found that provisioned, commercial cat foods had considerably higher and more variable C:N ratios (mean C:N = 8.7, SD = 2.0, range = 4.4–13.4) than wild foods and did not show a strong or a linear relationship between $\delta^{13}C$ and C:N ratio ($r^2 = 0.06$). Therefore, we did not apply the Post et al. (2007) correction to $\delta^{13}C$ of provisioned cat foods. Rather, we chemically extracted lipids, following the method used by Chouvelon et al. (2011), from a sample of 105 cat foods (n dry foods = 56, n wet

foods = 49) and regressed $\delta^{13}C$ before and after extraction, deriving the equation:

$$\delta^{13}C_{after} = -3.76 + 0.83 \times \delta^{13}C_{before} \, (r^2 = 0.71)$$

which was then applied as a correction to the $\delta^{13}C$ values of all provisioned cat foods.

Trophic discrimination factors

The processes of ingestion, digestion, and assimilation by consumers are associated with a shift in isotopic ratios, the magnitude of which is often referred to as discrimination, fractionation, or enrichment (Inger and Bearhop 2008). Trophic discrimination factors (TDFs) quantify the offset in stable isotope ratios between consumers and their food, and are a requirement of dietary reconstruction methods based on stable isotope mixing models (Healy et al. 2018). There are few reference values for means or variance in TDFs for modern domestic cats available in the literature. McDonald et al (2020) provide TDFs for diet to hair of +1.9‰ for $\delta^{15}N$ and +2.6‰ for $\delta^{13}C$, derived from a single indoor-only cat. Maeda et al. (2019) report mean TDFs for diet to hair of +2.8‰ (SE 0.1‰) for $\delta^{15}N$ and +2.3‰ (SE 0.3‰) for $\delta^{13}C$, derived from shelter cats ($n = 14$; Y. Watari, *personal communication*). Among wild felids held in captivity, Parng et al. (2014) quantified TDFs for diet to hair for 7 felids of 4 species (1.1–5.5‰ for $\delta^{13}C$ and 3.3–4.5‰ for $\delta^{15}N$), while Mutirwara et al. (2018) provided diet to whisker TDFs for 5 lions *Panthera leo* (2.7 ± 0.1‰ for $\delta^{13}C$ and 2.5 ± 0.1‰ for $\delta^{15}N$).

For species where TDFs are not described in detail, it is possible to infer TDFs from species where they have been empirically determined using Bayesian phylogenetic regression approaches, that incorporate details of tissue types and feeding ecology (SIDER; Healy et al 2018). However, the nutritional state, feeding ecology, and macronutrient intake of wild felids, on which such an approach would be based, are very different from those of domestic cats. Aside from this, our main concern was that domestic cats are regularly fed with foods of diverse origins and highly variable macronutrient composition and derivation. Therefore, we determined diet to whisker TDFs directly using a sample of 10 domestic cats that were exclusively kept indoors and were fed on known foods. We clipped a whisker from each cat and sampled every food provided in the past three months. We calculated the mean difference between the averaged individual isotopic signature of all sections of the whisker and the averaged isotopic values of provisioned foods for both $\delta^{13}C$ (after correction for lipids) and $\delta^{15}N$.

Statistical analyses and isotope mixing models

All statistical analyses were conducted in R (R Development Core Team 2018). Cats that did not successfully complete the trial, and cats that had only one whisker clipped, were excluded from analyses.

ANOVA, followed by post hoc Tukey's pairwise tests, was used to quantify isotopic variation among food sources. Food sources were then grouped according to their broad origins (wild prey and provisioned cat foods) and the similarity of their isotope ratios (mean $\delta^{13}C$ ratios −26.0‰, SD ± 2.1‰ for wild prey and −24.4‰ ± 1.6‰ for provisioned foods; and mean $\delta^{15}N$ ratios 6.4‰ ± 1.0‰, 4.0‰ ± 0.9‰, respectively). We then used Bayesian isotopic mixing models with uninformative priors to estimate the relative contributions of wild and provisioned food source groups to cat diets in the pre-treatment and treatment periods for the overall cat population using the package "SIMMR" v.0.3 (Parnell et al. 2010). Models were built with three Markov chains with a burn-in of 50,000 and 1,000,000 iterations. Gelman diagnostics were used to check model convergence.

To test whether cats' diets were affected by experimental treatments that we had shown (Cecchetti et al. 2021b) were effective in reducing the numbers of animals captured and brought home by cats, we analyzed variation in $\delta^{13}C$ and $\delta^{15}N$ of individual cats as a function of experimental treatment, using two general linear mixed models. Fixed factors were treatment, period (pre-treatment and treatment), age class (6 months to 5 yr and 6 yr to 15 yr), sex, and outdoor access (restricted or unrestricted). The effect of treatment was tested by a treatment × period interaction term. Cat identity was set as a random effect. The significance of the interaction term was evaluated by comparing models with and without the interaction term, using ANOVA. Where a treatment was found significantly to affect variation in $\delta^{13}C$ or $\delta^{15}N$ of the treated cats, we estimated and compared the contributions of

the food source groups to the diets of the cats subject to that treatment and the control group, before and during treatment, using Bayesian stable isotope mixing models as described above. Estimates of diet composition at the level of treatment group should be viewed as a means of gauging the relative importance of food sources, rather than deriving precise estimates, due to the increased influence of uninformative priors in the models with lower numbers of observations (Swan et al. 2020).

RESULTS

Whiskers were sampled from 90 cats. Instrument process errors during analysis led to the exclusion of samples from 7 cats. One further cat was excluded because its diet was reported to be based primarily on fish and would introduce bias in estimates of population-level diet. Thus, 82 cats were included in analysis of the diet of the whole cat population in the pre-treatment period. For analyses based on individual prey returns, 25 cats were excluded because they lived in multiple cat households and prey items could not reliably be attributed to individuals, leaving 57 cats in this analysis. Six cats did not complete the experimental trial, and so 76 cats were included in analyses of variation in δ^{13}C and δ^{15}N and of the effect of treatments on wild prey consumption: 9 cats were in the Bell treatment, 15 in Food, 10 in Puzzle, 13 in Safe, 14 in Play, and 15 in the control group.

During the pre-treatment period, the median number of prey items brought home per cat ($n = 57$ cats) was 4 (Interquartile range = 2–8) and the median prey return rate was 0.1 items per day (IQ range = 0.1–0.2) of recording effort (median = 37 d). During the treatment period, the median number of prey items brought home per cat ($n = 58$) was also 4 (IQ range = 2–8) and the median prey return rate was 0.1 items per day (IQ range = 0.1–0.2) of recording (median = 36 d).

Two hundred thirty-two wild animal prey items were analyzed. Insects were not included as they contributed a very small proportion of the biomass of wild prey captured and brought home by cats. It was not possible to discern potential food sources to the species level on the basis of stable isotope signatures, but two broad groups of wild animals could reliably be discriminated: (1) herbivorous mammals ($n = 64$), comprising rabbits *Oryctolagus cuniculus*, field voles *Microtus agrestis* and bank voles *Myodes glareolus* and (2) omnivorous and carnivorous vertebrates, comprising shrews *Sorex* spp., wood mice *Apodemus sylvaticus*, rats *Rattus norvegicus*, birds and herpetofauna ($n = 168$). These two groups differed in their mean δ^{13}C ratios (−24.9 SD ±1.3‰ and −28.6 ± 1.4‰, respectively) but were similar in their δ^{15}N ratios (6.6 ± 1.6‰ and 6.0 ± 1.5‰, respectively; Fig. 1). One hundred sixty-seven provisioned cat foods were analyzed, and their δ^{13}C values were corrected for lipid content. Two groups of provisioned cat foods, dry ($n = 90$) and wet ($n = 77$), differed in their mean δ^{13}C ratios (dry = −23.7 ± 1.5‰, wet = −25.2 ± 1.2‰) but were similar in their δ^{15}N ratios (dry = 4.0 ± 1.0‰, wet = 4.0 ± 0.8‰) (Fig. 1). Consequently, we were able to discern four food source groups (two groups of wild prey and two groups of provisioned cat food) that differed significantly from one another in δ^{13}C: (ANOVA $F_{3,\ 395} = 171.9$, $P < 0.001$) and δ^{15}N ($F_{3,\ 395} = 115.9$, $P < 0.001$). Critically, wild and provisioned foods were distinct in their ratios of δ^{15}N, while within each of wild and provisioned foods, the two source groups were distinct in their ratios of δ^{13}C (Fig. 1).

Three whiskers displayed two fluorescent bands, with an average growth rate of 0.48 mm/d (range 0.4–0.5 mm/d). Given the mean length of cat whiskers was 65 mm (range 37–118 mm), this corresponds to approximately 136 d (SD 28 d) of growth, such that analysis of the average whisker reflects cat diet over a period of around 4 to 5 months. The mean length of the basal section was 12.9 mm, corresponding to growth of around a month (approximately 27 d).

Trophic discrimination factors calculated from nine indoor cats (one was excluded from analysis as its diet was fish-based) were 2.9‰ (SD ±1.3‰) for δ^{13}C and 1.9‰ (±0.7‰) for δ^{15}N.

In both periods, cat diets consisted almost entirely of provisioned cat foods (Fig. 2; Table 1). In the pre-treatment period, dry cat food was estimated to comprise 79.0% of cat diet (95% credible interval [CI] 69.4–88.0%) and wet cat food comprised a further 17.0% (95% CI 7.4–27.1%); while herbivorous
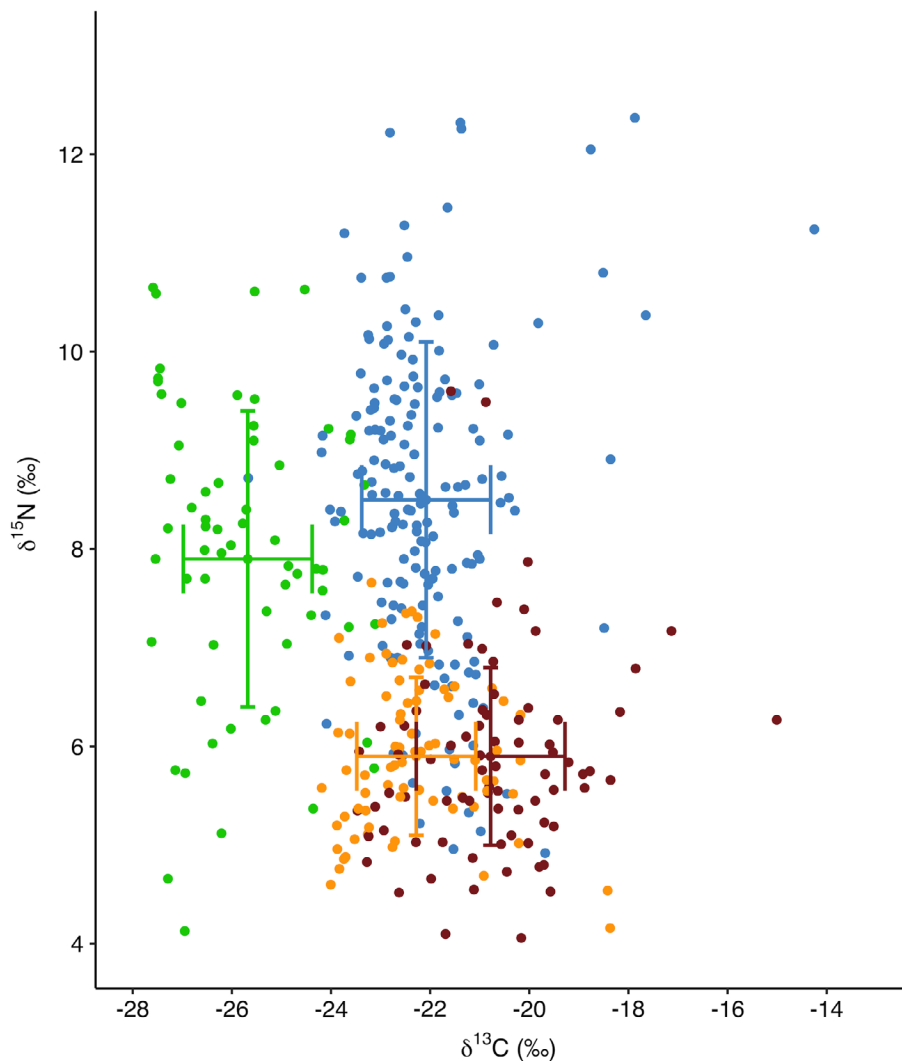
Fig. 1. Carbon and Nitrogen stable isotope ratios of potential food sources for domestic cats. Dots represent individual samples belonging to four putative food source groups: two provisioned cat food groups (orange = wet foods; brown = dry foods) and two wild animal food groups (green = herbivorous mammals; blue = omnivorous and carnivorous vertebrates). $\delta^{13}C$ and $\delta^{15}N$ values are per mil. Bars indicate the mean $\pm$ SD for each group.

mammals comprised 1.4% (95% CI 0.3–3.7%), and omnivorous and carnivorous vertebrates comprised 2.3% (95% CI 0.6–5.1%) (Fig. 2c). Cat diets overall were similar during the treatment period: Dry cat food comprised 77.5% (95% CI 68.2–86.4%) and wet food comprised 18.7% (95% CI 9.3–28.5%), while herbivorous mammals accounted for 1.3% (95% CI 0.3–3.5%), and omnivorous and carnivorous vertebrates for 2.1% (95% CI 0.6–4.7%).

Variation in $\delta^{15}N$ was significantly affected by the treatment × period interaction (ANOVA comparison of models, $\chi^2 = 11.6$, $P = 0.04$). Cats equipped with a Birdsbesafe collar cover showed reductions in $\delta^{15}N$, when compared to the control group and pre-treatment period (estimate for $\delta^{15}N = -0.6$, 95% CI −1.2–0.04, $P = 0.04$). Older cats (age class 6–15 yr) showed higher $\delta^{15}N$ ratios (estimate = 0.5, 95% CI 0.2–0.8, $P < 0.001$). The total variance explained by the model (R^2c)
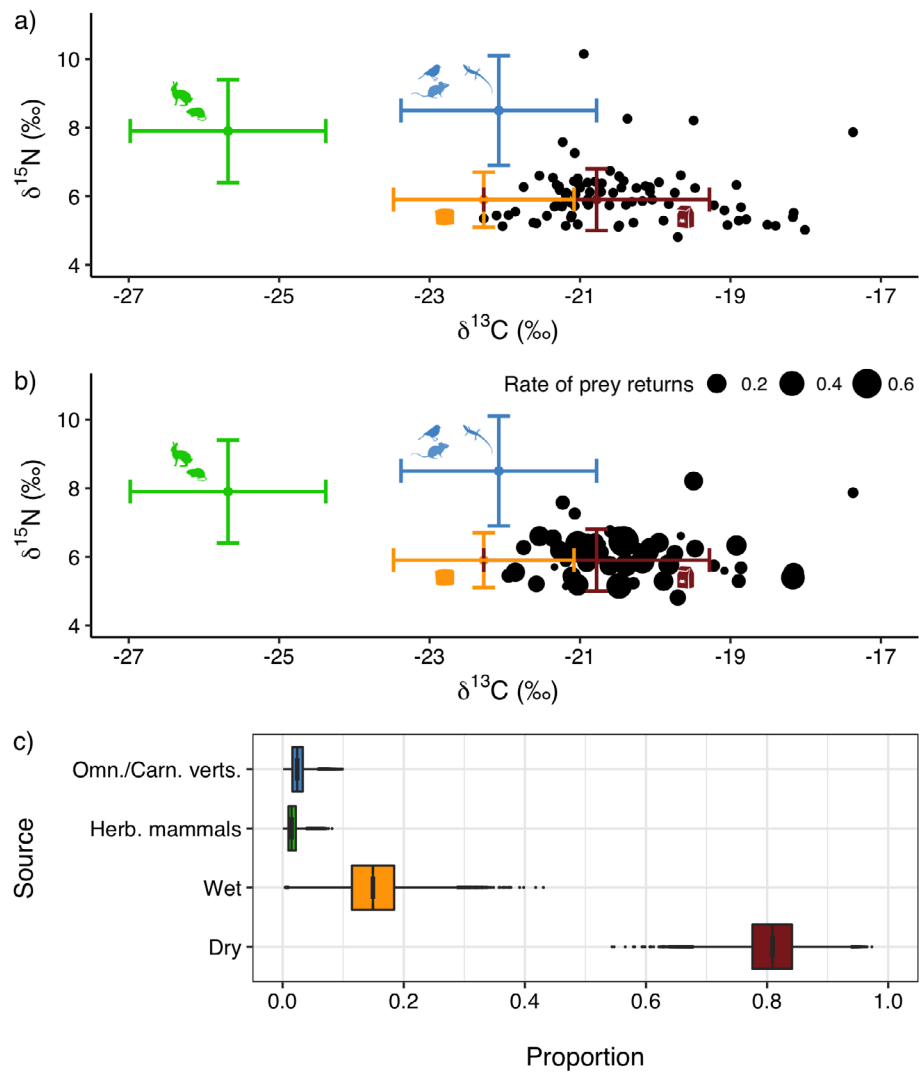
Fig. 2. Estimates of the composition of the diets of free-ranging domestic cats determined by stable isotope analyses of cat whiskers and of putative food sources. (a) Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of basal sections of whiskers sampled from domestic cats ($n = 82$) in the pre-treatment period and of their putative food source groups. Stable isotope ratios for cats are shown as black dots and for food source groups as the mean ± SD, adjusted upwards by the trophic discrimination factors. (b) Stable isotope ratios as in (a) but where the sizes of the dots are scaled by the rate of prey returns during the surveillance period, for individual cats ($n = 57$) where prey items could reliably be attributed to individuals. The rate of prey returns is given by the number of prey brought home divided by the number of days of recording (c) Estimates from Bayesian stable isotope mixing models of the proportional contributions of wild foods (omnivorous and carnivorous vertebrates, herbivorous mammals) and pet foods (wet, dry foods) to cat diets ($n = 82$). Each box represents the 25th and 75th percentiles, and whiskers represent 1.5 times the interquartile range.

was 0.7. There was no effect of any of the other interventions upon variation in $\delta^{15}N$. There was no effect of any interventions upon variation in $\delta^{13}C$.

In the Birdsbesafe treatment group, consumption of omnivorous and carnivorous vertebrates was estimated to be 11.3% (95% CI 2.0–31.1%) in the pre-treatment period but was reduced to

Table 1. Estimates of the composition of the diets of domestic cats that depredate wild animals.

	Pre-treatment period (n = 82 cats)		Treatment period (n = 76 cats)	
Food source group	Median	95% CI	Median	95% CI
Provisioned cat foods				
Dry cat foods	0.790	0.694–0.880	0.775	0.682–0.864
Wet cat foods	0.170	0.074–0.271	0.187	0.093–0.285
Wild animals				
Herbivorous mammals	0.014	0.003–0.037	0.013	0.003–0.035
Omnivorous and carnivorous vertebrates	0.023	0.006–0.051	0.021	0.006–0.047

Notes: Estimates are proportions from Bayesian stable isotope mixing models, based on analysis of cat whiskers and four putative food source groups of wild and provisioned foods. Diet composition was estimated for the whole sample of cats in treatment and control groups combined, before (pre-treatment) and during (treatment) an experimental evaluation of interventions aimed at reducing the killing of wild animals.

4.7% (95% CI 0.9–14.1%) during the treatment period (Fig. 3). Consumption of herbivorous mammals was estimated to be 4.7% (95% CI 0.9–14.3%) in the pre-treatment period and was similar at 3.6% (95% CI 0.7–10.8%) during the treatment period. In the control group, consumption of omnivorous and carnivorous vertebrates was estimated to be 3.0% (95% CI 0.7–8.3%) in the pre-treatment period and was unchanged at 2.9% (95% CI 0.6–8.4%) during the treatment period. Similarly, consumption of herbivorous mammals was estimated to be 2.8% (95% CI 0.6–7.9%) in the pre-treatment period and was unchanged at 2.7% (95% CI 0.6–7.8%) during the treatment period.

Discussion

Domestic cats that regularly capture and kill wild animals nevertheless rely almost entirely on commercial pet foods provided by their owners. Among our sample of cats, all of which regularly captured and killed wild animals, they tended overall to consume relatively small amounts of the wild foods they caught. Where anthropogenic foods are available, free-ranging, owned domestic cats clearly rely predominantly on them, suggesting that hunting and killing wild prey does not substantially contribute to the gross protein or energetic requirements of such cats. Rather, provisioned foods subsidize the cats, enabling hunting that might have potentially deleterious consequences for vulnerable species or ecosystems (Cove et al. 2018, Maeda et al. 2019).

Cats are obligate carnivores, requiring high levels of protein as the source of nitrogen and essential amino acids (McDonald and Rogers 1984). Notwithstanding our determination of a relatively low TDF for $\delta^{15}N$ of 1.9‰, which is suggestive of high protein quality (Robbins et al. 2005), it has nevertheless been proposed that some cats may hunt more because they are stimulated to seek additional or diverse food items to compensate for some aspects of deficiency in the food they are provided within the household. Our study suggests, however, that while some cats may be stimulated to hunt in this way, the contribution that wild prey then makes to most such cats' diets is very small, relative to provisioned food. It is therefore possible that despite hunting to address some need, this need may not be being addressed by hunting. Alternatively, if cats lack some micronutrient, it may be that even low levels of wild prey consumption suffice.

Because of the relatively recent domestication of the cat, it has retained many behavioral traits of its wild progenitor, among them the separation between hunting motivation and prey consumption (Leyhausen et al. 1956), not necessarily eating what is killed, and surplus killing when opportunities arise (Adamec 1976, Macdonald and Rogers 1984). Some cats tend to eat their prey *in situ* while others bring it to a safe place to eat immediately or later (Loyd et al. 2013, Seymour et al. 2020), and the human household is likely to represent such a place for most owned, domestic cats. Possible explanations for the disparity between the frequency of capturing and bringing prey home and the relative importance
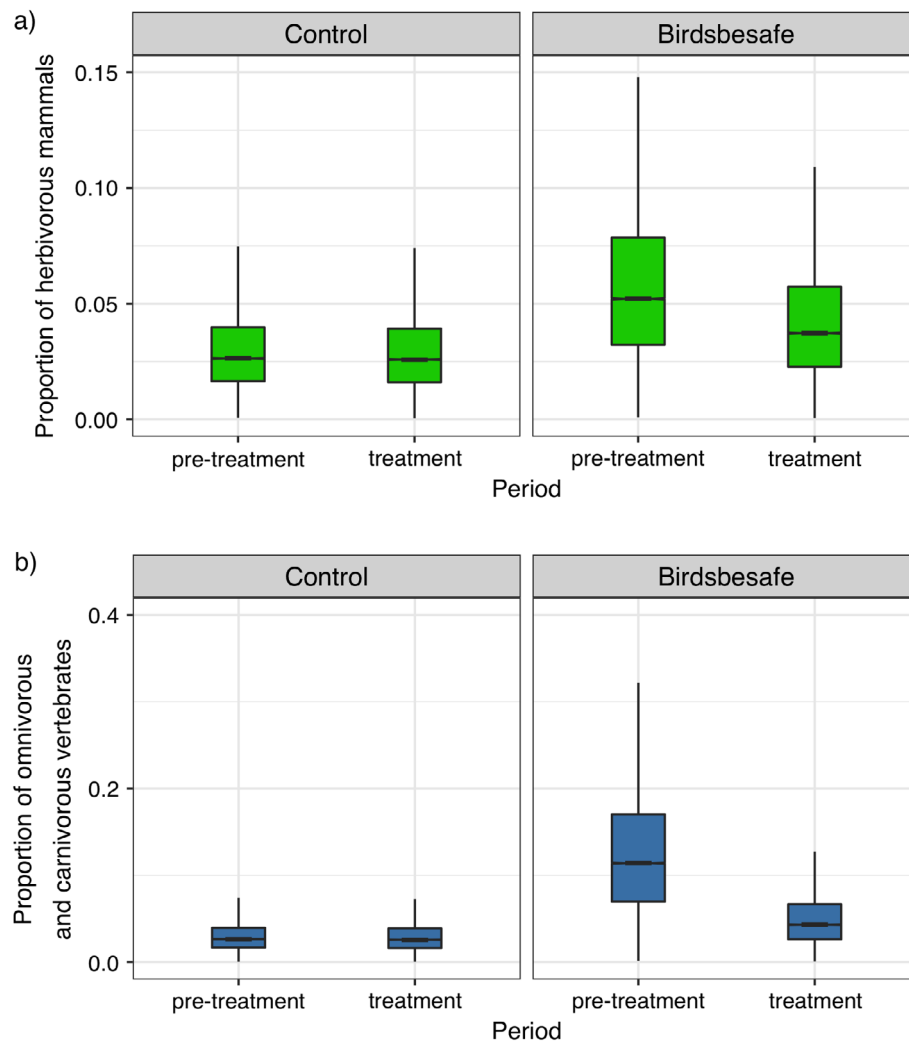
Fig. 3. Estimates of the proportional contributions of wild foods (a) herbivorous mammals and (b) omnivorous and carnivorous vertebrates to the diets of cats equipped with Birdsbesafe collar covers and a control group. Estimates are from Bayesian stable isotope mixing models of the composition of the diets of the whole sample of cats in the treatment and control groups, in the pre-treatment and treatment periods.

of wild prey consumed by cats might be (1) that once home, cats might be distracted by highly palatable provisioned food (Pekel et al. 2020) and eat it in preference to the wild prey or (2) that cats may have the intention of consuming their prey later (Niewold 1986), but in many cases the owner removes it before it can be partly or wholly consumed. Cats have retained a similar behavioral repertoire to that of their wild ancestors (Bradshaw 2006), and killing might be strongly driven by such inherited instincts and not necessarily by specific attempts to address

nutritional needs (Bradshaw et al. 1999). Killing prey can also be facilitated by owner husbandry and the degree of domestication of the cat, and by the environment where the cat lives, which determines the availability and diversity of potential prey (Cecchetti et al. 2021a).

In our wider study, provisioning of high meat protein food and object play led cats to capture and return wild prey with significantly reduced frequency (Cecchetti et al. 2021b). While these interventions significantly affected returns of wild prey by these domestic cats, their effects on

consumption of the prey they captured could not be discerned in this study. Instead, variation in the assimilated mass of wild prey was, in most cases, random with respect to treatment, both for interventions that reduced and increased prey capture rates.

The Birdsbesafe collar cover was the exception. This device effectively inhibits hunting success, particularly hunting of birds, by making cats more visible to their prey (Pemberton and Ruxton 2019). In our broader study (Cecchetti et al. 2021b), fitting this device reduced the capture and return of birds by 42% (albeit with large variation in individual responses: 95% CI 1–66%), but had no significant effect on returns of mammals. Our analysis of the diets of a subsample of this treatment group suggests that when wearing the collar covers, central estimates of the relative importance of omnivorous vertebrates, the food source group that included birds, in these cats' diets fell from 11.3% to 4.7%. Fitting cats with a Birdsbesafe cover collar therefore reduces both the frequency of capture and return of birds, and likely the consumption of a wild prey group that includes birds, even while the extent of such reduction is variable between individuals. For owners that are content to equip their cats with collars and collar-mounted devices, the Birdsbesafe is validated as an effective means of reducing the capture and consumption of wild birds, but not mammals. Some owners and animal welfare organizations, however, express reservations about fitting their cats with collars, stemming from concern about welfare, safety, or collar loss and cost (Lord et al. 2010) and so this measure may not be a general solution to the depredation of birds by cats.

Our study confirms that stable isotope analysis of cats' whiskers and potential foods can be a useful approach to estimating the contributions of broad categories of wild and provisioned foods to the diets of free-ranging domestic cats. The stable isotope ratios of δ^{13}C and δ^{15}N of cat foods and wild prey differed markedly, though at the scale at which we were operating, individual prey species were not distinguishable. We were able to discern two wild and two provisioned food sources: herbivorous mammals; omnivorous and carnivorous vertebrates; wet cat food and dry cat food. It was nonetheless disappointing not to be able to discriminate wild

birds, which are of particular conservation concern, from wild mice and rats, which tend to be considered pests. The use of more taxonomically precise techniques for identifying dietary components, like DNA metabarcoding, might be a complementary approach to identifying consumption of wild birds versus mammals (Forin-Wiart et al. 2018). Some greater resolution in dietary analyses might be achieved by sampling and quantifying both wild and provisioned food inputs at the level of individual cat or household, though the substantial between-batch variation in isotope ratios of provisioned foods would require such monitoring to be exhaustive in detail. Resolution might also be improved with greater understanding of variation among individual cats and, perhaps more importantly, among food sources, in affecting trophic discrimination factors. Our analysis of 9 individuals highlighted relatively large between-individual variation in estimates of this offset between food and consumer (coefficient of variance = 43% for δ^{13}C and 38% for δ^{15}N). Our mixing models incorporated this uncertainty, and we are confident of the robustness of our distinction between the broad groupings of wild and provisioned foods. However, this between-individual variation is consistent with bulk analysis of food isotope ratios not fully reflecting the bioavailability to cats of macronutrients in commercial foods. Commercial foods have high and variable C:N ratios and dry foods, in particular, contain high proportions of plant sugars and starches, including from distinctive C4 plants, much of which may be indigestible to cats. These have the potential substantially to affect δ^{13}C ratios and possibly the offsets between food and consumer tissues. To address this possibility, compound-specific isotope analytical approaches would allow the distinction of the nutritional importance of the diverse components of cat dietary intakes. Additionally, it would be interesting to detect variation in TDFs for δ^{15}N between cats provisioned with different foods, as a means of evaluating diet quality (Robbins et al. 2005).

In conclusion, domestic cats living as companion animals rely almost exclusively on provisioned cat foods, even when they regularly kill wild prey. If provisioned cats hunt to address some nutritional deficiency, what they kill is unlikely to alter macronutrient intake. Hunting

might nevertheless address some micronutrient requirement or behavioral motivation. Our studies together suggest that cat motivation for hunting and returning prey can be markedly reduced, even though domestic cats eat only relatively small amounts of wild prey, and further highlight the disconnect between hunting, capturing, and then eating wild prey and the motivations for these behaviors.

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Data Availability Statement

The data used in this study are available from Dryad: https://doi.org/10.5061/dryad.69p8cz920