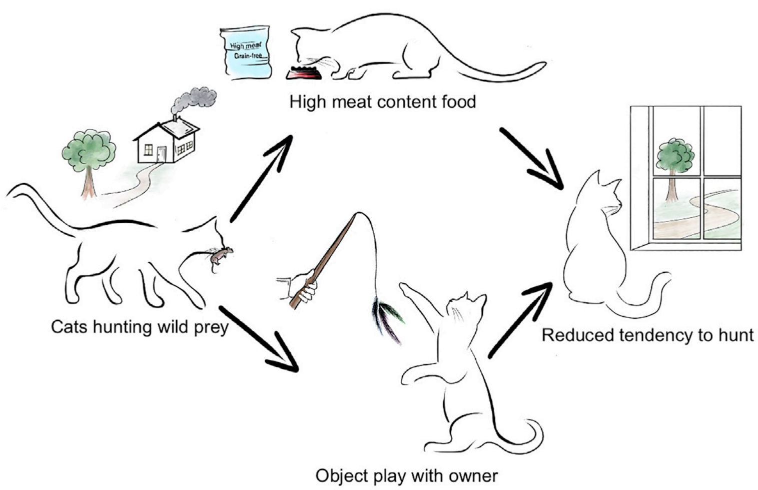
Current Biology

Report

Provision of High Meat Content Food and Object Play Reduce Predation of Wild Animals by Domestic Cats *Felis catus*

Graphical Abstract



Highlights

- Predation by domestic cats can be a threat to biodiversity and is a social problem
- Providing high-meat-protein food and object play both reduce predation by cats
- Rather than impeding hunting, these non-invasive measures reduce tendency to hunt
- Cat owners might engage more with measures that benefit cats as well as wildlife

Authors

Martina Cecchetti, Sarah L. Crowley, Cecily E.D. Goodwin, Robbie A. McDonald

Correspondence

r.mcdonald@exeter.ac.uk

In Brief

Cecchetti et al. address the contentious problem of wildlife predation by domestic cats. Providing grain-free food with meat-derived proteins and engaging in object play both reduced predation of wild animals. These non-invasive measures reduce the tendency to hunt rather than impede hunting, and might appeal to owners concerned about cat welfare.

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Current Biology

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Report

Provision of High Meat Content Food and Object Play Reduce Predation of Wild Animals by Domestic Cats *Felis catus*

Martina Cecchetti,[1] Sarah L. Crowley,[1] Cecily E.D. Goodwin,[1] and Robbie A. McDonald[1,2,3,*]
[1]Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK
[2]Twitter: @robbieamcdonald
[3]Lead Contact
*Correspondence: r.mcdonald@exeter.ac.uk
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SUMMARY

Predation by domestic cats *Felis catus* can be a threat to biodiversity conservation,[1–3] but its mitigation is controversial.[4] Confinement and collar-mounted devices can impede cat hunting success and reduce numbers of animals killed,[5] but some owners do not wish to inhibit what they see as natural behavior, perceive safety risks associated with collars, or are concerned about device loss and ineffectiveness.[6,7] In a controlled and replicated trial, we tested novel, non-invasive interventions that aim to make positive contributions to cat husbandry, alongside existing devices that impede hunting. Households where a high meat protein, grain-free food was provided, and households where 5–10 min of daily object play was introduced, recorded decreases of 36% and 25%, respectively, in numbers of animals captured and brought home by cats, relative to controls and the pre-treatment period. Introduction of puzzle feeders increased numbers by 33%. Fitting Birdsbesafe collar covers reduced the numbers of birds captured and brought home by 42% but had no discernible effect on mammals. Cat bells had no discernible effect. Reductions in predation can be made by non-invasive, positive contributions to cat nutrition and behavior that reduce their tendency to hunt, rather than impede their hunting. These measures are likely to find support among cat owners who are concerned about the welfare implications of other interventions.

RESULTS AND DISCUSSION

Depending on the ecological and cultural context in which domestic cats live, they are variously perceived as pets, pests, or pest controllers, leading to intense social debates about cat management.[4] Their adaptability to diverse environments, with and without human support, is connected to retention of hunting behavior from their wild ancestor *Felis silvestris lybica*, to which they are physiologically and behaviorally close.[8] The abundance of cats is associated with ecological impacts that are particularly severe in island ecosystems.[1] Although there is debate about the extent to which cat predation is compensatory or additive to natural mortality, high densities of cats have been convincingly linked to detrimental effects on vertebrate populations at continental scales.[2,3] In addition to any direct impacts of predation, cat presence can indirectly affect avian productivity, through reductions in nest provisioning rates and increases in nest predation by other predators,[9] which could markedly affect bird abundances where cat densities are high.[10]

Unless their cats are kept as pest controllers, owners rarely consider killing wild animals to be desirable.[6,7] To reduce killing, owners might completely or partly restrict outdoor access, or attempt to inhibit or impede hunting with collar-mounted devices such as bells, collar covers, and bibs, with varying success.[11–13] Cat owners vary in their use of such measures: roaming and hunting are often seen by owners as a natural component of cat behavior; the measures might, or might be perceived to, adversely affect cat welfare or safety; and cats may reject collars.[6] Moreover, although these measures might successfully impede hunting, they do not repress the cats' instinct, tendency, or desire to hunt.

The behaviors and perspectives of cat owners are clearly central to the problem of cat management. Permanent confinement of cats would eliminate depredation of wildlife, perhaps excepting commensal rodents. As effective as it might be in principle, permanent confinement is unpopular among cat owners in many societies, including in the United Kingdom, where outdoor access is considered by owners to be critical to cat welfare,[6,7] and New Zealand, where containment to enclosures and 24-h confinement were among the measures least likely to be adopted by owners.[14] In developing effective advocacy, there is a trade-off between effectiveness in principle and scale of uptake in practice. Prioritizing behaviors that are likely to be widely adopted by cat owners is likely to lead to more effective advocacy. Eventually, if adopted behaviors mitigate the problem, this would lead toward more effective conservation actions and incremental change in societal norms.[14]

Recognizing the importance of cat welfare to cats and their owners, we tested whether novel, non-invasive dietary and behavioral interventions, that would ostensibly benefit cats,

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Figure 1. Treatments Applied to Domestic Cats to Reduce the Numbers of Wild Animals Captured, Brought Home, and Recorded by Householders

(A) Bell: cats are fitted with a collar-mounted "standard" cat bell.

(B) Food: cats are provided with a high-quality, commercially available food that was high in meat-protein content and lacked grain.

(C) Puzzle: provision of existing dry foods in a standard, commercially available puzzle feeder.

(D) Birdsbesafe: cats are fitted with a collar and a Birdsbesafe collar cover.

(E) Play: cat owners engaged in object play with their cats, using a "fishing" toy (illustrated) and a "mouse" toy for a minimum of 5 min/day.

(F) Control: owners only recorded the numbers of wild prey brought home every day.

might reduce killing, not by impeding hunting but by reducing the cats' tendency to hunt. We recruited cat owners whose cats regularly hunted and captured wild animals and brought them back to the house. With a before-after-control-impact design, we evaluated two existing inhibitory measures: equipping collars with a bell, or with a Birdsbesafe collar cover; alongside three novel measures: provision of food in a "puzzle" feeder, provision of a commercial, grain-free food in which meat was the principal source of protein, and 5- to 10-min daily object play, plus a control group (Figure 1). Our response variables were the total numbers of prey animals, and of mammals and birds separately, captured and brought home by cats living in the same household and recorded by householders. When the trial ended, we surveyed participants about their intention to continue using their assigned interventions.

219 households in southwest England, owning 355 cats, completed the 12-week trial (Table S1). Relative to the control and pre-treatment period, total numbers of animals per cat were significantly reduced in households in the food (−36%, $p < 0.001$) and play (−25%, $p = 0.016$) treatments (Figure 2; Table S2). Conversely, households in the puzzle treatment recorded significantly increased numbers (+33%, $p = 0.009$). Bell and Birdsbesafe treatments had no discernible effects on total prey. For mammals only, food (−33%, $p = 0.002$) and play (−35%, $p = 0.002$) reduced numbers, puzzle increased numbers (+49%, $p = 0.002$), but bell and Birdsbesafe had no discernible effects. For birds only, food (−44%, $p = 0.032$) and Birdsbesafe (−42%, $p = 0.047$) reduced numbers, but bell, play, and puzzle had no discernible effects.

Of the survey respondents, 16 of 30 (53%) from bell, 7 of 33 (21.2%) from Birdsbesafe, 13 of 40 (33%) from food, 13 of 41 (32%) from puzzle, and 29 of 38 (76%) from play treatment groups reported that they planned to continue with the intervention (Table S3). Respondents from the Birdsbesafe and bell groups reported cat discomfort and loss of collars as reasons for discontinuing use. Low intention to continue in the puzzle group was primarily attributed to cat disinterest, and in the food group to low palatability of the wet, but not the dry, food.

Domestic cats are valued companion animals and owners tend to prioritize their perceptions of cat welfare over any potential hazard cats might present to wildlife.[6,7] The fulfilment of cats' physiological and behavioral requirements has not previously been considered important for managing hunting behavior,[5] yet our study has shown that modifications to diet, and behavioral enrichment with object play, both affect cats such that they capture and bring home significantly fewer wild animals.

Our study is consistent with the theory that some cats may hunt more because they are stimulated to address some deficiency in their provisioned food.[5] We are not, however, able to distinguish specific drivers of the beneficial effect of dietary change, because the trial food had multiple attributes that differed from most previous foods: freshly prepared meat was the primary source of proteins and the food lacked grains, rendered meat, or meat meal. It is possible that the effect arises from augmentation of a specific micronutrient or amino acid, the availability of which has the potential to be increased in a targeted way, without necessarily increasing any wider environmental impacts of providing meat-rich diets to companion animals.[15] It is therefore desirable and feasible to evaluate the precise nature of the relationship between food contents and hunting behavior in a blinded trial, with a view to targeting recommendations for owners and pet food manufacturers. As well as contents, palatability is important. Although there were no apparent differences in effectiveness between wet and dry foods, 50% of survey respondents from the food group reported that their cats found the experimental wet, but not the dry, food unpalatable.

Reproduction of natural behaviors in the home environment is beneficial for pet cats.[16] During hunting and play, similar behaviors are observed, and hunger increases both predation rate and play motivation in cats.[17] Again, we have made an ostensibly

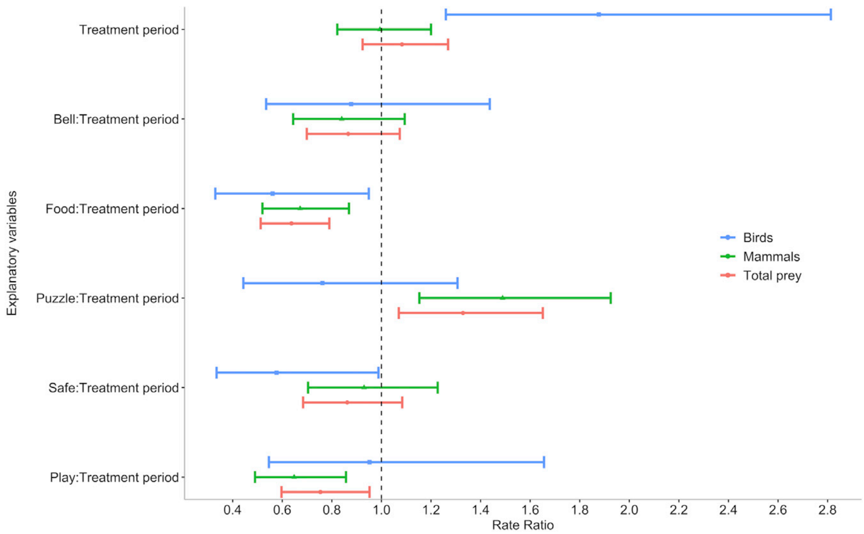

Figure 2. Comparisons of the Effects of Treatments Applied to Domestic Cats to Reduce the Numbers of Wild Animals Captured and Brought Home by Cats, and Recorded by Householders

Comparisons are based on analysis of the numbers recorded (see also Table S1) during the treatment period, relative to the control group and the pre-treatment period. "Safe" is the Birdsbesafe collar cover. The main effect of the treatment period reflects a seasonal increase in wild bird availability. Rate ratios are shown with 95% confidence intervals (see also Table S2).

positive intervention with the introduction of object play, associated with desirable reductions in hunting. Participant feedback indicated that most cats readily engaged with the toys, and that three-quarters of households planned to continue with regular play. Dietary and behavioral drivers of hunting may operate independently, and so it would be valuable to investigate potential additive effects of changes to diet and play.

Increased predation in the puzzle treatment might be attributable to device novelty, insufficient training of owners and/or cats, or inability to easily access food and resulting hunger or frustration. For owners willing to equip their cats with collars, and are concerned about their cats hunting birds, the Birdsbesafe collar cover was effective.

Given the value of applying a precautionary approach to this issue,[18] reduction in killing by domestic cats is a positive step in most ecological settings. However, the degree of impact that cat predation has upon prey populations varies with ecological and human social contexts, as will the effectiveness of mitigation attempts. In areas of low cat density, reductions in individual killing are likely to bring greater benefits than in areas of dense human settlement, where cats live at their highest densities.[19] Such conditions in some residential areas mean that reduced individual predation rates may still result in considerable cumulative impacts.[20] Similarly, reductions in individual killing might not suffice to mitigate impacts upon particularly vulnerable populations or species.

In managing predation by domestic cats, owner behavior is as important as cat behavior and so to reduce killing by cats, management strategies need to be both effective and implemented by owners.[14] Positive interventions, aimed at benefiting cats and appealing to owners, can reduce cats' tendencies to hunt, and might therefore form the basis of a conservation win-win.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.12.044.

ACKNOWLEDGMENTS

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AUTHOR CONTRIBUTIONS

The study was conceived by M.C., S.L.C., and R.A.M.; M.C. and S.L.C. conducted the experiment; M.C. analyzed the data with input from C.E.D.G.; and M.C. and R.A.M. drafted the manuscript with input from other authors.

DECLARATION OF INTERESTS

The food provided to cats was purchased by the project from the manufacturer (Lily's Kitchen) at a wholesale price, and was shipped at the company's expense to the study households. Lily's Kitchen provided a box of cat food and treats for a prize draw among the participants of our control group. We purchased Birdsbesafe collars directly from Birdsbesafe LLC with a 35% discount.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Raw and analyzed data	This paper	Dryad data repository https://doi.org/10.5061/dryad.cvdncjt3k
Software and Algorithms		
tidyr	Hadley Wickham and Lionel Henry (2019). tidyr: Tidy Messy Data. R package version 1.0.0.	https://CRAN.R-project.org/package=tidyr
tidyverse	Hadley Wickham (2017). tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1.	https://CRAN.R-project.org/package=tidyverse
dplyr	Hadley Wickham, Romain François, Lionel Henry and Kirill Müller (2019). Dplyr: A Grammar of Data Manipulation. R package version 0.8.3	https://CRAN.R-project.org/package=dplyr
lme4	Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.	https://CRAN.R-project.org/package=lme4
MuMIn	Kamil Bartoń (2019). MuMIn: Multi-Model Inference. R package version 1.42.1.	https://CRAN.R-project.org/package=MuMIn
DHARMa	Florian Hartig (2019). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.4.	https://CRAN.R-project.org/package=DHARMa
magrittr	Stefan Milton Bache and Hadley Wickham (2014). magrittr: A Forward-Pipe Operator for R. R package version 1.5.	https://CRAN.R-project.org/package=magrittr
ggplot2	H. Wickham. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.	https://CRAN.R-project.org/package=ggplot2
lubridate	Garrett Grolemund, Hadley Wickham (2011). Dates and Times Made Easy with lubridate. Journal of Statistical Software, 40(3), 1-25.	https://CRAN.R-project.org/package=lubridate

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Robbie McDonald (r.mcdonald@exeter.ac.uk).

Materials Availability

This study did not generate new materials.

Data and Code Availability

Anonymised data and code are available from the Dryad Digital Data repository https://doi.org/10.5061/dryad.cvdncjt3k

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study worked with adult and juvenile (> 6 months), male and female domestic cats *Felis catus* living as companion animals, as part of human households.

Cat owners were recruited through advertisements on broadcast, print and social media. During sign-up, owners completed a questionnaire for each cat in the household, regarding the cat's general characteristics (e.g., name, sex, breed), owners' perceptions of health and behavior, feeding and roaming habits, frequency of hunting, and any ongoing management strategy adopted for reducing hunting. To test owner willingness and continuity in recording for the study duration, we set the first two weeks as surveillance weeks. Power analysis based on a pilot study and on previous experimental studies suggested we had 80% power of detecting a statistically significant reduction of > 67% in numbers of animals returned to the household, over a period of three weeks with a sample of 40 cats that regularly captured and brought home wild animal prey. Allowing for drop out, our target sample per treatment was 70 cats. We selected households in which at least one prey item had been brought home during two weeks of preliminary surveillance. Owners not selected for inclusion in the intervention study kept recording prey but were not included in formal analyses.

The study protocol was approved by the ethics committee of the University of Exeter, College of Life and Environmental Sciences, Penryn Campus (Reference CORN000181). The project also received specialist veterinary guidance and the protocols were approved by an independent Project Advisory Group, comprising feline veterinary, behavioral and welfare specialists. Owners provided informed written consent.

METHOD DETAILS

Basis of treatments

It has been hypothesized that the selective basis for domestic cats retaining hunting behavior relates to the probability that diets provided by people have, at times, been unlikely to meet cat nutritional requirements in their entirety.[21] Cats are obligate carnivores with an absolute requirement for high levels of protein as the source of nitrogen and essential amino acids, and no essential requirement for carbohydrates.[22] They are incapable of synthesizing some essential nutrients that are readily available in their wild prey.[22] Among their nutritional peculiarities, cats have an absolute requirement for high protein diets, many water-soluble B vitamins (e.g., niacin), vitamin A, vitamin D, arginine, taurine, methionine, cysteine and some essential fatty-acids.[22,23] Nutritional deficiencies can have severe implications: arginine deficiency causes hyperammonemia and severe uremia and may lead to death within few hours,[24] while taurine deficiency causes central retinal degeneration[25] and leads to cardiac abnormalities.[26] An important aspect in characterizing cat foods is protein quality, evaluated in terms of digestibility and the relative abundance and bioavailability of amino acids. Bioavailability of dietary amino acids is the proportion of ingested dietary amino acids that is absorbed, and renders them potentially suitable for metabolism or protein synthesis.[27] The protein components of pet foods can comprise both animal and plant sources, though it is recognized that, compared to animal protein sources, plant protein sources have lower digestibility,[28,29] with lower bioavailability[30] and a less complete profile of amino acids.[31] Adult cats fed on a meat meal as protein source had higher apparent nitrogen absorption and retention, as well as higher dry matter digestibility, when compared to a corn gluten meal-based diet.[32] Cats fed plant-based diets in which protein content is provided largely by soybean had lower plasma concentrations of taurine[33,34] and such diets are also associated with arginine shortage.[30,35] Consequently, while essential taurine is found in animal proteins, it must be supplemented when plant sources are used in the diet.

The advent of pet food manufacturing has allowed cat owners to feed their cats with an ostensibly "complete" (providing adequate amounts of all the required nutrients) and "balanced" (the nutrients are present in the correct proportions) diet. Guidelines for pet food companies in countries of the European Union are established by Fédération Européenne de l'Industrie des Aliments pour Animaux Familiers (FEDIAF). This Federation provides guidelines for complete and complementary pet foods, to ensure adequate concentrations of macronutrients, micronutrients and amino acids for a daily ration to satisfy cat energetic and nutrient requirements. However, detailed examination of the composition of common commercial pet foods has revealed inconsistency in their provision of some essential elements[30,36] and some commercial foods do not meet all the nutrient minima, compared to dietary requirements, in terms of fatty acids, amino acids, and minerals.[30] Domestic cats have a target macronutrient intake of 52% of total energy from protein, 36% from fat and 12% from carbohydrates.[37] Instead, some pet food diets contain much higher proportions of energy content from carbohydrates (minimum 26% of energy from carbohydrates), which limits further food intake and creates a shortfall in protein and fat intake,[36] potentially leading cats to seek those nutrients elsewhere. Moreover, dry foods have higher carbohydrate content than wet foods because of the starches used as binding agents, making aspects of target intake for some cat macronutrients attainable only through provision and consumption of wet food.[38] Production of pet foods has a substantial environmental impact, stemming in particular from the use of meat.[15] Cats require specific nutrients but not necessarily specific sources for these nutrients. Detailed analytical examination of meat foods might provide insights into their chemical and nutritional attributes that influence hunting behavior. This would allow manufacturers to refine their composition without necessarily adding to environmental impacts.

To reduce adverse signs of stress in cats and to ensure their behavioral needs are met, as well as to address common pathologies like obesity and diabetes mellitus, various behavioral enrichment strategies have been evaluated[39] and are advocated by animal welfare organizations.[40] These have included the use of 'puzzle feeders' designed to mimic instincts for pursuit of food, while object play with toys engages cats in a pseudo-predatory activity.[40] A complete hunting sequence in domestic cats involves seeking prey, stalk, chase, manipulate, kill and consume[41] and playing and hunting activities increase with hunger, suggesting a shared motivational basis.[17] A lack of physical and mental stimulation in the home environment might therefore increase the time that companion animal cats spend outside, with associated increases in hunting, and the possibility that behavioral enrichment might reduce hunting and killing.

There are several collar-mounted devices that aim to inhibit hunting success that have been previously tested. Birdsbesafe is a colorful collar cover that works as a visual warning, increasing the visibility of cats to potential prey animals with color vision. It exhibits pronounced effectiveness in reducing killing of birds[12,42,43] and, more generally, prey with good color vision, including herpetofauna.[42] The Birdsbesafe is variably effective in affecting killing of mammals,[42,43] as might be expected given their lack of color vision and tendency to be more nocturnal. Studies on collars equipped with bells have reported divergent outcomes, with no effects on predation rates in Australia,[44,45] but a significant (by around 50%) reduction reported in UK.[11,46] In our earlier, observational study,[47] we found that cats fitted with bells tended to bring back fewer mammals but found no difference in numbers of birds.

Experimental design

The trial was carried out from 20th March to 21st June 2019. Participants were required to remove any existing device that potentially interfered with cat hunting activity immediately before entry to the trial. The trial followed a before-after-control-impact (BACI) design. Before interventions were applied, owners recorded all prey brought home by cats for a pre-treatment period of seven weeks (20th March to 9th May). There then followed a transition period of one week (from 10th to 16th 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 (17th May to 21st June). All cats in the same household were treated in the same way, except when one of the cats was exclusively kept indoors. The experimental unit for the trial was therefore the household.

The six treatment groups were: BELL, where cats were fitted with a quick-release reflective collar (Kittygo, Wink Brands, UK) to which a single cat bell was attached; BIRDSBESAFE, where the same quick-release collar was fitted with a rainbow-patterned Birdsbesafe (https://www.birdsbesafe.com) collar cover; FOOD, where owners provided cats with a commercial, grain-free food in which protein was predominantly derived from meat sources (Lily's Kitchen Everyday Favorites paté multipack 8x85 g as wet food; and Lily's Kitchen Delicious Chicken as dry food); PUZZLE, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser); PLAY, in which owners spent at least 5 minutes per day dedicated time playing 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); 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.

All food and equipment was provided by the project and was sent, with detailed guidance for the introduction of the treatment. For the BELL and BIRDSBESAFE interventions, detailed instructions were provided to ensure safe fitting and monitoring of the collar. In the case of households where cats exhibited prolonged intolerance of the collar, owners removed the collar and continued with prey recording but were excluded from further analysis. For the FOOD intervention, the food was purchased at wholesale price by the project from the manufacturer and shipped directly to the household. Food was presented in the same manner and quantities as the regular food, including relative proportions of wet and dry food. The new food gradually replaced regular food over the seven-day transition period (presenting a small amount of new food mixed with the normal food, then shifting the quantities until only the new food was provided). Owners were requested to monitor their cat and notify the research team if the cat refused the new food. In four households where cats exhibited complete aversion, the households continued recording but were excluded from analysis. Following the conclusion of the study, owners were provided with a further week's supply of food, to enable gradual transition back to regular food. The trial was not blinded, and owners in the FOOD group might have introduced recording bias. For the PUZZLE group, the puzzle feeder was introduced gradually over several days, following a procedure set by Dantas et al.[48] Cat treats (Lily's Kitchen Little Lovelies Delicious Chicken) were initially provided to increase cat motivation and, as the cat became more adept at using the puzzle feeder, owners could replace treats with the normal dry food. Part of the cats' normal daily ration of dry food was used in the ball (i.e., the ball did not become an additional source of food). The holes in the feeder were adjustable. It was initially put on an 'easy' setting. As cats became more familiar, the difficulty of the puzzle was increased, and an increasing proportion of the normal dry food was provided using the feeder. By the end of the transition week, cats received their entire daily dry food ration from the puzzle feeder. In the PLAY group, owners were provided with play guidance, to slowly move the 'fishing' toy away from their cat, allowing it to stalk and/or ambush it, and then provide the 'mouse' toy filled with bubble wrap to be caught and manipulated (catch, bite and kick) in order to reproduce a complete hunting sequence. Toys were removed when not in use, both to maintain their value to cats and for safety reasons. Play duration per day was 5-10 minutes, after which adult cat motivation in playing tends to reduce as a consequence of habituation.[49] It is therefore unlikely that the modest duration of object play affected the availability of time that cats might have spent outdoors. Because of the importance of CONTROL group owners to the study, we encouraged their active participation with a final gift consisting of a small pack of cat treats, and a discount voucher for future food orders.

Prey recording and basis of response variables

The main response variables were the numbers of animal prey items captured and brought home by cats and recorded by the owners. Cat owners regularly uploaded prey records online, using a unique participant number, identifying the cat responsible for the kill, 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 prey remains), species (an identification guide was available for facilitating species identification), whether prey was alive or dead, and comments.

A limitation of this and similar studies[11,12,42–47] relates to using the numbers of prey brought home by cats as a proxy for the numbers of animals they kill. Two studies[50,51] that have equipped domestic cats (n = 16 and 18 cats, respectively) with cameras ("KittyCams"), found that 9 of 39 (23%) and 11 of 62 (18%) prey items were brought home, while the remainders were left or eaten *in situ*. Similarly, direct observation of hunting by tracked indoor-outdoor cats (n = 12 cats) and of hunts resulting in kills (n = 4 kills), when compared to prey records, suggest that householders might record around 30% of the prey killed.[52] Notwithstanding the scale of these studies, they are consistent in their findings. Therefore, it is probable that some of the cats in our study killed and ate some of their prey while away from home, or killed and left them *in situ*, and so returned a proportion of their total kills to the household for recording. However, our study design accounts for this unquantified variation in multiple ways: 1. It is not quantified in the three observational studies,[50–52] but it is likely there is between-individual variation in the tendency of cats to bring home prey. We have accounted for this by adopting a before-after-control-impact design, whereby between-cat and temporal variation are controlled-for, by making paired observations of the same individuals before and after implementation of the treatment, and analyzing variance by period and by treatment group, including a control. 2. Not accounting for all the animals killed by cats is a critical bias in quantifying the totality of killing by domestic cat populations and their impact upon prey populations.[20,53] However, our study is of the effect of interventions on the relative frequency of prey returns and we do not extend our findings to the impact of killing upon prey populations. Hence our study conclusions are not subject to this bias. Rather, we work on the basic premise that any killing of wild animals by domestic cats is, in general, ecologically and socially undesirable[6,7] and that any reduction is beneficial. The same factor, i.e., cat abundance, that means their impacts can be locally and regionally substantial, also means that even small *per capita* reductions in killing are likely also to reduce substantially the total numbers killed. 3. In recognizing, *a priori*, the constraints upon directly observing killing by cats, we recruited households where their cats had a track record of bringing home animals they had captured. While this represents a sample that is biased toward the tendency to bring home prey, which we note above is problematic for impact assessment, this bias is not relevant to our interventions. We have only to assume that the tendency to bring home prey is randomly distributed with respect to any potential impact of our interventions upon hunting and killing. 4. An alternative experimental approach would be to equip cats with cameras or to track them directly during hunts, as in the studies above,[50–52] and then to implement our treatments. This more direct approach to quantification of predation has promise, though there are clear challenges of scale. Our power analysis suggested a necessary sample in the hundreds of cats that regularly killed prey, whereas previous camera studies were an order of magnitude smaller. More importantly, perhaps, equipping cats with collar-mounted cameras is itself a moderately invasive intervention, along similar lines to collar covers and bibs. Thus, the means of observation likely affects the observation. Also, the premise of three of our treatments is that they are non-invasive and are not dependent on collaring. This would further increase the challenges of scale, as camera deployment would itself require incorporation as a level in a factorial design. 5. Our aim is to use the numbers of animals brought home as a proxy, to test the effect of our interventions on the numbers of animals killed. An alternative hypothesis is that our interventions did not affect the numbers of animals killed, but instead affected the numbers of animals brought home while the killing continued unabated. We acknowledge that this alternative hypothesis cannot wholly be excluded with our design but we consider this to be a much less parsimonious explanation. In our long-standing study quantifying wildlife predation by cats,[47] we addressed this point: A proxy for the number of animals killed is adequate for a specific purpose "if we can assume that it is the cat's ability or inclination to capture prey that is influenced by the factors being investigated and not its inclination to bring prey home. That is, it seems safe to assume that by wearing a bell, a cat's ability to catch a mouse may be affected, but not the cat's tendency then to bring the mouse home."

The project team sent participants a weekly email prompt to provide data and to confirm ongoing participation using an update form. Participants inserted dates on which they were unable to record prey brought home by the cat (e.g., holidays) and dates on which the intervention was likely ineffective, for example if the bell or collar had been lost. In case of collar loss, a replacement was supplied and re-fitted as soon as possible and days on which cats were not wearing collars were excluded from the analysis. Overall, 15 households presented this problem with a median of 4 days excluded (IQR = 2.5-5.0 days) from the analysis. Two households reported cats not tolerating trial collars at all and these did not continue with the study.

Participant feedback

Owner participation was encouraged through project Facebook pages, in which they could share their ongoing experience with other members of the same treatment group, and through a series of in-person workshops held in different regions throughout the trial. We collected feedback on the owners' experiences of trialling the interventions through the weekly update forms, and conducted a short survey at the end of the trial, in which we asked participants whether they planned to carry on using their assigned interventions. Details of uptake and a summary of feedback for each intervention are provided in Table S3. For some cats, collars appeared to be a source of discomfort, causing cats to scratch the area and try to remove them. Nine owners reported that Birdsbesafe collars prevented cats from grooming effectively, an issue also identified in a previous study.[42] Some owners additionally reported disliking the appearance of the collars, stating they looked 'silly' or 'ridiculous'. Post-trial intent to continue with the FOOD intervention was limited by around 50% of owners reporting that the cats disliked the wet food provided; this is not considered to have affected trial outcomes, as cats continued to eat the wet food and the majority ate mixed diets of wet and dry foods. Cats who completely rejected the food were excluded from the analysis. Post-trial intention to continue with the PUZZLE feeder depended on cat engagement with the device, with some owners reporting cats becoming bored or disinterested. Cat engagement with puzzle feeders may rely on appropriate introduction and training, which could improve uptake and reduce frustration caused by cats' inability to access food. Post-trial intention to continue with object PLAY was high (76%), with owners reporting both engagement with, and sometimes solicitation of, play from cats, and their own enjoyment of the measure.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were conducted in R.[54] Our response variables were the total numbers of prey animals, and separately the numbers of birds and of mammals, captured and brought home by cats living in the same household and recorded by householders. The numbers of prey caught by multiple cats in the same household were combined, because prey could not in every case be confidently attributed to an individual cat. Households in which cats did not experience the intervention, for example where one of the cats was intolerant of a collar or diet change, were excluded from analyses. Records of prey brought home during the transition week were excluded from the analyses. In the treatment period, daily prey records were excluded from analysis if the cats in the house were not all following the treatment on that day (e.g., one of them had lost the collar, or owners were not using the puzzle feeder). Sampling 'effort' was calculated for each household as the total number of days when owners were active in recording prey, during the pre-treatment and treatment periods.

To analyze variation in the total numbers of prey brought home by cats as a function of treatment, a generalized linear mixed effect model with a Poisson error distribution and log link was used. Fixed factors were treatment (six levels, comprising five interventions and the control group), and period (pre-treatment and treatment). The effect of treatment was tested by the interaction term (treatment*period). To incorporate the dependency among observations of cats living in the same household, household identification number was a random variable. To adjust the value of the dependent variable by the number of cats in each house and owner recording effort, an offset for number of cat surveillance days was used (log(n_cats*effort)). The proportion of variance in the dependent variable explained by the model was expressed as a conditional R^2 (R^2c) value incorporating fixed and random effects. Model assumptions were verified by using the package DHARMa.[55] Descriptions of the effects in terms of reduction or increase in rates of animals killed are derived by exponentiating the estimate of the effect, to obtain the Rate Ratio (RR) and the corresponding percentage decrease in the response rate ([RR-1]*100%).

To test for a possible effect of the novelty of the trial food driving any effects of dietary changes, as opposed to the food content, we conducted a secondary analysis of the daily prey brought home by cats in the FOOD group during the treatment period. We tested whether records of animals killed and brought home tended to increase as the duration of the trial increased. We fitted a generalized linear mixed effect model with a Poisson error distribution and log link. Day of observation was a fixed quadratic term. Household identification number was a random variable. To adjust the value of the dependent variable by the number of cats in each house, an offset was used (log(n_cats)). Model fit was verified using the package DHARMa.[55] We found no significant effect or trend arising from day of trial ($p = 0.845$).

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Supplemental Information

Provision of High Meat Content Food and Object Play Reduce Predation of Wild Animals by Domestic Cats *Felis catus*

Martina Cecchetti, Sarah L. Crowley, Cecily E.D. Goodwin, and Robbie A. McDonald

Treatment group	N households	N cats	Period	Mammals	Birds	Reptiles	Amphibians	Insects	Unidentified	All prey
Bell	33	56	Pre-treatment	316	92	23	2	22	31	486
			Treatment	175	96	9	1	1	16	298
Food	39	66	Pre-treatment	418	79	28	0	5	46	576
			Treatment	188	57	5	0	3	18	271
Puzzle	38	51	Pre-treatment	278	64	8	4	8	27	389
			Treatment	253	55	7	0	8	16	339
Birdsbesafe	31	50	Pre-treatment	267	76	23	3	12	19	400
			Treatment	146	48	13	2	3	6	218
Play	46	65	Pre-treatment	318	51	3	1	1	24	398
			Treatment	129	55	3	1	2	12	202
Control	32	67	Pre-treatment	267	43	14	2	6	29	361
			Treatment	185	55	7	2	3	19	271
Total	219	355		2940	771	143	18	74	263	4209

Table S1. Summary of sample sizes in treatment groups and wild animal prey brought home by domestic cats and recorded by households in pre-treatment and treatment periods, related to Figure 1.

Owners living in 456 households with a total of 753 cats signed up to take part in the trial. After allocation to treatment groups and cleaning of data, a total of 219 households and 355 cats were included in the analyses. Median recording effort was 49 days (Interquartile range = 46-49 days) in the pre-treatment period and 34 days (IQR=28-35) in the treatment period. Treatments were: BELL, in which cats were fitted with a collar-mounted ‘standard’ cat bell; BIRDSBESAFE, in which cats were fitted with a Birdsbesafe collar cover; FOOD, in which cats were provided with a high-quality, commercially available food that was high in meat protein content and lacked grain; PUZZLE, in which cats were provided existing dry foods in a standard, commercially available puzzle feeder; PLAY, in which cat owners engaged in object play with their cats for a minimum of five minutes per day; and CONTROL, in which owners only recorded the numbers of wild prey brought home every day. Note that these are raw data as recorded and analyses incorporate duration of recording and other covariates.

	All prey					Mammals					Birds				
	Est.	(SE)	RR	(95% CI)	p	Est.	(SE)	RR	(95% CI)	p	Est.	(SE)	RR	(95% CI)	p
Intercept	-2.327	(0.153)			<0.001	-2.724	(0.184)			<0.001	-4.598	(0.224)			<0.001
Bell	0.422	(0.213)	1.52	(1.00-2.32)	0.048	0.241	(0.257)	1.27	(0.76-2.12)	0.349	0.892	(0.291)	2.44	(1.38-4.34)	0.002
Food	0.442	(0.205)	1.56	(1.04-2.33)	0.031	0.422	(0.246)	1.52	(0.94-2.49)	0.085	0.668	(0.287)	1.95	(1.11-3.44)	0.020
Puzzle	0.319	(0.208)	1.38	(0.91-2.08)	0.126	0.254	(0.250)	1.29	(0.78-2.12)	0.310	0.805	(0.292)	2.24	(1.26-3.99)	0.006
Birdsbesafe	0.341	(0.217)	1.41	(0.92-2.16)	0.117	0.302	(0.261)	1.35	(0.81-2.27)	0.247	0.938	(0.296)	2.55	(1.43-4.59)	0.002
Play	0.124	(0.201)	1.13	(0.76-1.69)	0.537	0.200	(0.241)	1.22	(0.76-1.97)	0.406	0.195	(0.296)	1.22	(0.68-2.18)	0.511
Treatment period	0.080	(0.080)	1.08	(0.92-1.27)	0.319	-0.006	(0.095)	0.99	(0.82-1.20)	0.950	0.629	(0.204)	1.88	(1.26-2.81)	0.002
Bell:Treatment period	-0.144	(0.109)	0.87	(0.70-1.07)	0.186	-0.175	(0.133)	0.84	(0.64-1.09)	0.191	-0.130	(0.252)	0.89	(0.53-1.44)	0.606
Food:Treatment period	-0.451	(0.109)	0.64	(0.51-0.79)	<0.001	-0.397	(0.129)	0.67	(0.52-0.87)	0.002	-0.577	(0.269)	0.56	(0.33-0.95)	0.032
Puzzle:Treatment period	0.285	(0.110)	1.33	(1.07-1.65)	0.009	0.398	(0.129)	1.49	(1.15-1.92)	0.002	-0.271	(0.276)	0.76	(0.44-1.31)	0.326
Birdsbesafe:Treatment period	-0.149	(0.116)	0.86	(0.68-1.08)	0.200	-0.072	(0.140)	0.93	(0.70-1.23)	0.604	-0.549	(0.276)	0.58	(0.33-0.99)	0.047
Play:Treatment period	-0.282	(0.117)	0.75	(0.60-0.95)	0.016	-0.433	(0.140)	0.65	(0.49-0.86)	0.002	-0.049	(0.283)	0.95	(0.55-1.66)	0.862

Table S2. Summary of analyses of variation in the numbers of wild animal prey brought home by domestic cats and recorded by households, related to Figure 1.

Model outcomes are summarised as the estimated regression parameters (Est.) with standard errors (SE), rate ratios (RR) and 95% confidence interval (95% CI), and p-values from a generalised linear mixed model, where the interaction between treatment and period is the term of interest. Descriptions of the effects in terms of reductions or increases in animals killed are derived by exponentiating the estimate of the effect, to obtain the Rate Ratio (RR), and the corresponding percentage decrease in the rate is given by ([RR-1]*100%). Estimated variance in total prey explained by the fixed and random variables was 0.87 (R^2c= 0.87), as well as in mammals (R^2c= 0.87), while in birds is 0.58 (R^2c= 0.58).

	n respondents	Will keep using intervention (%)	Will not keep using intervention / not sure (%)	Positive feedback summary	Negative feedback summary
Bell	30	16 (53.3)	14 (46.7)	Cat behaviour not affected by collars; perceived reduction in hunting	Cat discomfort with collars (scratching, efforts to remove); loss of collars
Food	40	13 (32.5)	27 (67.5)	Cats readily ate food; perceived reduction in hunting	Cats refused, or initially refused, wet food
Puzzle	41	13 (31.7)	28 (68.3)	Cats ate more slowly; cats engaged with puzzle feeder	Cats disinterested in, or became bored of, puzzle feeder
Birdsbesafe	33	7 (21.2)	26 (78.8)	Cat behaviour not affected by collars; perceived reduction in hunting	Cats had difficulty grooming; owners disliked collar appearance
Play	38	29 (76.3)	9 (23.7)	Cats engaged well with toys; owners enjoyed increased interaction	Cats lost interest in toys

Table S3. Summary of participant feedback and uptake, related to Participant Feedback section in STAR Methods.
At the end of the study, participants were surveyed about the interventions they trialled. They were asked whether they intended to keep using the intervention once the trial had finished, and for comments on the intervention they trialled. This table includes responses from households whose cats may not have been included in the final analysis, e.g. owners of cats in the puzzle group who never used the puzzle feeder.