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Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources

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Abstract Cat food left out for feral and domestic cats and bird seed spilled from backyard bird feeders are two common anthropogenic food sources that may attract non-target animals like urban mesocarnivores but no studies have quantified mesocarnivore visitation at these food sources. We used motion-activated video cameras to monitor mesocarnivore use of spilled bird seed below 25 bird feeders maintained by residents in four neighborhoods in Flagstaff, Arizona, June-September 2012 and 2014. During the first five nights of monitoring only seed that spilled naturally below feeders was available. On each of the subsequent five nights, we placed a bowl of commercially available dry cat food below feeders so that both spilled seed and cat food were present. In both years, after cat food was added, the number of visits by striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*) and domestic cats (*Felis cattus*) doubled and the number of times two animals were present simultaneously also increased. Aggressive interactions, in the form of displays or contacts, increased for all species combinations but significantly only between skunks in the presence of cat food. These results demonstrate that both spilled bird seed and cat food may be exploited frequently by urban mesocarnivores and that the type of food can elicit different behavioral responses that could have important implications for human-wildlife conflict and disease transmission.

Keywords Bird feeders · Bird seed · Disease · Pet food · Rabies · Skunk

Two commonly available food sources in urban environments, especially in the USA, are bird seed provided by humans for wild birds and pet food left out for domestic and feral cats. Approximately 47 % of households (50 million people) in the USA provided food for birds in 2011 (U.S. Department of the Interior et al. 2011) and a similar percentage did so in the United

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Kingdom (Davies et al. 2009) and Australia (Ishigame and Baxter 2007). Households in the USA and UK together have been estimated to provide over 500,000 tonnes of seed for wild birds annually (Robb et al. 2008). Though less prevalent in Europe, feeding of birds is apparently common enough in some areas to have allowed exotic bird species to establish by feeding primarily on seed made available by humans (Clergeau and Vergnes 2011). Likewise, feral and domestic cats can reach densities exceeding several hundred cats/km^2 primarily due to human food provisioning (Liberg et al. 2000). Studies in Massachusetts, California and Florida USA found that from 8 to 12 % of households fed an average of 2–4 feral cats (Levy and Crawford 2004) while studies in urban Brooklyn, New York estimated that humans provided enough supplemental pet food to support 4–5 feral cats/ha (Calhoon and Haspel 1989). Feeding of feral cats is also typically part of rapidly growing, trap-neuter-release (TNR) programs for managing feral cat populations in the United States (e.g., Centonze and Levy 2002). In spite of their prevalence, few studies have experimentally investigated the indirect effects of these two food sources on non-target species (Orros et al. 2014).

Foods provided by humans that increase wild animal density or visitation rates will increase probability of human-wildlife conflict and the potential for disease transfer (Daszak et al. 2000; Bradley and Altizer 2007). Increased availability of anthropogenic food sources is often cited as a driver for higher densities of mesocarnivores like skunks, foxes and raccoons in urban areas (Rosatte et al. 1991; Prange et al. 2004; Prange and Gehrt 2004; Bozek et al. 2007), but few studies have quantified visitation rates at different food sources or assessed how behavior may change with food type. Equally important is whether anthropogenic food sources increase the potential for animals to transfer disease either directly through contact or indirectly through scats or parasites that accumulate at feeding sites. The role of bird feeders as foci for disease has previously been investigated primarily in the context of indirect disease transmission via increased numbers of parasites such as ticks (e.g., Townsend et al. 2003) or roundworms (e.g., Page et al. 2009). However, in North America, rabies is an important disease that could be directly transmitted via contact among animals attracted to anthropogenic food sources. Rabies is a deadly disease transmitted via bite of an infected animal, and in North America skunks, raccoons and foxes are the primary wild terrestrial reservoirs for this disease (Dyer et al. 2014). Cross-species transmission of rabies is common, and the potential for transmission from wild skunks, raccoons and foxes to unvaccinated pets and potentially to humans remains a widespread health concern in the USA, Canada and Mexico (Dyer et al. 2014). Approximately 16,000-39,000 people in the United States are potentially exposed to rabies and receive post-exposure prophylaxis annually (Vaidya et al. 2010). Although transmission of diseases like rabies from wildlife to domestic animals is a concern, diseases can also be transmitted in the opposite direction, from domestic animals to wildlife, in some cases threatening already endangered wild populations (e.g., Roelke-Parker et al. 1996). If visitation rates or contacts among wildlife or between wildlife and domestic pets increase in areas where people feed birds or leave pet food out for feral or domestic animals, these areas could act as foci for disease transmission and may be of special concern as areas for the transfer of newly emerging infectious diseases (Daszak et al. 2000).

The types of food humans make available to wild mesocarnivores may also differ in the amount of aggressive behavior or interaction they elicit. Both the quality and spatial distribution of food can alter the probability and intensity of competition, with increased competition and aggression over high quality food distributed in spatially concentrated clumps and less aggression when lower quality food is more widely dispersed (Carr and MacDonald 1986; Milinski and Parker 1991). For example, studies of raccoons demonstrated that both contact rate among individuals and probability of endoparasitic infection were higher in an area where food was experimentally provisioned as concentrated clumps versus an area where food was

provisioned in a more widespread spatial distribution (Wright and Gompper 2005). Based on these studies, we predicted that seed spilled and scattered over several square meters below birdfeeders should represent a more widely dispersed, lower quality food source, while pet food, typically provided in a bowl or dish, should represent a clumped, high quality food source. Therefore, we predicted that aggression and contact among animals would increase in the presence of cat food. Although mesocarnivores have been documented using spilled bird seed and cat food anecdotally (e.g., Weissinger et al. 2009), we know of no studies that have quantified visitation rates or types of interactions at these resources in an urban setting. We specifically addressed two questions: 1) what is nocturnal visitation rate and visit length of mesocarnivores visiting bird feeders in suburban yards and 2) how does visitation rate, contact rate and behavior change when cat food is added?

Materials and methods

We studied animal visitation to established bird feeders in suburban neighborhoods of Flagstaff, Arizona (population 65,000, elevation =2170 m, 35°11′57″N 111°37′52″W). Three of these neighborhoods experienced outbreaks of rabies in 2001, 2005 and 2009, primarily in striped skunks but also infecting a domestic cat (Leslie et al. 2006, Kuzmin et al. 2012). Flagstaff is surrounded by extensive ponderosa pine (*Pinus ponderosa*) forest and the neighborhoods we studied were dominated by single family homes that retained an overstory of ponderosa pine. All neighborhoods were suburban and had similar moderate- to low-density housing interspersed with parks, golf courses and small areas of wildland. Each of the four neighborhoods was a minimum of 2 km distant from the others. Based on previous radiotelemetry studies of home range sizes of striped skunks in Flagstaff (Weissinger et al. 2009) and raccoons in other suburban areas (Hoffmann and Gottschang 1977), some of the same individual skunks and raccoons may have visited more than one of our feeders within a neighborhood, but it was unlikely that animals would have moved between neighborhoods.

During June, July, August and September 2012, we placed motion-activated video cameras (Advanced Security Model SSC-773, Eureka, California) at ten homes where residents had been feeding birds for several months or years. We repeated the experiment during the same months at 15 other homes in 2014 for a total of 25 different locations (Fig. 1). In each year we recruited homeowners opportunistically by contacting the local bird-watching society (Northern Arizona Audubon Society) and members of our university faculty and staff and asking anyone who regularly fed birds to volunteer their home. Our criterion for recruiting a homeowner was that the bird feeder had to have been in place for at least 3 months so that mesocarnivores would have had time to become accustomed to the presence of bird seed as a potential food source. We video-recorded visitation by nocturnal animals under each feeder between 2000 and 0500 h each night for a total of 10 days. During the first five nights, only bird seed that fell naturally from the feeders was present, as it had been for months before our monitoring began (Fig. 2a). On each of the successive five nights, we placed a bowl of approximately 75 g commercially-available, dry cat food below feeders at dusk (Fig. 2a). The same brand of cat food was used at all sites. Any cat food remaining in the dish the following morning was removed and a re-filled dish placed each evening, so cat food was only available at night. Homeowners maintained bird feeders with the same amounts and types of seed that they had been providing for the previous several months throughout the 10 day period. Bird seed at all sites included sunflower seeds but some homeowners also provided peanuts, millet or other seed types (e.g., thistle). We used existing feeders provisioned by homeowners instead of creating new sites where seed type and amount was controlled because we wanted to assess

visitation under conditions that reflected the inherent variability among existing feeders. Because bird feeders had been in operation for months, and in most cases years, prior to initiating filming, we assumed our initial five nights of filming represented baseline visitation rates typical of that at bird feeders maintained by Flagstaff residents. We based our five night sampling period on a pilot study conducted in May 2012 at one site where we monitored visitation for 15 consecutive days and then calculated the mean number of skunk visits/night based on 3, 4, 5, 6, 7, 8, 9 or 10 nights of observation. Means stabilized and standard deviation of those means reached an asymptote after four nights. Each feeder was videotaped once for ten nights between June and August as new homeowners were recruited to the study. This study followed American Society of Mammalogists guidelines (Sikes et al. 2011) and was approved by the NAU Institutional Animal Care and Use Committee (Protocol 11–002).

We quantified the number of visits by raccoons, skunks and cats, the number of simultaneous animal visits (any time two or more animals were present in the same field of view) and the number and type of interactions. Because an animal could move in and out of the field of view during a single visit, we considered video sequences in which an animal with similar pelage pattern came, left and then returned within 15 min to be a single visit. Post-hoc examination of the data showed that by using a 15 min cutoff, visits by similarly-colored individuals were then separated by at least 30 min.

Because our measures of number of visits/night could include repeated visits by the same individuals, we also estimated the total number of unique individual skunks and cats that visited bird feeders under each treatment based on differences in pelage coloration. Striped skunks in Flagstaff exhibit extensive variation in pelage, with individuals ranging from those with a continuous black stripe from mid-shoulder to tail tip to others with entirely white backs

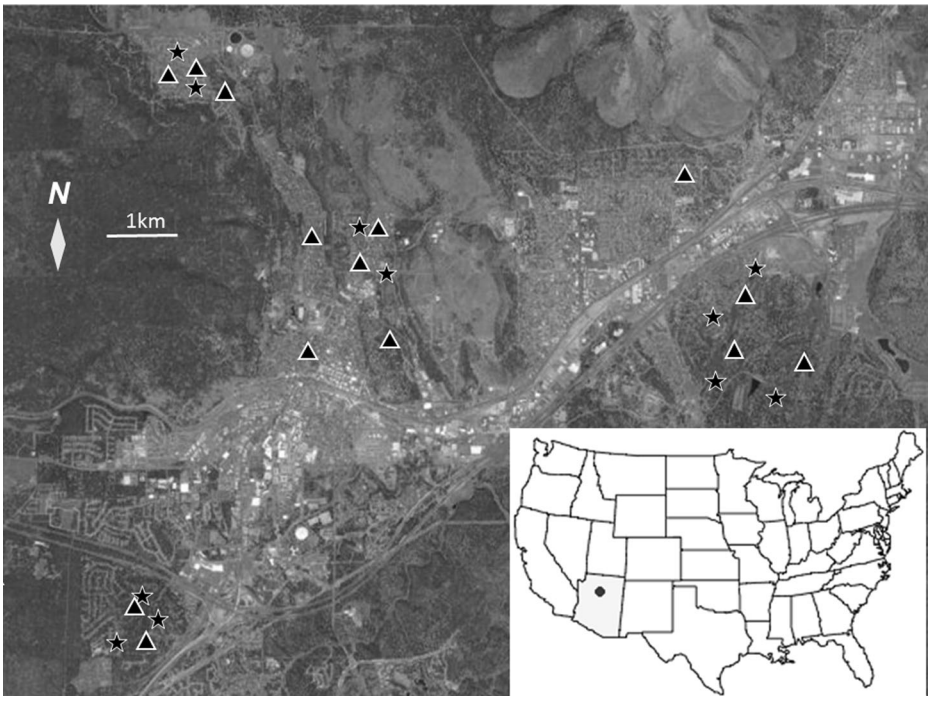

Fig. 1 Locations of bird feeders monitored in Flagstaff, Arizona, USA in summer of 2012 (10 stars) and 2014 (15 triangles). Inset shows location of Flagstaff (*dark dot*) within the state of Arizona within the United States

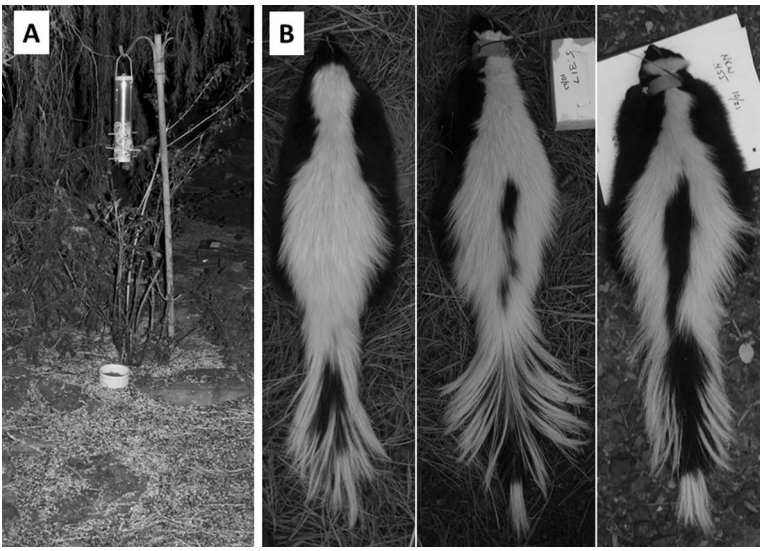

Fig. 2 **a**. Photograph of a typical bird feeder showing the extent of seed spillage below the feeder relative to the size of the cat food dish placed below the feeder. **b**. Photographs of striped skunks captured in Flagstaff, Az, USA illustrating how variation in pelage pattern allowed us to estimate minimum number of individuals visiting feeders

and tails (Fig. 2b). Although we could not identify every individual during every visit, this variation in coat pattern, combined with relative size of the animal (e.g., adult versus juvenile), allowed us to estimate a minimum number of unique individuals visiting each feeder. Cats likewise were recognized by unique pelage color and differences in hair length. Two different animals that were of similar size with similar coat and tail patterns could have been counted as the same individual at any one feeder, unless both were visible in the same frame simultaneously, so that our estimate of number of unique individuals visiting any one feeder is conservative. We could not distinguish among individual raccoons.

We categorized behavioral interactions during visits when two or more animals were present as either Ignore, Display or Contact. For skunks and raccoons, Ignore included visits in which animals behaved without acknowledging each other's presence. We also included in this category a common behavior exhibited by cats in which cats sat motionless in one location and watched other animals but never approached them. In these cases the other animal showed no sign that they were aware of the cat's presence and the cat exhibited no sign of aggression. In the category of Display we included visits in which animals exhibited some sort of behavior indicating they had seen and were reacting to the other animal. These were often species-specific. For cats we included 1) raising the fur on the back or tail, 2) hissing or 3) arching the back. For skunks we included 1) raising the tail, 2) stomping the front feet, 3) presenting the anal gland and 4) lunging in the direction of another animal. For raccoons we included 1) opening the mouth and exposing the teeth or 3) lunging in the direction of another animal. Within the category of Contact we included any behavior in which animals came in physical contact. This included 1) animals touching their bodies together while feeding with no apparent pushing, 2) animals pushing against each other in an attempt to displace each other, 3) one animal striking another animal with a forepaw, 4) one animal biting another and 5) two animals wrestling and biting each other. We viewed these categories as representing three levels of increasing aggression, with Ignore the lowest and Contact the greatest. Likewise, we

also assumed that the potential for disease spread, especially via contact and biting, increased across these three levels of behavior.

We used General Linear Model Repeated Measures Analysis of Variance to determine 1) whether the mean number of visits by cats, raccoons and skunks varied across species, treatments, neighborhoods and years and 2) whether mean visit length varied among species or across treatments. Mean visits/night and mean visit length/night over the first five nights compared to the values during the second five nights were modelled as our within-subjects repeated measure, while species, neighborhood, and year were between-subjects effects. We transformed data as ln(x) +1 in order to meet the requirements of normality. We verified that Mauchly's test of sphericity was met in each case. When factors were significant ($P<0.05$) we used Tukey's tests to determine differences among groups. We used paired t-tests to determine whether the mean number of individual skunks and cats visiting a feeder/night differed with the presence of cat food using each site as a replicate and combining data across years. We used Chi-square to test whether the total number of simultaneous visits (visits during which two or more animals were present) differed between the two 5 day periods and Chi-square Contingency Table analysis to determine whether the relative number of behaviors of skunks (Ignore, Display or Contact) differed when cat food was present by combining all data across all years.

Results

Striped skunks were the most common visitors to feeders when only bird seed was present. Skunks were recorded at 88 % of sites and on 68 % of nights, followed by cats at 72 % of sites and 30 % of nights and raccoons at 48 % of sites and 22 % of nights (Table 1). When cat food was added, the number of sites visited by skunks and cats increased by 10 % and not at all for raccoons, while the number of nights visited increased by 27 % for skunks, 92 % for cats and 70 % for raccoons (Table 1). Total number of visits increased when cat food was present for all three mesocarnivores in both years (Table 1).

We found a significant effect of both species and the presence of cat food on the mean number of cats, raccoons and skunks visiting bird feeders/night but no significant effect of

Table 1 Number of bird feeders (sites) visited out of total ($n=10$ in 2012, $n=15$ in 2014), number of nights visited out of total nights monitored ($n=50$ in 2012, $n=75$ in 2014) and total number of visits by striped skunks, domestic cats and raccoons at bird feeders when only seed was present and when both seed and cat food was present during June-September 2012 and 2014 in Flagstaff, Arizona, USA

		2012		2014	
Species	Variable	Seed	Seed + Cat Food	Seed	Seed + Cat Food
Striped skunk	# sites	10	10	12	14
	# nights	41	50	44	58
	Total #	167	384	103	204
Domestic cat	# sites	9	9	9	11
	# nights	20	29	17	40
	Total #	29	72	19	103
Raccoon	# sites	5	6	7	6
	# nights	9	23	18	23
	Total #	11	51	56	98

year, neighborhood or any interactions (Fig. 3a; Within-factor (no cat food vs cat food present): F=63.4, P<0.001; Between subjects effects: species F=22.9, P<0.001; year F=2.1, P=0.10; neighborhood F=1.0, P=0.13). Overall, mean number of visits per night doubled for skunks, cats and raccoons when cat food was present (Fig. 3a). For both skunks and cats, the mean number of unique individuals visiting feeders/night showed a similar pattern (Fig. 3b, skunks: t=5.3, df=23, P<0.001; cats: t=4.2, df=20, P<0.001), indicating that increased visitation was due in part to new animals being recruited to the site when cat food was present.

We found a significant interaction between species and the effect of cat food on mean visit length (Fig. 3c; F=6.2, P=0.02). Visit lengths were significantly longer for raccoons and skunks compared to cats (F=18.3, P<0.001) and post-hoc tests indicated that mean visit length increased significantly in the presence of cat food only for cats (Fig. 3c).

The mean number of times two or more animals were present simultaneously increased when cat food was present for all species' combinations except skunk-raccoon in 2014 and raccoon-raccoon in 2012 (Table 2). In all cases, interactions that were categorized as Display or Contact were more common when cat food was present (Fig. 4). Behaviors exhibited by skunks when only bird seed was present fell primarily into the categories of Ignore or Display,

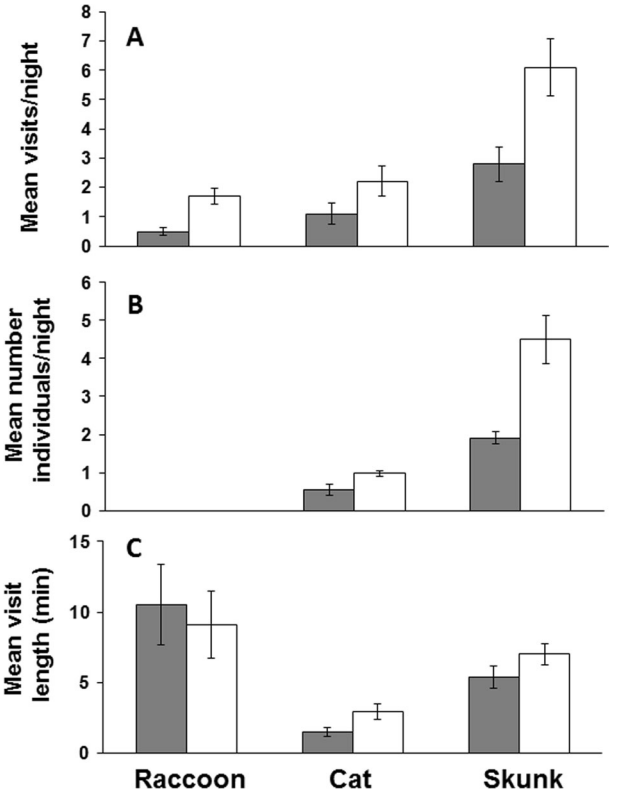

Fig. 3 **a**. Mean (± SE) number of visits/night by raccoons, cats and striped skunks when only spilled bird seed was present (*gray bars*) and after cat food was added (*open bars*). **b**. Mean (± SE) number of unique individuals visiting bird feeders/night when only bird seed was present (*gray bars*) and after cat food was added (*open bars*). We could not recognize individual raccoons so no data for number of individuals are presented. **c**. Mean (± SE) visit length (min) for animals visiting feeders when only spilled bird seed was present (*gray bars*) and after cat food was added (*open bars*)

Table 2 Total number of times more than one individual was present (simultaneous visits) among cats, skunks and raccoons over five nights at 25 bird feeders when only seed was present and when both cat food and seed was present during June-September 2012 and 2014 in Flagstaff, Arizona USA. No cat-cat simultaneous visits were observed. * indicates Chi-squared test comparing number of simultaneous visits when seed only vs seed + cat food present was significant at $p=0.05$, ** $p\leq0.01$, *** $p\leq0.001$

	2012		2014	
Visitors	Seed	Seed + Cat Food	Seed	Seed + Cat Food
Skunk-skunk	20	53***	14	50***
Raccoon-raccoon	8	8	16	19
Skunk-raccoon	1	12**	8	8
Skunk- cat	2	11*	1	6*
Raccoon-cat	0	7**	1	5
Total	31	91***	40	88***

whereas behaviors categorized as Contact (pushing, wrestling, and biting) were two times more prevalent when cat food was present (contingency table $\chi^2=16$, 2 df, $P<0.001$, Fig. 4). In 26 cases when cat food was present, skunks charged at each other, bit, nipped and rolled each other over, an intensity of interaction we never recorded when only bird seed was present. In the case of skunk-raccoon interactions, the only times we saw contacts in the form of nips and bites were when cat food was present, though this species combination was far less frequent (Table 2, Fig. 4). When bird-seed was present, we recorded cats and raccoons visiting simultaneously only once and skunks and cats only three times (Table 2). In each case, cats watched from a few meters away and skunks and raccoons did not acknowledge the cat's presence. When cat food was present, simultaneous visits by cats and raccoons and cats and skunks increased (Table 2). We recorded skunks displaying by foot-stomping or lunging at cats but never a physical contact. Likewise, when cat food was present we saw cats and raccoons charge or lunge at each other, and in two instances one animal scratched the other's face. Raccoon-raccoon simultaneous visits were typically either adults that arrived together or an adult with juveniles. Contact we recorded in these cases was from animals feeding side-by-side with no apparent aggression between them.

Discussion

Our study confirmed that striped skunk use of spilled bird seed below feeders was widespread and frequent, even during the summer months when other food sources were plentiful. Use by raccoons was less widespread but raccoons are generally much less common than skunks in Flagstaff (Weissinger et al. 2009). Skunks and raccoons were not merely passing by feeders en route to other feeding locations, as they would typically forage below feeders for extended periods of time (5–10 min). Although simultaneous visits at feeders when only seed was present were relatively rare, the low but consistent number of simultaneous visits indicates potential for direct as well as indirect transmission of disease.

The most striking finding of our manipulation was the increased number of individuals, visits, and contacts in the presence of cat food. Although our manipulations were carried out across a time period of 3 months, during which behavioral states and population size likely changed (e.g., parturition in striped skunks occurs in May and June, weaning and dispersal in July and August (Wade-Smith and Verts 1982)), response to the addition of cat food was

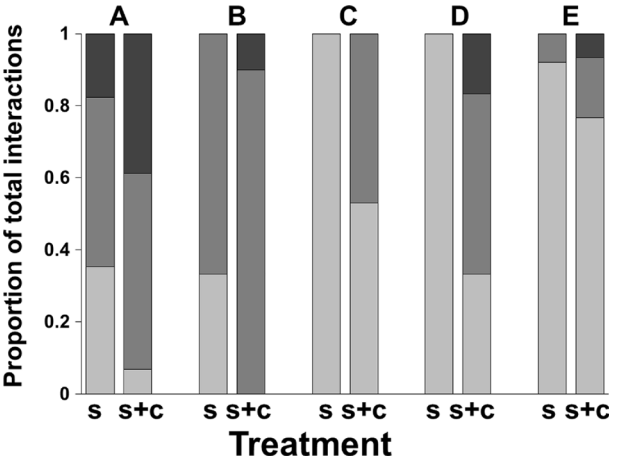

Fig. 4 The proportion of interactions classified as Ignore (*light gray*), Display (*medium gray*) or Contact (*dark gray*) when only spilled bird seed was present below bird feeders (Treatment 'S') versus when cat food was added (Treatment 'S + C') for **a**: skunk-skunk interactions, **b**: skunk-raccoon interactions, **c**: skunk-cat interactions, **d**: raccoon-cat interactions and **e**: raccoon-raccoon interactions. In each case there was a shift to more display and contact interactions in the presence of cat food. Sample size for each bar is the sum across years of the numbers given in Table 2 for that species combination

consistent across our locations regardless of these differences in timing. Although we did record more young animals in our videos as the season progressed, they were typically present in the 5-night periods both before and after addition of cat food, and the increase in numbers in the second 5-night period was dominated by arrival of new adults rather than new young-of-the-year. Thus, the increase in individuals between the initial 5-nights and the second 5-nights could not be attributed simply to an increase in population size due to juvenile recruitment through time.

The increase in both the number of individual skunks and the number of simultaneous visits we documented when cat food was present indicated that cat food increased both the probability of contact among animals and the pool of animals that came in contact with one another. This is important because an increase in the number of unique individuals visiting feeders increases the probability of disease spread, as it is the number of different individuals contacted during the infectious period that is a key driver in disease dynamics (Anderson and May 1985).

Aggressive behavior also increased in the presence of cat food, including biting and nipping, that could lead to direct transmission of diseases spread through bite, especially among skunks. Our study could not distinguish between whether this heightened aggression was due to animals perceiving cat food as a higher quality resource than bird seed, and therefore more aggressively defending it, or to the difference between defending a point source (cat food dish) versus a more widely dispersed resource (scattered seeds) (Carr and Macdonald 1986). Regardless of the reason, our study was designed to test responses to the most typical way in which each resource would actually be encountered in urban neighborhoods. In our experience, homeowners typically provide cat food in some sort of dish or bowl, while bird seed is scattered below feeders. Raccoons and skunks are two of the most important terrestrial reservoirs for rabies in North America (Dyer et al. 2014) and rabies has broken out repeatedly among skunks in the last decade in the Flagstaff neighborhoods we studied (Kuzmin et al. 2012). Increased visitation and interaction at bird feeders or where domestic and feral cats are

fed therefore could act as foci for disease transmission. Although we have no evidence that any of the animals we videoed were infected by rabies, studies that have followed rabid skunks using telemetry have documented home ranges and movements similar to those of non-rabid animals except in the final days before death (Storm and Verts 1966; Greenwood et al. 1997). These studies suggest that the visitation behaviors of rabid animals would not be strikingly different from those we recorded. Skunks experimentally infected with rabies showed increased aggressiveness in the initial stages of infection (Charlton et al. 1984) which could potentially increase the chance of bites during simultaneous visits over that we recorded.

Both the community of mesocarnivores and the relative abundances of those mesocarnivores likely varies from city to city and those differences could shift the frequency of use and encounters at bird feeders. For example, raccoons are relatively uncommon in Flagstaff compared to other urban areas where they can reach remarkable densities (e.g., Smith and Engeman 2002) and in some suburban areas raccoons may be common while skunks are absent (e.g., Kays and Parsons 2014). Repeating this study in other urban areas with different mesocarnivore communities and abundances would likely reveal patterns somewhat different than the ones reported here, but we predict the overall increase in visitation and aggressiveness in the presence of cat food would hold in those areas as well. Likewise, how cat food might alter wild mesocarnivore-cat interactions in the presence of a large feral cat population remains an important question, especially in those areas where trap-neuter-release (TNR) is being used in feral cat management, as TNR programs often include ongoing feeding of feral cats after neuter and release (Levy and Crawford 2004). Our results indicate that provisioning feral cats with cat food would be a more powerful attractant to mesocarnivores compared to other anthropogenic food sources like bird seed and thereby increase the potential of feral cat-mesocarnivore interaction and disease transmission.

Our study demonstrated that provisioning birds with seed and domestic and feral cats with food can have important indirect effects on wild urban mesocarnivores. To reduce wild mesocarnivore visitation at homes with bird feeders, spilled seed should be removed regularly and/or caught using hoop nets that can be suspended below feeders (e.g., SeedHoop ™, Songbird Essentials, Inc) or feeders should be placed inside fenced yards or enclosures that effectively prevent access by mesocarnivores. Likewise, if cat food is left outside in areas accessible by other mesocarnivores, it should be brought indoors at night. Given the higher visitation rate and increased aggressiveness exhibited by animals in the presence of cat food, removal and management of that resource should be a priority in public education campaigns to reduce spread of diseases like rabies. Residents should be encouraged to maintain current rabies vaccinations for their pets in areas where rabies is still prevalent in wild carnivores and cats should be vaccinated against diseases they could either spread to or receive from wild mesocarnivores attracted to areas where cats are provisioned. Birdfeeders and areas where pet food was traditionally provided could act as foci for disease control efforts such as trap-vaccinate-release and could be identified by contacting relevant citizen's groups (e.g., local bird watching organizations) prior to management efforts.

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Conflict of interest The authors declare they have no conflict of interest.

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