

Supplementing non-target taxa: bird feeding alters the local distribution of mammals

J. HUNTER REED,^{1,3} AND DAVID N. BONTER^{2,4}

¹Department of Animal Science, Cornell University, Morrison Hall, 507 Tower Road, Ithaca, New York 14853 USA

²Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850 USA

Abstract. Although the effects of bird feeding on avian species have been extensively examined, few studies evaluate the indirect effects of bird feeding on non-target taxa. Bird seed could provide direct nourishment to several mammalian species (e.g., *Lagomorpha*, *Rodentia*, and *Cetartiodactyla*), potentially altering their distribution and behavior with possible unintended consequences for some avian populations, particularly those not directly benefiting from the resource. To examine how bird feeders may influence the presence and behavior of mammals, we used camera traps to quantify differences in the distribution and richness of mammal species frequenting sites with bird feeders and control sites (lacking feeders) in Ithaca, New York, USA. We recorded 15,684 images capturing 12 mammal species with gray squirrel (*Sciurus carolinensis*) and raccoon (*Procyon lotor*) detected significantly more often at feeder sites than at control sites. Detections of white-tailed deer (*Odocoileus virginianus*) marginally increased near feeders whereas detections of several carnivorous species were unrelated to the presence of bird feeders. We recorded larger gray squirrel and raccoon group sizes and greater mammal richness at feeder sites than at nearby control sites. We detected squirrels and raccoons less when snow covered the ground than on snow-free days. Ambient temperature was not a strong predictor of mammal detections. Camera trapping revealed strong, species-specific patterns in the timing of daily visitation to areas with feeders. Because many mammals depredate bird nests, the local increases in mammal richness and activity near bird feeders may create an ecological trap for avian species nesting in close proximity to supplemental feeding stations.

Key words: bird feeding; camera trapping; ecological trap; gray squirrel; mammals; supplemental food.

INTRODUCTION

Wild bird feeding is a popular and rapidly growing hobby with more than 50 million Americans spending approximately \$4 billion dollars on the activity annually (U.S. Fish & Wildlife Service 2011). This expenditure represents a substantial resource subsidy for millions of birds (Orros and Fellowes 2015). Bird feeding is also a common pastime in other Western societies, with upwards of 75% of households in the United Kingdom and 57% of households in Australia provisioning wild birds (Jones and Reynolds 2008). As such, the practice of bird feeding is the focus of recent research and debate. Supplemental feeding can increase survival and reproductive success of bird populations (Seward et al. 2013), which is often a goal of supplemental feeding efforts (Ewen et al. 2015). Bird feeding also engages and connects the public with the natural world, potentially contributing to human well-being (Shanahan et al. 2015, Cox and Gaston 2016) and concern for the environment (Russell et al. 2013, Zelenski and Nisbet 2014). Potential negative implications of bird feeding include increased disease transmission (Becker and Hall 2014, Adelman et al. 2015), increased risk of predation (Dunn and Tessaglia 1994) or mortality related to window-strikes near feeders (Kummer and Bayne 2015) and changes in evolutionary trajectories (Plummer et al. 2015). Despite

the ubiquity of bird feeding, the potential influence of this subsidy on non-target taxa remains relatively unexplored (Galbraith et al. 2015, Sánchez-García et al. 2015).

Though difficult to quantify, a sizable portion of birdseed offered at supplemental feeders is dropped below the feeders rather than being consumed by birds. Individual birds often reject a portion of the food subsidy due to species-specific preferences associated with the presence of a seed hull, seed nutritional content, or bill-to-seed volume ratios, making the rejected resource available for other taxa (Johansen et al. 2014). The most common seeds used for wild bird feeding, including sunflower seed (*Helianthus annuus*), millet (*Panicum miliaceum*), nyjer (*Guizotia abyssinica*), and corn (*Zea mays*), are all rich in energy and nutrients (Lin 2005). Any waste seed made available to non-target species could serve as a substantial resource, especially during times of food shortage or unfavorable weather conditions. As demonstrated by intentional food supplementation studies, small mammal populations limited by food availability can increase in abundance following feeding (Cittadino et al. 1994, Banks and Dickman 2000, Forbes et al. 2014). Further, supplemented individuals may increase their body condition (Cittadino et al. 1994), reproductive performance (Forbes et al. 2014), and alter the timing of breeding (Sullivan 1990). The provisioning of clumped, supplemental food sources may also alter home ranges, increase territorial overlap, and affect social structures (Wehtje and Gompper 2011).

The supplemental feeding of mammals as a byproduct of bird feeding could affect trophic interactions with unintended consequences or even create an ecological trap for wild birds. Ecological traps occur when an environment changes such

Manuscript received 22 June 2017; revised 7 December 2017; accepted 21 December 2017. Corresponding Editor: John M. Marzluff.

³Present address: Cornell University College of Veterinary Medicine, Ithaca, New York 14853 USA.

⁴Corresponding Author. E-mail: dnb23@cornell.edu

that the former indicators of high quality habitat are no longer indicators of the habitat's true current quality (Robertson and Hutto 2006, Demeyrier et al. 2016, Hale et al. 2016). While supplemental food in the form of bird feed may attract birds to the area and may potentially enhance overwinter survival (Brittingham and Temple 1988), reproductive success (Robb et al. 2008b), and body condition (Brittingham and Temple 1988, Schoech and Bowman 2003) for species that make use of the supplemental resource, there may also be negative consequences (e.g., Harrison et al. 2010). If supplemental food resources facilitate local population increases of mammals that depredate bird nests, then feeding could indirectly compromise bird reproduction (Cooper and Ginnett 2000, Cain et al. 2006, Selva et al. 2014, Hanmer et al. 2016), particularly for bird species that do not directly benefit from the resource but may suffer the consequences of increased risks of nest depredation.

Another unintended consequence of bird feeding may be changes to the normal activity patterns of non-target animals. Because mammal populations tend to be food limited (Prevedello et al. 2013), a novel supplemental food source provides a strong incentive for individuals to alter their behavior or movements. For instance, mammals may immigrate to sites with food subsidies (Boutin 1990, Morris et al. 2011) or delay migratory movements (Jones et al. 2014). Resource subsidies can also decouple predator-prey relationships (Rodewald et al. 2010) and increase local mammal abundance (Kearns and Rodewald 2017).

To our knowledge, few studies have examined the influence of bird feeding on non-target bird species (but see Galbraith et al. 2015), and no replicated and controlled studies have examined the effects of bird feeding on non-target mammals. Here, we examine the potential effects of bird feeding on local activity patterns of mammals by quantifying the detections and species richness of mammals at sites with bird feeders and at nearby control sites. Further, we investigate how the detection of mammals at these sites varies with weather (snow cover and temperature). Because mammals are likely to exploit the spatially concentrated and temporally predictable food resources available at bird feeders, we predicted that the detections and richness of mammals would be greater at feeder sites than at control sites. We expected concentrations of mammals feeding on the waste from bird feeders to increase with decreasing temperatures and on snow-covered days due to increases in metabolic demands. Further, we expected that the feeding activity of small mammals and birds might lead carnivorous mammals to frequent feeder sites more often than control sites.

STUDY AREA

We established study sites near Cornell University's Liddell Field Station in Ithaca, New York, USA (42°27'28.46" N, 76°26'55.71" W). The study area included an approximately 7-ha plot of mixed deciduous/coniferous forest largely composed of maples (*Acer* spp.), oaks (*Quercus* spp.), hickories (*Carya* spp.), eastern hemlock (*Tsuga canadensis*), and pine (*Pinus* spp.) and flanked a perennial stream. The surrounding landscape included agricultural land planted with hay, corn, and soybeans as well as suburban development.

METHODS

Camera trapping

We deployed three Bushnell (HD Aggressor model) and three Covert (MP6 model) infrared-detection trail cameras to record mammal activity. We installed feeders near forest-agricultural edges at locations >0.75 km from the nearest human dwelling to limit access to non-experimental sources of bird food. We recorded camera trap data on 163 d between 31 January and 12 December 2015 for 467 complete camera-days of trapping with up to six cameras in operation per day. Sampling was conducted in two bouts (31 January–5 May and 28 August–12 December) with no supplemental food provided at any sites from early May to late August. We deployed a single camera at each of three supplemental feeding sites and three control sites. Following the January–May sampling period, feeder and control sites were swapped wherein the January–May feeder sites thereby became control sites for August–December. Feeder sites were located approximately 100 m from each other and each site had a single custom-built bird feeder made of a 1-m section of PVC pipe with a single feeding port (Bonter et al. 2013). We filled feeders continuously with black-oil sunflower seeds. We hung feeders from poles fitted with stovepipe-style baffles (Advanced Pole System Raccoon Baffle; Wild Birds Unlimited, Carmel, Indiana, USA) that effectively prevent mammals from climbing the poles and directly accessing the food. Mammals acquired supplemental food resources, therefore, from the ground beneath the feeders. We placed control sites at the midpoint between feeder sites (patches of forest without a feeder). At each site, we installed a trail camera on a metal stake at 0.25 m above the ground and located 5 m from the feeder or control point (Fig. 1). We rotated cameras weekly within the sampling grid so that all cameras operated at all sites in case individual cameras differed in trigger sensitivity. All cameras were set to the same settings: delay between photos = 1 min, normal sensitivity (10–80° F), photo burst (number of photos taken per detection) = 1, and 24-h operation. The 1-min time delay between camera images likely leads to a lack of independence among "captures." Multiple daily captures of the same individual squirrel, therefore, were likely across sampling days. The purpose of our study, however, was to quantify differences in the activity of mammals between locations near bird feeders and nearby locations lacking supplemental food. As such, repeated captures of the same individual over time provides important information—it shows that the mammal remained active in the vicinity for an extended period.

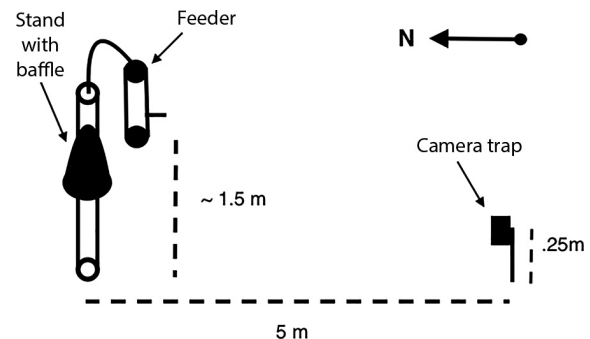


FIG. 1. Schematic of camera trap and feeder set-up.

TABLE 1. Total detections (photographs) of each species during entirety of the study.

Scientific order	Scientific name	Common name	Detections (photos)
Cetartiodactyla	<i>Odocoileus virginianus</i>	White-tailed deer	145
Carnivora	<i>Canis latrans</i>	Eastern coyote	13
Carnivora	<i>Pekania pennanti</i>	Fisher	2
Carnivora	<i>Mephitis mephitis</i>	Striped skunk	1
Carnivora	<i>Procyon lotor</i>	Raccoon	1,304
Carnivora	<i>Urocyon cinereoargenteus</i>	Gray fox	6
Carnivora	<i>Vulpes vulpes</i>	Red fox	7
Didelphimorphia	<i>Didelphis virginiana</i>	Virginia opossum	229
Lagomorpha	<i>Sylvilagus floridanus</i>	Eastern cottontail	4
Rodentia	<i>Sciurus carolinensis</i>	Gray squirrel	13,552
Rodentia	<i>Tamias striatus</i>	Eastern chipmunk	275
Rodentia	<i>Tamiasciurus hudsonicus</i>	American red squirrel	36
—	<i>Aves</i> sp.	Bird species	110
No animal visible in image			7,954
Unidentified species			10

We did not harm, physically capture, or handle animals in this study and we conducted the research under the animal care guidelines of the Cornell University Institutional Animal Care and Use Committee (protocol # 2014-0023). We conducted the research on private property with no threatened or endangered species and neither state nor federal permits were required.

We downloaded weather data from the Northeast Regional Climate Center for the Game Farm Road, Ithaca, New York, USA weather station that is located 0.9–1.2 km from the sampling locations and at nearly the same elevation (~300 m above sea level; data *available online*).⁵ Weather data included mean hourly temperature values. We recorded snow cover from the camera images (presence or absence) due to variation and patchiness in snow cover throughout the study site. We acquired sunrise and sunset times for Ithaca, New York from the Astronomical Applications Department of the U.S. Naval Observatory (data *available online*).⁶

Statistical methods

We limited the data set to days in which individual cameras were operational for the entire 24-h period to eliminate problems associated with missing data due to battery failure or snow obstructing the lens. Each image was visually inspected by the same observer (J. H. Reed) to identify the species photographed (Table 1). We recorded the total number of individuals detected and snow cover (presence/absence) along with date and time. We then zero-filled the data set by species (zeros added for site-day combinations lacking information on a focal species) and merged with the weather data and sunrise/sunset times by date.

To test for relationships between mammal detections and the presence of supplemental food and weather conditions, we constructed a series of models run independently for each species and compared model fit using Akaike Information Criterion (Burnham and Anderson 2002). We modeled

the total number of photo detections at a site per day (response variable) as a function of the presence or absence of a supplemental feeder, average daily temperature (continuous variable), the presence or absence of snow cover (binary variable), and the unique identifier of the camera used to account for potential differences in trigger sensitivity among cameras. Because the zero-filling procedure resulted in a zero-inflated distribution, we implemented zero-inflated Poisson regression models (PROC GENMOD with “ZIP” distribution, SAS 9.4 [SAS Institute 2012]). To account for potential site-based differences, we included site in all models and the site \times feeder interaction in models that included the feeder variable. Reduced models included various combinations of feeder presence, average temperature, and snow cover (Table 2). Sufficient detections allowed for analyses of data from gray squirrel (*Sciurus carolinensis*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*; hereafter “opossum”), white-tailed deer (*Odocoileus virginianus*), and “other carnivores” combined including gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), fisher (*Pekania pennanti*), and coyote (*Canis latrans*).

To determine how the presence of bird feeders may influence the richness of mammals in the area, we next calculated species richness for each location/date combination where a species was included if it was detected at least once at the location on the date. We then constructed a Poisson-distributed mixed model (PROC GLIMMIX) where total species richness (response variable) was modeled as a function of the presence/absence of a feeder, average daily temperature, snow cover, and the identifier of the camera, with site as a random variable.

Camera images generally captured only a single individual of most species, although multiple gray squirrels (range 1–8), raccoons (range 1–3), and white-tailed deer (range 1–4) were occasionally recorded in the same field of view. Large samples of squirrel and raccoon photos allowed us to investigate the relationship between the presence or absence of bird feeders and abundance of these mammals. We thus calculated mean abundance of each species detected per image per day at each location. We then used this mean value as the response variable in additional models (mixed

⁵ <http://www.nrcr.cornell.edu/wxstation/ithaca/ithaca.html>

⁶ <http://aa.usno.navy.mil>

TABLE 2. Model selection results from the zero-inflated Poisson models testing for relationships between species detections and the presence/absence of supplemental food (feeder), mean daily temperature (temperature), and the presence/absence of snow cover (snow).

Feeder	Temperature	Snow	AIC	Δ AIC	Model weight
Gray squirrel					
0.97	-0.01	-0.85	9935.38	0	1.00
0.98	.	-0.64	10054.83	119.45	0.00
1.01	.	.	10509.35	573.97	0.00
1.01	0.00	.	10509.43	574.05	0.00
.	-0.02	-0.65	14966.98	5031.6	0.00
.	.	-0.32	15242.21	5306.83	0.00
.	-0.01	.	15331.89	5396.51	0.00
.	.	.	15376.50	5441.12	0.00
Raccoon					
1.07	0.00	-1.11	1927.17	0	1.00
1.08	0.01	.	2000.90	73.73	0.00
1.10	.	.	2003.86	76.69	0.00
1.07	.	-1.11	2258.46	331.29	0.00
.	-0.01	-0.99	2258.46	331.29	0.00
.	.	-0.92	2259.16	331.99	0.00
.	.	.	2314.03	386.86	0.00
.	0.00	.	2315.56	388.39	0.00
White-tailed deer					
0.06	.	.	500.18	0	0.30
.	.	.	501.19	1.01	0.18
0.18	.	-0.66	501.68	1.5	0.14
0.08	0.00	.	502.16	1.98	0.11
.	-0.01	.	502.35	2.17	0.10
.	.	0.21	503.00	2.82	0.07
0.21	0.01	-0.68	503.50	3.32	0.06
.	-0.01	0.07	504.33	4.15	0.04
Other carnivores					
.	.	.	185.94	0	0.41
.	0.01	.	187.03	1.09	0.24
.	.	-0.38	187.10	1.16	0.23
.	0.01	-0.19	189.00	3.06	0.09
2.92	.	.	191.63	5.69	0.02
2.76	0.01	.	193.55	7.61	0.01
2.80	.	-0.32	193.55	7.61	0.01
2.73	0.00	-0.22	195.51	9.57	0.00

Notes: All models included camera identity, site identity, and the site \times feeder interaction if feeder was included in the model. "Null" models include only camera and site identities. Model coefficients (values column for each variable) are reported if the variable was included in the model. A period (.) indicates that the variable was not included in the model. Results are not shown for opossum (models did not converge).

Poisson model for squirrel, zero-inflated Poisson model for raccoon) with the same predictor variables detailed above.

To compare daily activity patterns between feeder and control sites for gray squirrels, we created a zero-filled data set for all hours on all dates when cameras were operational. We created a zero-inflated Poisson model with the total detections per hour as the response variable and camera identifier and the hour \times feeder interaction as the predictor variables to calculate predicted mean detections by hour as related to the presence/absence of a feeder.

To test for temporal (daily) patterns in mammal activity near supplemental feeders, we merged sunrise and sunset

times with the camera data to control for changes in day lengths. Days were divided into four categories: "sunrise" included the hour before and after sunrise on each day, "sunset" included the hour before and after sunset on each day, "day" included all daylight hours except the first hour after sunrise and the last hour before sunset, "night" included all night-time hours except for the hour after sunset and the hour before sunrise. We restricted the data set to feeder locations and included all days where the focal species was recorded at least once on the day. Because variation in day length changed the amount of time sampled during "day" and "night," we standardized the response variable (detections) to the proportion of the 24-h period in each time category for each day. We then zero-filled the data set prior to running another zero-inflated Poisson model where we modeled the number of detections (standardized) as a function of camera identifier, time of day, and location (site).

RESULTS

Camera traps recorded 15,684 images of identifiable animals comprising 12 mammal species (Table 1). The camera traps detected gray squirrels on 437 of 467 (93.6%) sampling days, more than any other animal with 13,552 images recorded. Gray squirrels were more likely to be detected at sites with supplemental feeders than at control sites ($\beta = 0.97 \pm 0.06$ [estimate \pm standard error], Fig. 2a) as the full model received the greatest support from the data for this species (Table 2). Squirrels were less likely to be detected on days with snow cover than on days without snow cover ($\beta = -0.85 \pm 0.04$). Although temperature was included in the top model, the number of detections did not vary considerably with temperature ($\beta = -0.01 \pm 0.00$). With regard to group size, the mean number of squirrels captured in each camera image was greater at sites with feeders than at sites without feeders ($\beta = 0.36 \pm 0.04$) and was greater on days with snow cover than without snow cover ($\beta = 0.15 \pm 0.07$), but was unrelated to average temperatures ($\beta < 0.00 \pm 0.00$).

Camera traps detected raccoons in 1,304 photographs with more detections at sites with supplemental feeders than at control sites ($\beta = 1.07 \pm 0.37$, Fig. 2b). Raccoons were less likely to be detected on days with snow cover than on snow-free days ($\beta = -1.11 \pm 0.14$). The two top models included average temperature, but the influence of temperature was not strongly supported in the full model ($\beta < -0.01 \pm 0.00$). The number of raccoons (mean group size) detected was greater at sites with feeders than at sites without feeders ($\beta = 1.26 \pm 0.17$) and increased slightly with increasing temperatures ($\beta = 0.03 \pm 0.01$) but was unrelated to snow cover ($\beta = -0.10 \pm 0.26$).

Camera traps captured 145 images of white-tailed deer on 64 of 467 sampling days (13.7%). The model including feeder best fit the data with more deer detections at feeder sites than at control sites, but the beta estimate included zero ($\beta = 0.06 \pm 0.71$, Fig. 2c). There was little support for a relationship between temperature or snow cover and detections (Table 2).

Detections of the combined carnivores were limited at both feeder and control sites with only coyote ($N = 13$ photos), red fox (7), gray fox (6), and fisher (2) recorded. The

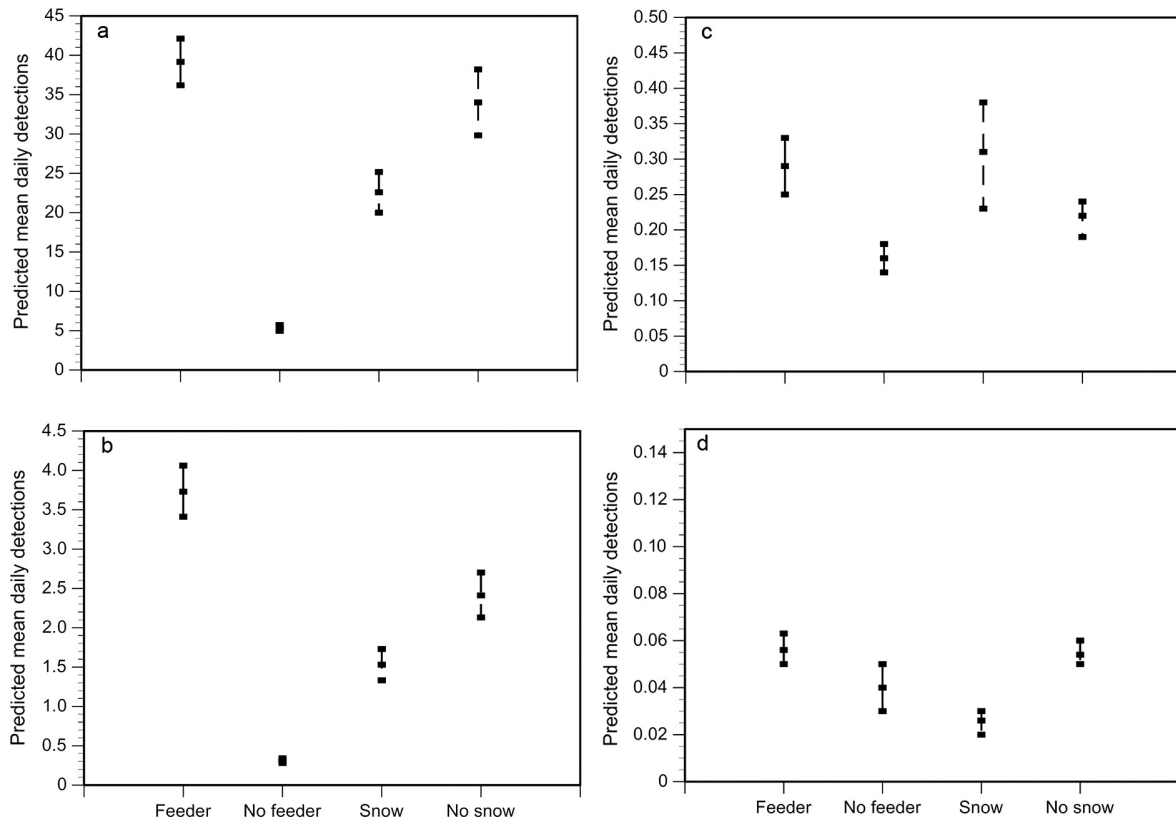


FIG. 2. The relationship between daily detections and the presence or absence of a bird feeder and the presence or absence of snow cover for (a) gray squirrel, (b) raccoon, (c) white-tailed deer, and (d) other carnivores. Mean and 95% CI of predicted values from the full models are shown.

null model best supported the data when all four species were combined as “other carnivores” (Table 2), suggesting no influence of bird feeders on the distribution or activity of these species within our study area.

Daily mammal species richness was greater at sites with feeders ($\bar{x} = 2.15 \pm 0.06$) than at sites without feeders ($\bar{x} = 1.42 \pm 0.05$, $\beta = 0.47 \pm 0.07$), marginally increased with increasing temperatures ($\beta = 0.01 \pm 0.00$), and was not correlated with snow cover ($\beta = -0.10 \pm 0.12$).

Analysis of the daily patterns of detections at sites with supplemental feeders demonstrated substantial differences in activity patterns by species. Gray squirrels were active around the feeding stations during the day, with activity increasing around sunrise and peaking during daylight hours (Fig. 3a). The other species demonstrated strong nocturnal patterns with nearly all detections of raccoon (Fig. 3b) and opossum (Fig. 3c) taking place after dark. Most detections of white-tailed deer also took place at night with little crepuscular activity detected (Fig. 3d). We failed to detect species in the “other carnivore” group during daylight hours. Squirrels were active throughout the day but demonstrated distinct peaks in activity (detections) at camera trapping locations (Fig. 4a). We detected nocturnal species (raccoon, opossum, and white-tailed deer) at all hours of the night (Fig. 4b).

Hourly activity patterns for the gray squirrel differed between feeder sites and control sites with squirrel detections spiking in the morning at feeder sites and occurring at

a relatively constant rate throughout daylight hours at control sites (Fig. 5).

DISCUSSION

This study highlights potential unintended community-level effects of the widespread practice of wild bird feeding as non-target taxa opportunistically take advantage of subsidies intended for birds. We demonstrate clear changes in the local detections of various mammalian taxa in response to the presence of bird feeders. Squirrels and raccoons were more likely to be detected at sites with feeders than at nearby control sites, a result similar to previous food supplementation experiments that explicitly targeted mammals (Havera and Nixon 1980, Sullivan 1990, Schuttler et al. 2015). Because mammal populations in temperate environments can be food limited, particularly in winter, the novel food source unintentionally provided by humans via bird feeding can incentivize changes in movement patterns and feeding behaviors of mammals (Prevedello et al. 2013). The aggregation of birds near feeders may also attract mammals. The increase in detections of certain mammal species at the feeder sites is potentially the result of home range shifts and immigration of individuals seeking access to this novel food source (Mares et al. 1976, Boutin 1984, Banks and Dickman 2000, Wehtje and Gompper 2011).

Attracting mammals to areas with bird feeders may result in unintended consequences for birds. Many mammal species,

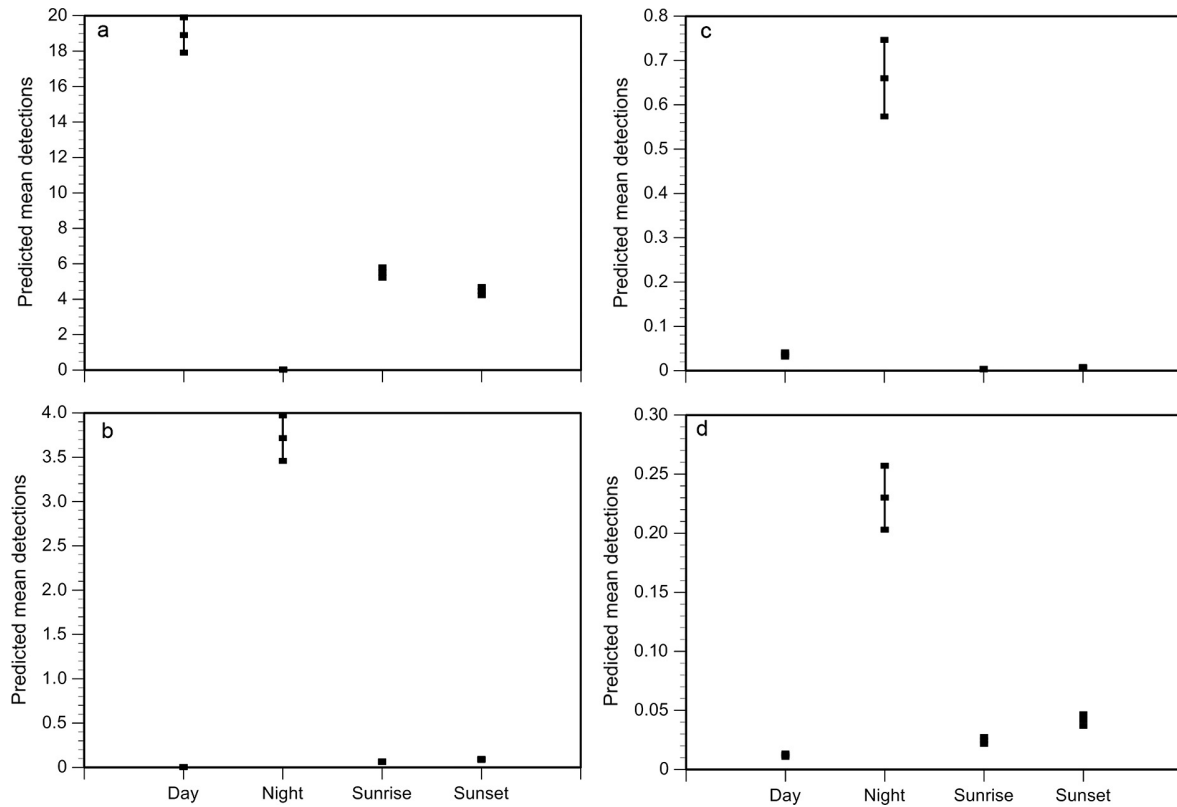


FIG. 3. Mammals detected by cameras at supplemental bird feeding locations demonstrated strong temporal patterns in visitation with the (a) diurnally active gray squirrel and (b) nocturnally active species including raccoon, (c) opossum, and (d) white-tailed deer. "Day" includes daylight hours except for the hour after sunrise and the hour before sunset. "Night" includes nighttime hours except for the hour before sunrise and the hour after sunset. "Sunrise" and "sunset" include a 2-h window on either side of sunrise or sunset. Predicted means and 95% CI are reported from a zero-inflated Poisson regression of data collected only at locations with bird feeders. Models did not converge for "other carnivores" because nearly all detections were at night.

including several of the focal species in this study, are known to prey upon adult birds and depredate their nests, directly reducing reproductive success (Heske et al. 2001, Cain et al. 2006, Schmidt et al. 2008, Hanmer et al. 2016, but see Newson et al. 2010). High local density of deer may reduce the reproductive success of birds because deer browse understory vegetation thereby reducing available nest sites or making nests more visible to predators. Consequently, birds aggregating around or nesting near bird feeders to take advantage of the resource could potentially experience decreased survival or reproduction; in effect, waste seed from feeders may create an ecological trap for the birds.

Clearly, not all species of birds benefit from supplemental feeding. Backyard bird feeders typically provide seed, suet or nectar, benefitting a limited suite of species. While meta-analyses of food supplementation studies indicate a general improvement in reproductive parameters for the species targeted by the supplementation, many studies focus only on the reproductive success of granivorous passerines that nest in cavities (Robb et al. 2008a, Ruffino et al. 2014). Few studies examine the secondary effects of providing supplemental food on non-target birds. Resource subsidies may create source habitats for synanthropes while decreasing the quality of the local environment for species that do not take advantage of the subsidies. For instance, open-cup-nesting passerines with insect-based diets will not benefit from seed

feeders but may suffer the consequences of increased local predation pressure as potential nest predators (avian or mammalian) congregate near feeders. Predation of eggs or chicks is the leading cause of nest failure in birds, with small rodents (Bradley and Marzluff 2003) and corvids (Marzluff and Neatherlin 2006) among the leading threats. The breeding success of cavity nesting species tends to be greater than that of species that build open cup nests (Wesołowski 2017), particularly if those species are nesting in boxes with anti-predator guards provided by humans (Bailey and Bontar 2017).

Changes in predator movement patterns may reduce nest survival, particularly at local scales (Marzluff et al. 2007, Kearns and Rodewald 2017). For instance, the nest success of Northern Cardinals (*Cardinalis cardinalis*) declined in areas with high mammal activity (Kearns and Rodewald 2017), and nest depredation by corvids is more likely near sites with anthropogenic subsidies than at sites farther from human developments (Marzluff and Neatherlin 2006). Previous research shows that one species of corvid (Steller's Jay, *Cyanocitta stelleri*) occurs at greater densities, is in superior body condition, and has greater reproductive success at subsidized sites (campgrounds) than at unsubsidized sites (West and Peery 2017). Because both small mammal and corvid populations respond positively to supplemental food, removing anthropogenic food resources from the landscape

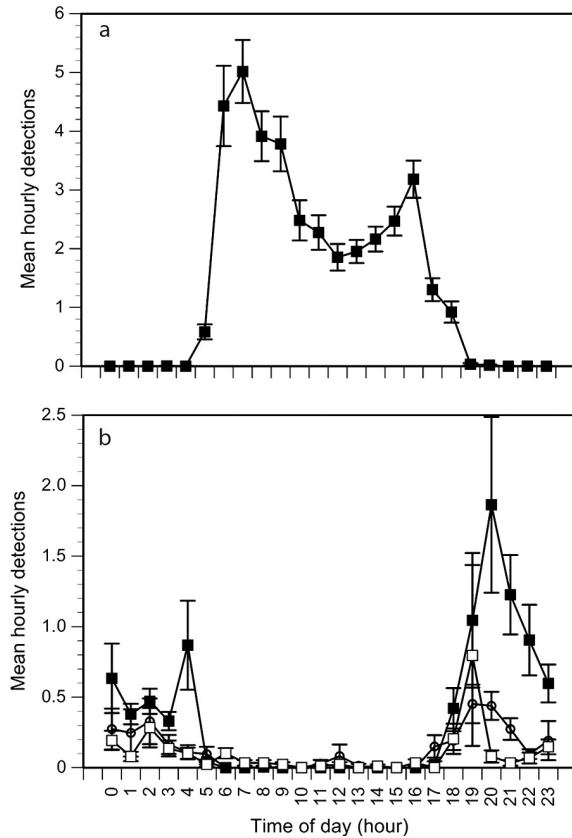


FIG. 4. Daily patterns in mammal activity as recorded by camera traps at feeder and control sites combined. (a) Gray squirrels showed diurnal activity patterns. (b) Nocturnal species include raccoon (solid squares), opossum (open circles) and white-tailed deer (open squares). Detections (mean \pm SE) per hour per day are shown from a zero-filled data set.

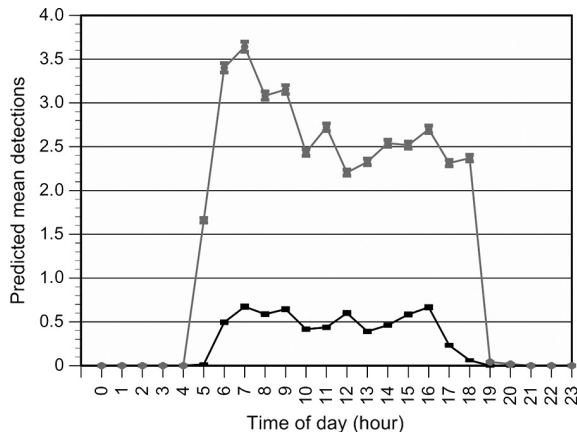


FIG. 5. Patterns of hourly detections of gray squirrels varied by treatment with feeder locations (gray) recording peaks in activity while control sites (black) recorded relatively consistent detections (predicted model means, 95% CI).

may be effective for increasing local nesting success. The presence of mammalian predators can also change the behavior of nesting birds. For instance, increased predator activity may force nesting birds to reduce provisioning rates

(Bonnington et al. 2013) or avoid potential nesting areas altogether, particularly at smaller spatial scales (Marzluff et al. 2007).

We used guards that effectively prevented mammals from directly accessing the food intended for birds. The results presented here, therefore, are likely minimal effects. Many people do not adequately guard their bird food against easy access by mammals, so changes in mammal richness and abundance would likely be greater at locations where mammals have direct access to food or at sites that feed squirrels and other mammals alongside birds. At sites where mammals have direct access to food, direct competition for resources can reduce the benefits of supplemental feeding. One recent study found that interference competition with gray squirrels reduced the ability of birds to access supplemental food by upwards of 98% (Bonnington et al. 2014). In another supplemental feeding initiative targeting gamebirds in England, non-target taxa accounted for 54% of feeder visits with mammals consuming upwards of 67% of the food provided (Sánchez-García et al. 2015).

In our study, detections of carnivores (eastern coyote, gray and red fox, and fisher) were unrelated to the presence of a feeding station. The relative lack of carnivores at our sites made it difficult to detect any relationship between bird feeding and these species. Large individual home ranges and low population densities of carnivores likely contributed to the low overall detection rates (Thompson and Colgan 1987, Grindler and Krausman 2001, Magle et al. 2014). Increases in the abundance of prey species around feeder sites would likely attract more carnivores over the long term (Thompson and Colgan 1987). Although we detected no relationship between feeders and carnivore activity, previous research demonstrates that supplemental feeding can lead to changes in the distribution of predators. For instance, the spatial distribution of bobcats (*Lynx rufus*, Godbois et al. 2004) and Red-tailed Hawks (*Buteo jamaicensis*; Turner et al. 2008) changed in response to supplemental feeding of Northern Bobwhite (*Colinus virginianus*), with the predators found closer to feeding stations than expected.

Of the three species with variable group sizes recorded in the camera images (gray squirrel, raccoon, and white-tailed deer), we found that gray squirrel and raccoon group sizes were greater at feeder sites than at control sites. This increase in squirrel and raccoon group size near feeders, 1.3-fold and 4.3-fold respectively, is consistent with other food supplementation studies and is reflective of the bottom-up nature of small mammal populations (Prevedello et al. 2013). The likely mechanisms by which waste birdseed could promote this increased density are numerous and may include increased immigration, reproductive success, survival, or annual recruitment (Havera and Nixon 1980, Boutin 1990, Gurnell 1996, Prange et al. 2004). Increased concentrations of small mammals at feeder sites will reach an asymptote, however, as larger group sizes may facilitate disease and parasite transmission (Becker and Hall 2014, Sorensen et al. 2014, Forbes et al. 2015) and intraspecific competition.

In addition to increased detections and group sizes of certain mammal species, sites with bird feeders also recorded localized increases in daily mammal richness. A local increase in richness is compelling because it indicates that species richness can differ even within small, fragmented

habitats and via provisioning of limited supplemental resources. Greater local mammal richness and abundance could also lead to the depletion of other food resources and increased intra- and interspecific competition, especially for mammals with small territories (Wauters et al. 2000). Alternatively, increasing species richness could lead to decreases in disease transmission via the “dilution effect” whereby interactions among competent hosts decrease (Keesing et al. 2006, 2010).

Development and human activity patterns are known to alter the distribution and temporal activity patterns of mesopredators (Wang et al. 2015), which can then influence the spatial distribution and nesting success of birds (Marzluff et al. 2007). Here, we were able to study daily activity patterns in the context of introducing limited supplemental food in a rural landscape. The temporal activity patterns we report generally agree with known life-history characteristics of the diurnal gray squirrel and crepuscular/nocturnal habits of raccoon, opossum, and white-tailed deer. Consequently, bird feeders did not impact the typical temporal activity patterns of local mammal species, although supplemental feeders may change temporal activity patterns in other taxa (Corcoran et al. 2013, Jones et al. 2014).

Hourly activity patterns in squirrels were consistent with another study that identified a bimodal activity distribution with activity peaking in the early morning and late afternoon during the fall and spring months (Thompson 1977). Daily gray squirrel activity at control sites, however, was greatly reduced and lacked a bimodal distribution. This finding suggests that bird feeding does not affect the temporal activity patterns of squirrels, but rather changes the local geographic distribution. Bird feeders, in effect, become “hot spots” for small mammal activity, the implications of which warrant further research attention. Future studies of reproductive success in birds should focus on species building open-cup nests in close proximity to bird feeders, particularly those species that do not benefit from supplemental food resources.

MANAGEMENT IMPLICATIONS

Providing supplemental food for birds potentially creates cascading ecological effects. Supplemental feeding of birds can lead to localized decreases of invertebrate prey that are presumably targeted by the birds attracted to feeders (Orros and Fellowes 2012). Moving up the food chain, bird feeding may unintentionally attract animals that compete with birds for resources (e.g., food or nesting sites), or attract animals that depredate the species that the supplemental food was intended to assist. Our work and previous studies suggest that several species of mammals are either modifying their home ranges and/or immigrating to areas with bird feeders in order to take advantage of waste seed (Boutin 1990, Prevedello et al. 2013). While the fitness implications of these behavioral changes for both mammals and birds require further study, altering bird feeding practices to limit spillage of waste seed from bird feeders is prudent. Preventing direct access to feeders by non-target taxa via installing baffles on support structures, by higher feeder placement, or by increasing the distance between feeders and trees can reduce inefficiencies. Additionally, suspending devices to catch waste seed

below the feeders and feeding birdseed without hulls (e.g., “no-waste” mixes) can be simple, cost-effective ways to limit the amount of food available to non-target taxa. Lastly, suspending bird feeding during the breeding season may minimize concentrations of potential nest predators. The public can, therefore, enhance their bird-watching experience while reducing the financial costs of bird feeding via modifying bird feeding practices and limiting the potentially negative effects of attracting non-target taxa.

ACKNOWLEDGMENTS

We thank the S. and R. Morley Student Research Grant for research funding (J. H. Reed) and the Cornell Botanic Gardens for providing access to the study area. Special thanks to E. Shertzer for her assistance in data collection and feeder maintenance and to B. McGuire for her essential advice in designing this study. W. Hochachka provided statistical advice and two anonymous reviewers provided appreciated feedback. Thanks to the Cornell Lab of Ornithology for support and to I. Lovette, P. Rodewald, and the Bonter lab group for constructive feedback.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p5k25>.