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RESEARCH ARTICLE

Species-dependent effects of bird feeders on nest predators and nest survival of urban American Robins and Northern Cardinals

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ABSTRACT

The abundance of anthropogenic foods in urban areas offers an excellent opportunity to examine the effects of supplementary food on animal communities, but few studies have examined the consequences of these supplements on relationships between predators and prey. We used observational and experimental approaches to investigate how supplementary food (i.e. bird feeders) affected predator abundances and nest survival of American Robins (*Turdus migratorius*) and Northern Cardinals (*Cardinalis cardinalis*) in 7 neighborhoods of Columbus, Ohio, USA. From April to August of 2011–2014, we quantified supplementary foods, the relative abundance of 6 common nest predators, and the nest survival of 2 songbirds. In April–August of 2013 and 2014, we supplemented 3 neighborhoods with additional bird feeders, the supplementary food most frequently available to predators. The effects of bird feeders varied among predator and prey species. Bird feeders were positively associated with the relative abundance of American Crows (*Corvus brachyrhynchos*) and Brown-headed Cowbirds (*Molothrus ater*). Neighborhoods with at least 15 feeders had on average 2.7× more crows and 3.2× more cowbirds than neighborhoods with 3 or fewer feeders. Relationships among bird feeders, predators, and nest survival were complex. Nest survival of robins declined with increasing numbers of bird feeders only where crows were most frequently detected. In neighborhoods with the most bird feeders and crows, fewer than 1% of robin nests were expected to survive to fledging (i.e. to 28 days), while in neighborhoods with fewer feeders and/or crows, up to 34% of robin nests were expected to successfully fledge young. In contrast, nest survival rates of cardinals were not related to either feeders or predators. Differences between robins and cardinals in vulnerability to specific predators and diet may partially explain the different patterns that we observed. Thus, although bird feeders generally did not promote nest predation, there may be nuanced and species-specific responses that have the potential to affect common breeding birds.

Keywords: nest survival, predation, food subsidies, suburban matrix, urban ecology

Efectos especie-dependientes de los comederos de aves sobre los depredadores de nidos y la supervivencia de los nidos en dos aves urbanas

RESUMEN

La abundancia de los alimentos antropogénicos en las áreas urbanas brinda una oportunidad excelente para examinar los efectos de los suplementos alimenticios en las comunidades animales, pero pocos estudios han examinado las consecuencias de estos suplementos en las relaciones entre depredadores y presas. Empleamos enfoques observacionales y experimentarlas para investigar como los suplementos alimenticios (i.e. comederos de aves) afectaron las abundancias de los depredadores y la supervivencia del nido de *Turdus migratorius* y *Cardinalis cardinalis* en 7 vecindarios de Columbus, Ohio, EEUU. Desde abril a agosto de 2011–2014, cuantificamos los suplementos alimenticios, la abundancia relativa de 6 depredadores comunes de nidos y la supervivencia del nido de 2 aves canoras. Desde abril a agosto de 2013 y 2014, suplementamos de 3 vecindarios con comederos de aves adicionales, que representan el suplemento alimenticio más frecuentemente disponible para los depredadores. Los efectos de los comederos de aves variaron entre las especies de depredadores y de presas. Los comederos de aves estuvieron positivamente asociados con la abundancia relativa de *Corvus brachyrhynchos* y de *Molothrus ater*. Los vecindarios con al menos 15 comederos tuvieron en promedio 2.7× más individuos de *C. brachyrhynchos* y 3.2× más individuos de *M. ater* que los vecindarios con 3 comederos o menos. Las relaciones entre los comederos de aves, los depredadores y la supervivencia del nido fueron complejas. La supervivencia del nido de *Turdus migratorius* disminuyó con el aumento del número de comederos de aves solo donde *C. brachyrhynchos* fue detectado más frecuentemente. En los vecindarios con la mayor cantidad de comederos de aves y de individuos de *C. brachyrhynchos*, menos del 1% de los nidos de *T. migratorius* se esperó que sobreviviera hasta el emplumamiento (i.e. hasta los 28 días), mientras que en los vecindarios con menos comederos y/o individuos de *C. brachyrhynchos*, hasta el 34% de los nidos de *T. migratorius* se esperó que emplumara exitosamente un volantón. En contraste, las tasas de supervivencia del nido de *Cardinalis*

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cardinalis no estuvieron relacionadas ni con los comederos ni con los depredadores. Las diferencias entre *T. migratorius* y *C. cardinalis* en términos de vulnerabilidad a los depredadores específicos y de dieta podrían explicar parcialmente los diferentes patrones que observamos. Por ende, aunque los comederos de aves por lo general no promueven la depredación de nidos, pueden haber respuestas matizadas y específicas de las especies que tienen el potencial de afectar a las aves reproductoras comunes.

Palabras clave: depredación, ecología urbana, matriz suburbana, subsidios alimenticios, supervivencia del nido

INTRODUCTION

Resource subsidies, particularly in the form of food, can strongly shape animal communities through their effects on behavior, population dynamics, and species relationships. Within species, access to supplementary food can change movement patterns and enhance population productivity (Arcese and Smith 1988, Polis et al. 1997, Beckmann and Berger 2003, Eide et al. 2004, Prange et al. 2004, Rastogi et al. 2006, Longcore et al. 2009). Among species, supplementary food can alter species relationships to the extent that community composition shifts (Brown and Munger 1985, Boutin 1990, Prange and Gehrt 2004). In addition, supplementary food may enhance or reduce predation risk (Dahle et al. 1998, Takimoto et al. 2002, Preston and Rotenberry 2006, Borgmann et al. 2013, Newsome et al. 2014, 2015).

Urban areas provide an excellent opportunity to examine how supplementary foods may influence relationships among predators and prey because abundant and diverse anthropogenic foods are a defining characteristic of cities (Warren et al. 2006). These supplementary foods, provided through both intentional means such as bird feeders and unintentional means such as poor refuse management, often make patchy resources more continuously available in space and time (Beckmann and Berger 2003, Shochat et al. 2006, Bozek et al. 2007, Robb et al. 2008). Relationships between breeding birds and their nest predators in developed landscapes may be especially influenced by supplementary foods because both songbirds and generalist predators readily exploit these resources, and thus congregate in the same areas (Marzluff et al. 2001, Prange and Gehrt 2004, Robb et al. 2008, Theimer et al. 2015). However, despite many studies on avian reproduction in urban landscapes, no clear pattern has emerged regarding the effect of urbanization and associated supplementary foods on the relationship between predators and nest survival (Chamberlain et al. 2009). Current understanding is limited because few field experiments have provided supplementary food directly to predators (Preston and Rotenberry 2006, Borgmann et al. 2013, Theimer et al. 2015).

Supplementary foods can affect nest predation risk in different ways, depending upon the underlying mechanisms by which these foods affect predators at the individual and population levels. As such, supplementary food may have a positive, negative, or neutral indirect effect on nest survival, depending on the consequences of food availability for nest predators. It is possible that supplementary foods may relax predation pressure because predators may switch their diet from natural prey (e.g., bird nest contents) to supplementary foods (Preston and Rotenberry 2006, Rodewald et al. 2011, Fischer et al. 2012). Alternatively, supplementary foods could be associated with lower rates of nest survival due to increased encounter rates between predators and nests (Stracey 2011, Borgmann et al. 2013). For example, abundant supplementary foods may support larger predator populations than could exist given the natural prey base, leading to hyperpredation, or these foods might attract predators to an area, leading to greater rates of incidental predation (Kristan and Boarman 2003, Schmidt and Ostfeld 2003). Lastly, greater levels of consumption of supplementary food by predators may partially satiate them and, in this way, balance out the negative effects on nest survival of higher numbers and/or activity of predators. In this final scenario, rates of nest survival may be similar across a wide spectrum of availability of supplementary foods. Experiments in which free-ranging predators are supplemented are relatively rare but have great potential to identify mechanisms by which predators and prey are influenced by supplementary foods (Preston and Rotenberry 2006, Borgmann et al. 2013, Theimer et al. 2015).

We focused our research on American Robins (*Turdus migratorius*; hereafter, robins) and Northern Cardinals (*Cardinalis cardinalis*; hereafter, cardinals), 2 species that commonly nest in the understory and midstory of residential neighborhoods where food supplementation is common. Robins and cardinals differ in their use of supplementary food: cardinals often consume seeds at bird feeders, whereas robins do not (Halkin and Linville 1999, Vanderhoff et al. 2016).

We investigated relationships among the nest survival of these 2 prey species (robins and cardinals) and 6 common nest predators: Brown-headed Cowbird (*Molothrus ater*), Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*), eastern gray squirrel (*Sciurus carolinensis*), American Crow (*Corvus brachyrhynchos*), and domestic cat (*Felis catus*). Each of these predators has been video-documented depredating eggs and/or nestlings of robins and cardinals in our study system, although in some instances predation events did not result in nest failure (i.e.

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complete loss of nest contents; Rodewald and Kearns 2011, Malpass 2015). We considered the effects of Brown-headed Cowbirds as nest predators only, not as brood parasites. Collectively, these 6 predator species accounted for the majority of predation events on both robin and cardinal nests in our system (74% and 66%, respectively; Malpass 2015). The diets of Brown-headed Cowbirds, American Crows, Common Grackles, Blue Jays, and eastern gray squirrels incorporate anthropogenic foods, including birdseed from feeders in suburban neighborhoods (Lowther 1993, Bowers and Breland 1996, Peer and Bollinger 1997, Marzluff et al. 2001, Verbeek and Caffrey 2002, Marzluff and Neatherlin 2006, Parker and Nilon 2008, Smith et al. 2013).

We measured the abundance of predators and the nest success of robins and cardinals in neighborhoods differing in the availability of supplemental food from bird feeders. We also experimentally supplemented food in 3 neighborhoods. Our objectives were to determine: (1) the relationship betwen bird feeders and nest predators; and (2) how bird feeders affected the nest success of robins and cardinals.

METHODS

Data Collection

We conducted our research in 7 residential neighborhoods (~3.5 ha each) in the greater metropolitan area of Columbus, Ohio, USA. We selected neighborhoods that were adjacent to riparian forest parks being used for complementary long-term research (Rodewald and Shustack 2008). The 7 neighborhoods had similar ranges of building density and landscape composition (Rodewald and Shustack 2008). With the permission of residents, we worked in 150 private yards in 2011, 173 in 2012, 151 in 2013, and 135 in 2014 (11–32 yards per neighborhood; >50% of the area of each neighborhood). We visited each neighborhood twice weekly between dawn and 16:00, with additional visits as necessary (e.g., to confirm fledging).

Nest monitoring. We attempted to find every robin and cardinal nest within the 3.5-ha area of each neighborhood using a combination of systematic searching of potential nest substrates and behavioral observations of adult birds (e.g., carrying of nesting material, defensive displays). We systematically searched for nests at least once per week in each property to which we had access as well as along public rights-of-way, and located nests through behavioral observations at least twice weekly during each visit to our focal neighborhoods. Nest searching continued through August because both species raise multiple broods. Once found, robin and cardinal nests were checked every 1–4 days, either by directly examining nest contents or by observing parental behavior from a position >10 m from the nest to determine the nest stage (nest building, incubation, nestlings). To avoid exposing nests to predators as a result of our visits, we varied our routes to nests, checked contents briefly, and delayed checking nests if nest predators were observed in the vicinity.

Predator surveys. We conducted diurnal surveys of potential nest predators weekly from May 16 to August 27, 2011, April 16 to August 12, 2012, April 22 to August 10, 2013, and April 21 to August 7, 2014. Surveys consisted of a 10-min point count of unlimited radius conducted between 07:00 and 13:00, during which time we used aural and visual cues to detect a wide variety of small mammals, raptors, corvids, and mesopredators known to be nest predators in this study system, including Brown-headed Cowbirds (hereafter, cowbird), Common Grackles, Blue Jays, eastern gray squirrels (squirrel), American Crows (crow), domestic cats (cat), eastern chipmunks (*Tamias striatus*), Cooper's Hawks (*Accipiter cooperii*), Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*Buteo lineatus*), red squirrels (*Tamiasciurus hudsonicus*), raccoons (*Procyon lotor*), Sharp-shinned Hawks (*Accipiter striatus*), eastern fox squirrels (*Sciurus niger*), American Kestrels (*Falco sparverius*), black rat snakes (*Pantherophis obsoletus*), Broad-winged Hawks (*Buteo platypterus*), Norway rats (*Rattus norvegicus*), and striped skunks (*Mephitis mephitis*; Appendix Table 4; Rodewald and Kearns 2011). During surveys, we recorded all predators that we detected, but detections of nocturnal species were expected to be low given that our surveys were diurnal. Observers were trained in distance estimation and provided with rangefinders (Buckland et al. 2001). We recorded predator species, method of detection (visual, aural, or both), distance to each individual detected, and method of distance measurement (rangefinder or visual estimate).

Within each of our 7 focal neighborhoods, we randomly selected 8 yards in which to conduct surveys from the pool of yards to which we had access. We centered surveys 10 m from the front door of the building for 6 of the yards, and we centered surveys 10 m from the back door of the building in the remaining 2 yards (total survey locations across all neighborhoods = 56). In most cases the survey center was in an open part of the yard; while this meant that observers were visible to potential nest predators, it also ensured that there was high detection probability at the survey center (Buckland et al. 2001). The same survey locations were used throughout the study, with the exception of 9 surveys that were moved because permission changed between years; these were relocated to the next nearest yard to which we had access. Of the 8 surveys in each neighborhood, half were conducted between 07:00 and 10:00 and half between 10:00 and 13:00 to minimize potential bias of differences in activity patterns of predators throughout the morning; survey start times were random within these 2 time periods. Surveys were not conducted during periods of heavy rain.

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Supplementary food surveys. We surveyed each neighborhood monthly between April and August, 2011–2014, to determine the locations and extent of supplementary foods (i.e. birdseed, pet food, trash, compost). Surveys across all 7 neighborhoods were conducted within the same 7-day period of the month. We created aerial maps for focal neighborhoods using GIS data for parcel boundaries, roads, and buildings from the Ohio Geographically Referenced Information Program (http://ogrip.oit.ohio.gov/). Trained observers spent 35–55 min per survey walking the neighborhood and identifying the locations of supplementary foods on these maps. Observers entered all properties to which we had access for nest monitoring, and visually inspected remaining properties from a distance (i.e. from public property). Every effort was made to survey the extent of the neighborhood included in nest monitoring studies, but we were not able to survey every yard due to access restrictions or visual obstruction (e.g., a privacy fence). Therefore, our results represent conservative estimates of supplementary food resources in these neighborhoods.

For each food source detected, we recorded food type (i.e. type of birdseed, pet food, trash, or compost), whether or not it was accessible to avian and/or mammalian nest predators, and whether nest predators were present. We recorded each food item separately, including cases when there were multiple foods present at a single location (e.g., several bird feeders hanging from the same pole), which occurred for ~40% of foods. Because birdseed accounted for 82% of all of the supplementary food accessible to nest predators (Appendix Table 5), other types of food were excluded from analyses. The number of bird feeders was not correlated with either trash ($r = -0.38$) or pet food resources ($r = 0.05$). All compost piles were either inaccessible to predators or did not contain food (e.g., consisted of only grass clippings). Feeders with no baffle and/or with seed on the ground were considered accessible to both avian and mammalian predators, while feeders with a baffle below the feeder and no seed on the ground were considered accessible to avian predators only, and feeders with a weight baffle and no seed on the ground were considered inaccessible to nest predators. Hummingbird feeders were considered inaccessible to nest predators, as were thistle-specific feeders, provided that there was no seed under the feeder. Only feeders that were accessible to nest predators were included in analyses. We used the number of bird feeders available to avian and/or mammalian nest predators as our predictor variable because the majority of feeders (82%) were available to both types of predator.

Experimental Supplementation

To test how supplementary foods influenced nest predators and nest survival, we experimentally supplemented 3 of the 7 focal neighborhoods by providing a consistent quantity and quality of birdseed. We chose to manipulate birdseed because birdseed: (1) accounted for the vast majority of supplementary food available to potential nest predators in our system (82%); (2) was consumed by most predator species included in our analyses; and (3) was deliberately provided by residents, unlike other supplementary food resources (e.g., trash). Moreover, >40% of U.S. households participate in bird feeding, possibly making this the most common wildlife management activity in the country and a pertinent area for further ecological research (Brittingham and Temple 1992, Martinson and Flaspohler 2003, Jones and Reynolds 2008, Robb et al. 2008).

For the supplementation experiment, we selected 3 neighborhoods with low numbers of feeders and no permanent sources of trash (dumpsters) in 2011–2012 (Appendix Table 5). During April–August of 2013 and 2014, we provided 13–16 feeders to each supplemented neighborhood ($n_{total} = 45$) to increase the number of feeders to 20–25, which reflected the greatest number of bird feeders observed across all neighborhoods in 2011–2012 (Table 1). Experimental feeders were designed to be accessible to songbirds and generalist nest predators and consisted of a shallow platform mounted on a 1.2 m pole or hung from a tree. Feeders were located within sight of ≥1 predator survey locations to enhance our ability to detect changes in diurnal predator activity as a function of feeder availability, and/or in proximity to areas where we had documented robins or cardinals nesting in 2011 and 2012 to enhance our ability to identify whether supplementary food increased or decreased nest survival rates. The mean distance between a predator survey location and the nearest bird feeder was similar for feeders provided by residents (35.6 m) and those provided by researchers (37.4 m). Because multiple feeders often occurred in individual yards (43% of yards in 2011 and 63% in 2012), most experimental feeders (84%) were placed in pairs on the same pole or tree. The same locations were used for supplementary feeders in 2013 and 2014, except in 2 instances in which residents requested that we move or remove feeders because residents were concerned that the feeders were attracting undesirable wildlife.

Spatial and temporal heterogeneity in the availability of bird feeders is common in urban environments, and the supplementation experiment provided a predictable, but not continuous, alternative food resource (Davies et al. 2009). We provided 9 kg (0.45–1.36 kg of seed per feeder) of high-quality birdseed to each supplemented neighborhood once per week. The seed blend consisted of 30% white millet, 30% milo, 22% black oil sunflower, 11% safflower, and 3% peanuts (>9% protein, >11% fat, <15% fiber). This seed blend was used because it was comparable to the most common mix detected during food surveys in

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TABLE 1. Minimum, maximum, and mean number of bird feeders accessible to avian and/or mammalian nest predators in control and experimental neighborhoods in Columbus, Ohio, USA, during April–August, 2011–2014. Experimental neighborhoods were supplemented with 9 kg of birdseed weekly across 13–16 feeders during April–August.

			Number of bird feeders		
Neighborhood	Year	Treatment	Minimum	Maximum	Mean
Casto	2011	Control	0	2	1.2
	2012	Control	1	5	2.2
	2013	Control	1	5	2.6
	2014	Control	0	5	2.4
Kenny	2011	Control	9	20	13.8
	2012	Control	6	21	14.4
	2013	Control	7	20	12.4
	2014	Control	3	16	8.4
Rush Run	2011	Control	9	15	12.0
	2012	Control	11	21	16.0
	2013	Control	11	14	12.6
	2014	Control	6	12	8.0
Tuttle	2011	Control	0	3	1.8
	2012	Control	0	3	1.8
	2013	Control	0	4	1.2
	2014	Control	0	1	0.4
Cherry	2011	Presupplemented	4	9	7.2
	2012	Presupplemented	5	13	8.8
	2013	Supplemented	12	28	19.4
	2014	Supplemented	8	15	12.6
Elk Run	2011	Presupplemented	0	6	4.4
	2012	Presupplemented	2	9	6.2
	2013	Supplemented	10	20	14.0
	2014	Supplemented	3	9	6.8
Woodside	2011	Presupplemented	2	6	4.8
	2012	Presupplemented	4	6	4.8
	2013	Supplemented	18	25	21.4
	2014	Supplemented	6	21	16.0

2011 and 2012 (used at 35% and 30% of all available feeders, respectively). We filled experimental feeders only once per week (i.e. we did not provide supplementary food ad libitum), and most experimental feeders were depleted within 7 days. Monthly food surveys were conducted 3 or 4 days after filling the feeders.

Statistical Analysis

Relationships between predators and bird feeders. We tested for spatial autocorrelation of predator survey data within neighborhoods using Mantel tests (Mantel 1967). We modeled detection probability for predator species for which we had at least 450 diurnal detections after removing the 5% most distant observations using the distance package in R 3.0.1 (Buckland et al. 2001, R Core Team 2013). Only these species were included in subsequent analyses. These models account for differences in detectability associated with increasing distance between observers and nest predators, and allow for comparisons of relative differences in abundance among surveys (Buckland et al. 2001). Half-normal, uniform, and hazard-rate key functions with the option of cosine series expansions are robust models for point survey data, but each of these may not fit the data equally well (Buckland et al. 2001). As such, we used an information-theoretic framework that compared the relative weight of evidence among these models with Akaike's Information Criterion (AIC) to identify models with strong support for detection probability (Burnham and Anderson 2002). We confirmed the best-fitting model within this set using visual inspections of plots (MacKenzie and Bailey 2004, Buckland et al. 2015).

After correcting for imperfect detection during surveys, we used linear mixed models to examine the relationship between bird feeders and the relative abundance of predators, running separate models for each predator species and each month. We analyzed predator data by month because weekly data did not provide a sufficient sample to calculate detection probability and because food surveys were conducted monthly. Monthly relative abundance was used as the response variable, and predictors included the number of bird feeders available in that month, neighborhood (as a random effect, to account for neighborhood-specific dependencies and our repeated measures design), and year (as a fixed effect, to address our supplementation experiment and direct interest in this

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effect). We calculated *P*-values based on Student's *t*-distributions and accepted significance at $\alpha = 0.05$.

Nest survival. We used the logistic exposure model to estimate the daily nest survival rate (DSR) of 521 robin nests and 428 cardinal nests monitored during April–August, 2011–2014. The logistic exposure model is a generalized linear model that uses a binomial error distribution and a link function to estimate the probability of nest survival between each visit to the nest, thereby eliminating potential bias due to different exposure periods (Shaffer 2004). Nest fate at each nest check was modeled as either failing (0) or surviving (1) the nest-check interval. We excluded nests for which failure was confirmed to be unrelated to predators (e.g., weather; <1% of failed nests), and nests abandoned during building or for which we did not confirm that a clutch was laid prior to nest failure (17%). We also excluded nests for which ≥1 nest checks were missing associated predator or food survey data (e.g., nests that fledged in September; $n < 5$).

Relationships among bird feeders, predators, and nest survival. We compared the relative weight of evidence for multiple mixed-effects models with AIC corrected for small sample sizes (AIC_c) to assess the ability of bird feeder and predator metrics to explain variation in predicted DSR, testing robins and cardinals separately (Burnham and Anderson 2002). Nest predators in this study system were identified using video recordings at nests as part of complementary research, and only known nest predators were included in analyses (Rodewald and Kearns 2011, Malpass 2015). Known predators of robins for which we had relative abundance estimates included crows and cats, and all 6 predators for which we had relative abundance estimates had been documented depredating cardinal nests. Global models included the number of bird feeders and relative abundance of predators as main effects, as well as interaction terms for feeders and relative abundance for the predators that consume birdseed. A feeder * cat interaction was not considered because cats do not use birdseed as an alternative food source, and although cats may hunt birds and small mammals around bird feeders, feeders may not expose birds to higher predation risk (Dunn and Tessaglia 1994, Woods et al. 2003). For cardinal models, we combined all avian predators into a single metric of relative abundance, firstly because avian predators rely on similar (i.e. visual) cues to detect nests, and secondly to maintain a lower ratio of number of predictor variables in relation to sample size (Söderström et al. 1998, Grueber et al. 2011). All models included neighborhood (as a random effect, to account for neighborhood-specific dependencies and our repeated measures design) and year (as a fixed effect, to address our supplementation experiment and direct interest in this effect), as well as the day of year of the nest check (as a fixed effect) because previous work in this study system has shown that nest survival increases as the breeding season progresses (Rodewald and Shustack 2008).

We centered and scaled the number of bird feeders and relative abundance of predators: (1) to minimize the likelihood of models failing to converge due to variables on vastly different scales; and (2) to enhance interpretability of interaction terms (Schielzeth 2010). We evaluated support for models within $\Delta AIC_c < 7$ of the top model (Burnham et al. 2010). Akaike weights (w_i; weight of evidence for each model) indicated the relative support for each model and the likelihood that any given model was the true best model of the candidate model set (Burnham and Anderson 2002). When candidate models had support, we used the natural averages method to calculate parameter estimates and to predict values for DSR (Burnham and Anderson 2002, Grueber et al. 2011).

Effect of experimental supplementation. We used linear mixed models to examine the effect of experimental supplementation on the relative abundance of predators, testing each predator species separately. Models included the following fixed effects: year (to address our supplementation experiment and direct interest in this effect), treatment (i.e. experimental or control), and year * treatment. Year within neighborhood was included as a random effect in models to account for neighborhood-specific dependencies and our repeated measures design. We used log-likelihood ratio tests to identify the most appropriate variance structure and modeled variance as different across years, treatments, and year * treatment when there was heteroscedascity in predator detections (Zuur et al. 2009).

We used the logistic exposure model to estimate DSR for each species, year, and neighborhood combination using a custom R package (nestsurvival; M. Herzog personal communication). The resulting DSR estimates for robins and cardinals were used as the response variable in separate linear mixed models to examine the effect of experimental supplementation on DSR. Predictor variables included the fixed effects of year, treatment (experimental or control), and year * treatment, and the random effect of year within neighborhood to account for our repeated measures design. We excluded DSRs from neighborhoods where we monitored fewer than 5 nests in ≥1 yr ($n = 6$).

RESULTS

Relationships between Predators and Bird Feeders

We completed 778 predator surveys in 2011, 945 in 2012, 868 in 2013, and 880 in 2014. In total, we recorded 15,115 diurnal detections of 19 nest predator species (Appendix Table 4). The following predators had sufficient detections to be included in further analyses: cowbird ($n = 3,376$), Common Grackle ($n = 3,282$), Blue Jay ($n = 3,258$), squirrel

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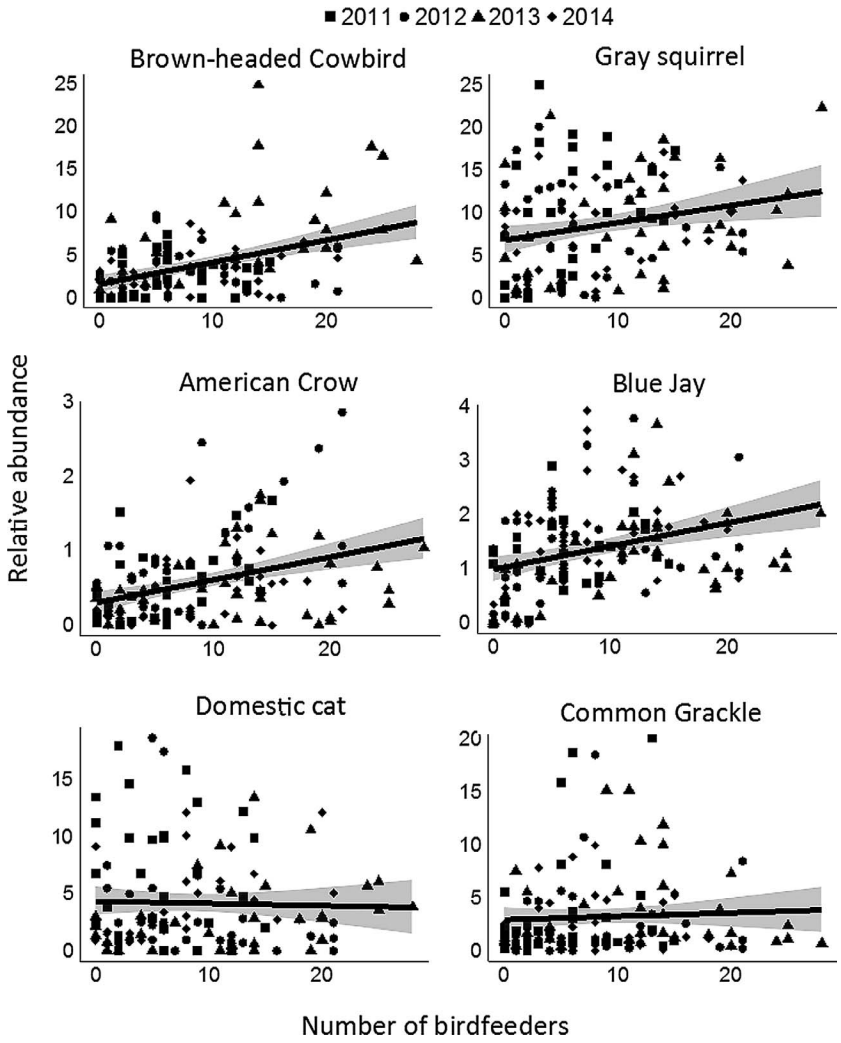


FIGURE 1. The relationship between the number of bird feeders available to avian and/or mammalian predators and the relative abundance of predators was positive for Brown-headed Cowbirds and American Crows, and neutral for gray squirrels, Blue Jays, domestic cats, and Common Grackles, sampled during 3,471 diurnal surveys in 7 suburban neighborhoods in Columbus, Ohio, USA, 2011–2014. Monthly bird feeder and predator data are plotted (points), and solid lines represent linear trend lines and 95% CIs (gray shading).

($n = 2{,}340$), crow ($n = 1{,}776$), and cat ($n = 526$). Each of these 6 species was also video-documented depredating songbird nests in yards included in this study or in adjacent forest parks (Rodewald and Kearns 2011, Malpass 2015). Mantel tests indicated that positive spatial dependence of predator survey data occurred only on one occasion (Elk Run in August, 2015). Thus, any effects of spatial dependence on our results are likely minimal. For each species per month per year combination, we used the detection probability model with the most support based on the lowest AIC value and where visual inspection did not indicate overfitting. We lacked predator survey data from April, 2011, because surveys started in May of that year. We also lacked sufficient diurnal detections to accurately model detection probability for cowbirds in August, 2013, and for cats in August, 2014; values for the relative abundance of these species in these months were excluded from further analyses.

The number of bird feeders available to nest predators differed across years and among neighborhoods (Table 1). The extent to which the number of available bird feeders predicted the relative abundance of predators varied among species (Figure 1). The relative abundance of cowbirds was positively associated with the number of bird feeders ($\beta \pm$ SE: 0.192 ± 0.055; $t_{125} = 3.482$, $P < 0.001$) but varied among years, with relative abundance in 2013 higher than in other years ($t_{125} = 4.445$, $P < 0.001$). The relative abundance of crows also was positively associated with the number of bird feeders (0.026 ± 0.007; $t_{132} = 3.896$, $P < 0.001$). The number of bird feeders was not

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TABLE 2. Model selection for American Robin daily nest survival rates in 7 suburban neighborhoods in Columbus, Ohio, USA, 2011–2014; models were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c). Models with interaction terms included those main effects, and all 10 candidate models also included year (fixed effect, $n = 4$), day of year of the nest check (fixed effect), and neighborhood (random effect). Only species known to depredate robin nests in this system were used in analysis. K = the number of model parameters, LL = model log-likelihood, ΔAIC_c = distance from the top model, and w_i = Akaike weight.

Model	K	LL	ΔAIC_c	w_i
Crow + Feeder + Crow * Feeder	9	−1185.11	0.00 [a]	0.60
Cat + Crow + Feeder + Crow * Feeder	10	−1185.11	2.01	0.22
Crow + Feeder	8	−1188.06	3.90	0.09
Cat + Crow + Feeder	9	−1187.99	5.76	0.03
Feeder	7	−1190.53	6.83	0.02
Crow	7	−1190.82	7.40	0.01
Crow + Cat	8	−1190.28	8.33	0.01
Cat + Feeder	8	−1190.44	8.66	0.01
Null	6	−1192.94	9.64	0.00
Cat	7	−1192.25	10.26	0.00

[a] The AIC_c value of the top model = 2388.27.

significantly related to the relative abundance of squirrels (0.080 ± 0.073; $t_{132} = 1.084$, $P > 0.05$), Blue Jays (0.016 ± 0.012; $t_{132} = 1.315$, $P > 0.05$), cats (–0.058 ± 0.066; $t_{125} = -0.887$, $P > 0.05$), or Common Grackles (–0.019 ± 0.061; $t_{132} = -0.314$, $P > 0.05$).

Nest Survival

Of the 10 candidate models for DSR of robins, the crow + feeder + feeder * crow model best predicted DSR, and no other models had a $\Delta AIC_c < 2$ (Table 2). Of the 5 models with $\Delta AIC_c < 7$, 3 were simplified additive models of the top-ranked model and cats entered the model in the remaining 2 cases (Table 2). However, evidence suggested that the cat variable provided no additional information; its addition resulted in >2 AIC_c change, and 95% confidence intervals for the model-averaged estimate for cats (–0.210, 0.214) overlapped 0 (Arnold 2010). The top-ranked model predicted robin DSR as: DSR = 3.41 – 2.28(crow) – 0.368(feeders) – 0.581(crow * feeders) + 0.751(day of the year of nest check) – 0.378($year_{2012}$) – 0.160($year_{2013}$) – 0.578($year_{2014}$), using $year_{2011}$ as a reference category. Bird feeders and the relative abundance of crows interacted such that DSR was especially low for robins nesting in neighborhoods with many feeders and many crows (Figure 2).

All of the 26 candidate models for DSR of cardinals had $\Delta AIC_c < 7$, with 11 of these models, including the null model, with $\Delta AIC_c < 2$ (Table 3). Effect sizes for feeder and predator parameters were small and confidence intervals for each of these overlapped 0 after model-averaging the parameter estimates across the 11 top models (Appendix Table 6).

Experimental Supplementation

Relative abundances of predators were highly variable among years and treatments (Figure 3). However, we did not observe an increase in mean relative abundance for any predator species in response to experimental supplementation after accounting for differences in variance across years (squirrel, Blue Jay), or years and treatments (cowbird, cat, Common Grackle). Mean relative abundance decreased from 2011 to 2014 for squirrels (β ± SE: –1.134 ± 0.515; $t_{15} = -2.200$, $P = 0.04$) and crows (–0.118 ± 0.050; $t_{19} = -2.375$, $P = 0.03$), independent of treatment, while relative abundance within a species was comparable across years and treatments for Blue Jays, cowbirds, cats, and Common Grackles. In addition, DSR estimates were similar among years and between experimental treatments for both cardinals and robins (Figure 4).

DISCUSSION

We found evidence that supplementary food has the potential to increase the relative abundance of certain predators, but not necessarily in a way that raises the risk of nest predation. Although the relative abundance of 2 nest predators, crows and cowbirds, was greater in areas with bird feeders, there was no consistent relationship between the number of bird feeders and predation of either robin or cardinal nests. Rather, we found that the number of bird feeders interacted with the relative abundance of nest predators, such that nest survival rates decreased only for robins in neighborhoods with many feeders and many crows. Thus, our results show that supplementary food does not necessarily increase the risk of predation for breeding birds, and instead likely has nuanced and species-specific consequences.

Contrary to our original expectations, the number of bird feeders did not consistently promote the use of neighborhoods by common nest predators. Crows, cowbirds, Common Grackles, Blue Jays, and squirrels were observed at bird feeders during our supplementary food surveys and readily consumed birdseed in residential

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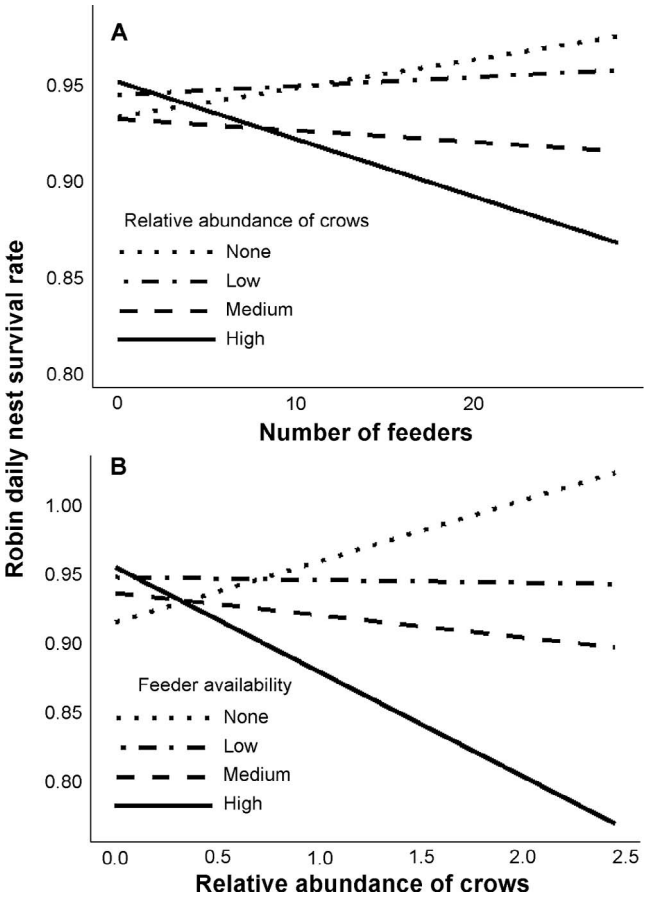


FIGURE 2. The relationship between bird feeders and daily nest survival (DSR) of American Robins in suburban neighborhoods in Columbus, Ohio, USA, 2011–2014, depended on the relative abundance of American Crows; the number of bird feeders available to nest predators in the month that the nest was checked had negative effects on robin nest survival only in neighborhoods with medium to high relative abundance of crows. For illustrative purposes, we have graphed robin DSR at 4 levels of (**A**) relative abundance of crows and (**B**) feeders: None = no observations; low = minimum nonzero observation to first quartile; medium = interquartile range; and high = above third quartile.

neighborhoods (avian species: feederwatch.org; squirrels: Parker and Nilon 2008). However, the relative abundances of only crows and cowbirds were positively related to the numbers of bird feeders, and relative abundance did not increase for any predator species in response to experimental supplementation. Although quantifying the amount of supplementary food consumed by our focal predators was outside the scope of our research, others have shown that anthropogenic foods, including birdseed, can have significant effects on the population demography of generalist species (e.g., Robb et al. 2008, Fischer and Miller 2015). Bird feeders attract cowbirds from great distances and support populations to the extent that reducing bird feeding during the breeding season is one management recommendation for decreasing the risk of brood parasitism and nest predation by cowbirds (Coker and Capen 1995, Chace et al. 2003). Crows are also known to heavily exploit supplementary foods associated with human habitation, and such foods are thought to promote both high densities and reproductive success of crows in suburbs (Marzluff et al. 2001, McGowan 2001, Marzluff and Neatherlin 2006). Although crows are not strongly associated with bird feeders in some regions, they are common visitors to feeders in Ohio, where they are reported at 16–30% of bird feeders included in the FeederWatch citizen science project (feederwatch.org).

The high levels of spatial and temporal variability in detections of predators may partly explain the lack of a strong response of most predators to the number of bird feeders in our study. Another contributing factor may have been the diverse diets of the omnivorous predators in this study system, which likely made these species less reliant upon any single food item compared with carnivores or other dietary specialists (e.g. Cooper's Hawks; Estes and Mannan 2003). The likelihood of a generalist omnivore becoming more specialized is further reduced when the supplementary food is not consistently available. Although common in urban areas, bird feeders may be intermittently filled, and at any given time the majority of feeders may be empty (Robb et al. 2008, Davies et al. 2009). We also recognize that species that lactate to meet the nutritional needs of their young may be more flexible in their dietary requirements, e.g., able to rely on supplementary foods to meet the energetic needs of themselves and their young. In addition, some generalist predators may respond to the availability of bird feeders at spatial scales beyond those that we measured. Other research has shown that supplementary foods may attract generalist species from several kilometers away, and the ubiquity of bird feeders in residential neighborhoods may mean that feeders do not function as point sources of supplementary food (Coker and Capen 1995, Kristan and Boarman 2003, Robb et al. 2008).

Although some previous research has suggested that bird feeders may enhance the survival of bird nests by satiating nest predators, we found no evidence of this in our study system. Prey switching is one mechanism proposed to account for weak correlations between predator densities and predation pressure in urban areas where supplementary foods are abundant (Rodewald et al. 2011, Fischer et al. 2012). However, results of evaluations of this mechanism have been mixed and few field experiments have been conducted (Preston and Rotenberry 2006, Borgmann et al. 2013, Theimer et al. 2015). In one experiment, researchers increased the probability that Wrentits (*Chamaea fasciata*) would successfully fledge young by providing bird feeders within the territories of their most frequent nest predator, California Scrub-Jays

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TABLE 3. Model selection for Northern Cardinal daily nest survival rates in 7 suburban neighborhoods in Columbus, Ohio, USA, 2011–2014; models were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c). Models with interaction terms included those main effects, and all 26 candidate models also included year (fixed effect, $n = 4$), day of year of the nest check (fixed effect), and neighborhood (random effect). Only species known to depredate cardinal nests in this system were included in analysis. K = the number of model parameters LL = model log-likelihood, ΔAIC_c = distance from the top model, and w_i = Akaike weight.

Model	K	LL	ΔAIC_c	w_i
Squirrel	7	−972.33	0.00 [a]	0.10
Cat + Squirrel	8	−971.49	0.32	0.09
Squirrel * Feeder	9	−970.50	0.37	0.09
Cat	7	−972.75	0.83	0.07
Cat + Squirrel + Feeder + Squirrel * Feeder	10	−969.78	0.94	0.07
Null	6	−973.93	1.17	0.06
Avian + Squirrel	8	−971.93	1.21	0.06
Avian	7	−973.05	1.43	0.05
Avian + Cat	8	−972.08	1.50	0.05
Avian + Cat + Squirrel	9	−971.16	1.68	0.05
Squirrel + Feeder	8	−972.24	1.82	0.04
Avian + Squirrel + Feeder + Squirrel * Feeder	10	−970.37	2.12	0.04
Cat + Feeder + Squirrel	9	−971.41	2.18	0.04
Cat + Feeder	8	−972.69	2.72	0.03
Cat + Avian + Squirrel + Feeder + Squirrel * Feeder	11	−969.68	2.76	0.03
Feeder	7	−973.83	2.99	0.02
Avian + Feeder + Squirrel	9	−971.89	3.15	0.02
Avian + Feeder	8	−973.04	3.43	0.02
Avian + Cat + Feeder	9	−972.07	3.51	0.02
Avian + Cat + Feeder + Squirrel	10	−971.13	3.65	0.02
Avian + Squirrel + Feeder + Squirrel * Feeder + Avian * Feeder	11	−970.37	4.14	0.01
Cat + Avian + Squirrel + Feeder + Squirrel * Feeder + Avian * Feeder	12	−969.68	4.78	0.01
Squirrel + Avian + Feeder + Avian * Feeder	10	−971.75	4.88	0.01
Avian + Feeder + Avian * Feeder	9	−972.86	5.07	0.01
Cat + Avian + Feeder + Avian * Feeder	10	−971.88	5.14	0.01
Cat + Squirrel + Avian + Feeder + Avian * Feeder	11	−970.99	5.38	0.01

[a] The AIC_c value of the top model = 1958.72.

(*Aphelocoma californica*; Preston and Rotenberry 2006). In contrast, a different experiment that subsidized predators with birdseed early in the nesting season (i.e. when other food sources were not as readily available) resulted in low nest success rates near feeding stations, likely because the supplementary food attracted predators (Borgmann et al. 2013). To our knowledge, ours is the first study to provide supplementary food during the breeding season in a large-scale, diffuse manner that mirrors how residents engage in backyard bird feeding (Robb et al. 2008, Davies et al. 2009). Our results do not corroborate either of the previous findings. Rather, in our system, adding bird feeders to neighborhoods where this food resource had been lacking had no measurable effect on daily nest survival rates for our 2 focal species. The lack of consensus regarding the effect of supplementary foods on nest survival suggests that further studies and experiments across a wider geographic range and suites of potential nest predators are warranted (Robb et al. 2008).

The observational component of our work, which spanned a larger area over a longer time period, suggested that supplementary foods might have affected nest survival in some situations. Specifically, data from all 7 neighborhoods across 4 yr provided evidence that the nest survival of robins declined with higher numbers of bird feeders only where the relative abundance of crows was highest, which suggests that crows may have been attracted to areas with high numbers of bird feeders, but that birdseed did not replace robin nest contents as a food source. In neighborhoods with the highest numbers of bird feeders and relative abundance of crows, fewer than 1% of robin nests were expected to survive to fledging (i.e. to 28 days), while in neighborhoods with fewer feeders and/or fewer crows, up to 34% of robin nests were expected to successfully fledge young. Crows are adept at depredating shrub and canopy nests and were the most frequent predator of robin nests in this study system, with 53% of documented predation events attributed to this species (Marzluff and Balda 1992, Malpass 2015). Even though adult crows consumed supplementary foods such as birdseed and trash, they likely switched to foods more rich in animal protein when provisioning young, as do

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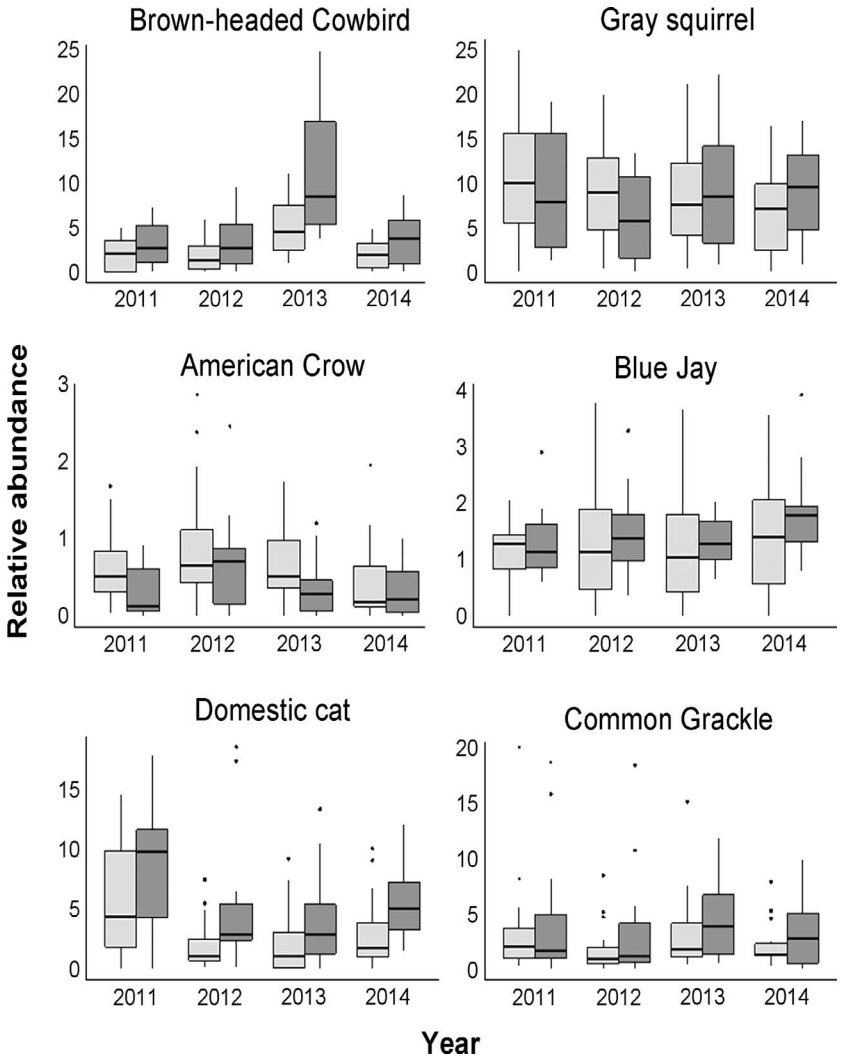


FIGURE 3. The relative abundance of 6 nest predators was highly variable among years and treatments (control = light gray, experimental = dark gray; whiskers = 1.5*IQR) in Columbus, Ohio, USA. Experimental neighborhoods were supplemented weekly with 9 kg of birdseed during April–August of 2013 and 2014.

many species that use anthropogenic foods (Pierotti and Annett 2001, Verbeek and Caffrey 2002, Kristan and Boarman 2003).

Differences in diet and vulnerability to predators may explain why the nest survival of cardinals was unrelated to either the number of bird feeders or the relative abundance of predators and showed no response to experimental supplementation. First, the diversity of species that depredated cardinal nests ($n = 10$ for cardinals vs. $n = 4$ for robins; Malpass 2015) made it unlikely that any single species, even if it responded positively to the presence of feeders, would have driven changes in nest survival rates for cardinals. Indeed, no individual species was responsible for >30% of predation events on cardinal nests in our focal neighborhoods or adjacent forest parks (Rodewald and Kearns 2011, Malpass 2015). In addition, most (>70%) documented predation of cardinal nests was attributed to species (i.e. mammals and cowbirds) that do not need to switch to natural foods during the breeding season to support growing young, as do crows. Second, bird feeders may have buffered the risk of nest predation for cardinals that directly consume birdseed, unlike adult robins (Halkin and Linville 1999, Vanderhoff et al. 2016). Access to supplementary food such as birdseed may reduce nest predation risk for cardinals by minimizing the time spent foraging or the frequency at which birds leave and return to nests (Martin 1992, Komdeur and Kats 1999, Rastogi et al. 2006, Lima 2009). Our understanding of the effects of supplementary food on predators and prey would be greatly enhanced if future research were to address both the direct and indirect effects of supplementation (e.g., through structural equation modeling or path analysis) and

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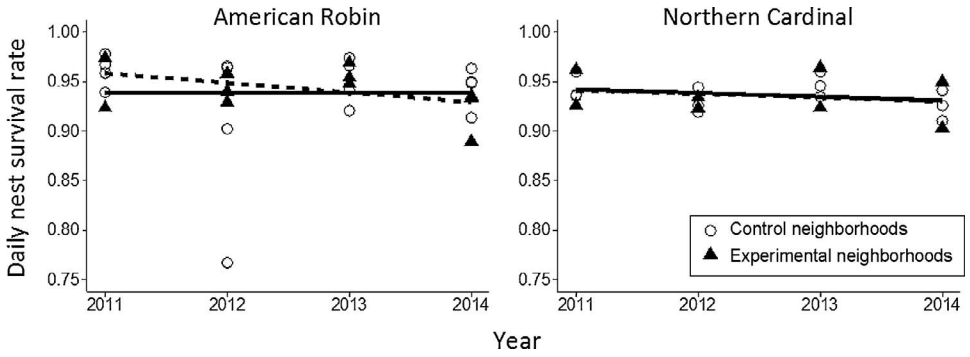


FIGURE 4. Daily nest survival rates for American Robins and Northern Cardinals were similar between control (hollow circles and solid line; $n = 4$) and experimental neighborhoods (filled triangles and dashed line; $n = 3$) in Columbus, Ohio, USA. Experimental neighborhoods were supplemented weekly with 9 kg of birdseed during April–August of 2013 and 2014.

quantify the amount of supplementary food consumed. In addition, our results suggest that supplementation over several years may be necessary to provoke measurable changes in the relative abundance of predators.

One important caveat of our work is that our use of diurnal surveys likely limited our ability to survey the full suite of species known to depredate robin and cardinal nests in our system (Rodewald and Kearns 2011, Malpass 2015). Conducting surveys at other times of day may better sample some known nest predators (e.g., at night for species such as raccoons and opossums), and using different methods may be necessary to reliably survey other species (e.g., trapping or track surveys for certain small mammals). However, the suite of 6 predators that we did include in our analyses together accounted for the majority of predation events on both robin and cardinal nests in our neighborhoods (74% and 66%, respectively; Malpass 2015), and we sampled these species sufficiently to account for detectability. In addition, although we had adequate diurnal detections for cats, future research should also consider nocturnal surveys of cats because of differences in cat movement patterns throughout the diel cycle and because avian nests may be more vulnerable to cat predation at night (Barratt 1997, Metsers et al. 2010, Thomas et al. 2014; but see van Heezik et al. 2010, Horn et al. 2011, Stracey 2011, Malpass 2015).

Bird feeding is an immensely popular activity and, although its ecological effects are only beginning to be explored, the social effects of bird feeding are usually positive (Brittingham and Temple 1992, Martinson and Flaspohler 2003, Jones and Reynolds 2008, Robb et al. 2008, Kummer et al. 2016). Residential neighborhoods provide a key venue for reconnecting city dwellers to wildlife, and urban birds are generally perceived favorably and provide a likeable link to nature (DeStefano and DeGraaf 2003, Jones and Reynolds 2008, Belaire et al. 2015). Bird feeders allow residents to more closely engage with wildlife and may help to foster environmental awareness (Galbraith et al. 2014). In addition, the development of best management practices can help to limit any potential negative ecological effects of bird feeders on birds, such as disease transmission and risk of window strikes (Fischer and Miller 2015, Kummer et al. 2016). Although results from our research suggest that providing supplementary food may not enhance nest survival for 2 species that frequently breed in residential yards in our system, the cultural benefits of bird feeding may outweigh the potential negative effects of bird feeders for common backyard birds (Jones and Reynolds 2008).

This research shows that the responses of predators and prey to bird feeders may be complex and context dependent, even if most of the species considered are known to consume birdseed. Species-specific responses of predators and prey to supplementary foods may partially explain the lack of a consistent pattern among studies of nest survival in the face of urbanization and increasing amounts of supplementary food (Chamberlain et al. 2009). In addition, while other research has shown that anthropogenic resources may dampen fluctuations in resource availability in urban areas (Shochat et al. 2006), our results provide evidence that food availability, nest predators, and nest survival may show tremendous inter- and intra-annual variation. In this way, our work highlights the fact that human-dominated environments are highly variable systems and thus may not be amenable to simple generalizations about the effects of supplementary foods on nest survival.

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Author contributions: J.S.M. and A.D.R. conceived the idea, design and experiment; J.S.M. collected data and conducted the research; and all authors analyzed data and wrote the manuscript.

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APPENDIX TABLE 4. Numbers of detections of nest predator species during diurnal surveys in residential yards in the metropolitan area of Columbus, Ohio, USA, during April–August, 2011–2014. Species in bold were included in analyses.

Nest predator species	*n*
Brown-headed Cowbird (*Molothrus ater*)	**3,376**
Common Grackle (*Quiscalus quiscula*)	**3,282**
Blue Jay (*Cyanocitta cristata*)	**3,258**
Eastern gray squirrel (*Sciurus carolinensis*)	**2,340**
American Crow (*Corvus brachyrhynchos*)	**1,776**
Domestic cat (*Felis catus*)	**526**
Eastern chipmunk (*Tamias striatus*)	217
Cooper's Hawk (*Accipiter cooperii*)	108
Red-tailed Hawk (*Buteo jamaicensis*)	81
Red-shouldered Hawk (*Buteo lineatus*)	41
Red squirrel (*Tamiasciurus hudsonicus*)	30
Raccoon (*Procyon lotor*)	14
Sharp-shinned Hawk (*Accipiter striatus*)	9
Eastern fox squirrel (*Sciurus niger*)	8
American Kestrel (*Falco sparverius*)	3
Black rat snake (*Pantherophis obsoletus*)	1
Broad-winged Hawk (*Buteo platypterus*)	1
Norway rat (*Rattus norvegicus*)	1
Striped skunk (*Mephitis mephitis*)	1

APPENDIX TABLE 5. Incidence of supplementary food resources available to avian and/or mammalian nest predators, recorded during monthly surveys in April–August of 2011–2014 in 7 residential neighborhoods in the metropolitan area of Columbus, Ohio, USA. Asterisks indicate neighborhoods in which bird feeders were added as part of a supplementary feeding experiment in 2013 and 2014; values for the numbers of bird feeders in these years reflect those provided by residents as well as researchers.

Neighborhood	Year	Bird feeder	Trash	Pet food
Casto	2011	6	0	0
	2012	11	0	5
	2013	13	0	1
	2014	12	0	0
Cherry*	2011	36	3	2
	2012	44	2	10
	2013	97	1	3
	2014	63	0	0
Elk Run*	2011	22	1	0
	2012	31	2	3
	2013	70	0	1
	2014	34	1	0
Kenny	2011	69	2	1
	2012	72	0	0
	2013	62	1	0
	2014	42	0	0
Rush Run	2011	60	0	2
	2012	80	0	2
	2013	63	0	1
	2014	40	0	0
Tuttle	2011	9	43	5
	2012	9	45	4
	2013	6	44	0
	2014	2	13	0
Woodside Green*	2011	24	0	3
	2012	24	0	4
	2013	107	0	5
	2014	80	0	0

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APPENDIX TABLE 6. Parameter estimates for the effects of feeders and predator activity on Northern Cardinal daily nest survival rates in 7 suburban neighborhoods in Columbus, Ohio, USA, 2011–2014, averaged across 11 plausible models (with $\Delta AIC_c < 2$; Table 3) to illustrate lack of certainty in parameter estimates. RI = relative importance (i.e. summed Akaike weights).

Parameter	Estimate	SE	*z*	$P(>\|z\|)$	95% CL	RI
Intercept	2.742	0.163	16.797	<0.001	2.422, 3.061	
Day of year	0.510	0.116	4.386	<0.001	0.282, 0.738	1.00
2012 [a]	−0.170	0.177	0.961	0.337	−0.518, 0.177	0.25
2013	0.112	0.188	0.595	0.552	−0.256, 0.479	0.25
2014	−0.196	0.169	1.162	0.245	−0.527, 0.135	0.25
Squirrel	−0.221	0.147	1.502	0.133	−0.510, 0.067	0.68
Cat	−0.177	0.133	1.331	0.183	−0.438, 0.084	0.44
Avian	0.179	0.178	1.008	0.313	−0.169, 0.528	0.28
Feeder	0.137	0.169	0.807	0.419	−0.195, 0.468	0.27
Feeder*Squirrel	−0.416	0.221	1.877	0.061	−0.849, 0.018	0.21

[a] 2011 was used as the reference category.

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