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Original article

Direct and indirect effects of anthropogenic bird food on population dynamics of a songbird

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ABSTRACT

Anthropogenic bird foods are frequently credited with affecting avian population dynamics, but few studies have tested this assertion over broad spatial scales. Human-derived foods could directly impact population sizes or indirectly affect them by mediating the influence of another factor, such as disease. In 1994, a novel disease outbreak (mycoplasmal conjunctivitis) substantially reduced populations of the house finch (*Haemorhous mexicanus*) in the eastern United States, creating an opportunity to test whether bird feeding indirectly exacerbated or ameliorated the impacts of the disease. We assessed the effects of bird food availability on house finch populations using data from the National Survey on Fishing, Hunting, and Wildlife-associated Recreation and the Christmas Bird Count. House finch densities were positively related to the density of people providing food for birds prior to the spread of mycoplasmal conjunctivitis, suggesting that the availability of bird seed can limit the size of finch populations. Following the disease epidemic, house finch declines were greatest where the density of people feeding birds also fell dramatically. This pattern suggests that bird food could have a positive indirect effect on disease-related mortality. Our findings suggest that the collective actions of individual people have the potential to influence resource availability and population dynamics of wildlife in human-modified landscapes.

1. Introduction

Anthropogenic foods (i.e., derived from human activity) are frequently credited with impacting population dynamics of wildlife (Adams et al., 2006; McKinney, 2006). Such supplements to natural food sources (e.g., garbage, pet food, and foods purposely provided for wildlife; Adams et al., 2006) can reduce starvation and increase reproductive output (Robb et al., 2008; Kanda et al., 2009), and are abundant and continuously available (Adams et al., 2006; Jones and Reynolds, 2008). Consequently, anthropogenic foods may affect bottom-up regulation of some populations (Faeth et al., 2005; Shochat et al., 2006). Despite the potential importance of anthropogenic food, few studies have examined its influence on populations at landscape or regional scales (Robb et al., 2008; Francis and Chadwick, 2012; but see Fuller et al., 2008).

In addition to direct demographic effects, anthropogenic foods may have indirect effects on biotic interactions (Robb et al., 2008). Clustered, predictable resources like feeding tables and bird feeders produce unnaturally high concentrations of foragers (Adams et al., 2006; Daniels and Kirkpatrick, 2006), which could lead to higher mortality rates (i.e., negative effects) by attracting predators or increasing disease transmission (Brittingham and Temple, 1986; Dunn and Tessaglia, 1994; Süld et al., 2014). Conversely, anthropogenic foods could have positive indirect effects. Such predictable and abundant resources reduce the amount of time that animals spend searching for food and exposed to predators (Brodin and Clark, 2007). For birds, larger numbers at feeders could also confer a survival advantage if collective vigilance is greater than in smaller flocks away from feeders or if the per capita risk of depredation is lower due to a dilution effect (Robb et al., 2008).

Abbreviation: FHWAR, National Survey on Fishing, Hunting, and Wildlife-associated Recreation.

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We investigated the direct and indirect effects of anthropogenic food on wildlife population dynamics in a case study involving bird feeding and the house finch (*Haemorhous mexicanus*) in the eastern United States. A native of the southwestern United States, the house finch was introduced to New York in the 1940s and has since spread throughout the contiguous United States (Elliott and Arbib, 1953; Badyaev et al., 2012). This species is an obligate granivore and in its introduced range is found primarily in association with human development where bird feeding is prevalent (Badyaev et al., 2012). These factors suggest that bird seed may be an important resource for the house finch in the eastern United States that could affect bottom-up population regulation (i.e., direct effect hypothesis).

Beginning in 1994, house finch populations were decimated by the emergence of mycoplasmal conjunctivitis (Dhondt et al., 1998), a novel infectious disease that has provided an opportunity to examine the indirect effects of bird feeding on disease-related population change. Mycoplasmal conjunctivitis is caused by a bacterium (*Mycoplasma gallisepticum*) found in domestic poultry that spread throughout house finch populations in the eastern United States in two years, causing density-dependent mortality rates of 50–70% (Hochachka and Dhondt, 2000; Badyaev et al., 2012). The disease causes swelling of ocular tissues and discharge from the eyes and is typically transmitted through direct contact between infected and healthy birds (Luttrell et al., 1998; Kollias et al., 2004). The pathogen can also survive for up to 12 h on surfaces touched by infected birds (Dhondt et al., 2007), which suggests that bird feeders could have been transmission hotspots that facilitated the spread of the disease and exacerbated the severity of the epidemic (Hartup et al., 1998; Hotchkiss et al., 2005; Hawley et al., 2007). We refer to this potential negative indirect effect as the “transmission hotspot hypothesis”.

While feeders are likely to facilitate the spread of diseases (Hotchkiss et al., 2005; Hawley et al., 2007), they could also ameliorate negative population-level effects by reducing mortality. Because mycoplasmal conjunctivitis impairs vision (Luttrell et al., 1998), predictable and abundant food resources could provide finches with the time needed to recover from the disease by preventing starvation. In addition, infections that result from eating at a contaminated feeder lead to less severe symptoms from which finches recover more quickly (Dhondt et al., 2007). Less severe symptoms and a reduction in starvation are both mechanisms that could reduce disease-related mortality, a potential positive indirect effect of bird feeding that we term the “crutch hypothesis”.

To assess the indirect and direct effects of bird feeding on house finches, we compared densities of people feeding birds in the eastern United States with estimates of house finch densities before and after the spread of mycoplasmal conjunctivitis. If anthropogenic food availability directly affects population regulation (direct effect hypothesis), then house finch densities should have been positively related to the densities of people feeding birds prior to the disease outbreak. To determine whether bird feeding had positive or negative indirect effects on house finches during the epidemic, we compared declines in house finch populations to changes in the density of people providing food for birds. If bird feeding exacerbated the negative effects of mycoplasmal conjunctivitis (transmission hotspot hypothesis), then reductions in house finch densities should have been lower where people stopped feeding birds and higher where feeder densities remained unchanged or increased (i.e., negative relationship between change in feeder density and change in house finch density). If, on the other hand, bird feeding ameliorated the population-level effects of mycoplasmal conjunctivitis (crutch hypothesis), then decreases in finch densities should have been greatest where fewer people fed birds and lower where feeder densities were consistent or increased (i.e., positive relationship).

2. Methods and materials

This study focused on 22 states in the eastern United States from 1991 to 2006 (Fig. 1). By the 1990s, all of the eastern United States had been invaded by the house finch (Dhondt et al., 1998), but states on the western and southern edges of the range expansion were not colonized until the 1980s (National Audubon Society, 2013). These more recently established populations were small and, consequently, unlikely to be food limited because of the abundance of anthropogenic foods (Adams et al., 2006). States with such populations were excluded from the study and delineated the western and southern borders of the study area (Fig. 1).

We obtained estimates of the number of people feeding birds per state in 1991, 1996, 2001, and 2006 from the FHWAR (US Census Bureau, 2013). This survey on outdoor recreational activities is sponsored by the US Fish and Wildlife Service and carried out by the US Census Bureau. The FHWAR has been conducted every 5 years since 1955, but data are only comparable from 1991 to 2006 because the survey methodology was altered in 1991. The survey consisted of screening a random sample of households (1991 – 128,000; 1996 – 77,100; 2001 – 80,000; 2006 – 85,000) to identify individuals eligible for one of two in-depth interviews conducted by phone or in person. One interview was for hunters and anglers whereas the second was for people that pursued other wildlife-related recreational activities such as watching or feeding birds. For the purposes of this study, we focused on the results from one question in the second interview—“From January 1 to December 31 [of the survey year], did you feed wild birds around your home?” (sample size by year: 1991 – 22,723; 1996 – 11,759; 2001 – 15,303; 2006 – 11,279). Responses to this question were reported in FHWAR publications as estimates of the number of people per state that fed birds in a given year (US Census Bureau, 2013). We divided these estimates by the land area of each state to obtain the density of people feeding birds per state (US Census Bureau, 2004).

We obtained an index of house finch densities in 1991, 1996, 2001, and 2006 from the Christmas Bird Count (National Audubon Society, 2013). Every year since 1900, the National Audubon Society has organized volunteers to count the number and species of all birds observed or heard within 24-km diameter circles in a 24-hr period sometime between December 14th and January 5th (National Audubon Society, 2013). There are multiple designated circles in each state ($n = 3–69$), and an index of density for a species is calculated by adjusting the number of birds detected by the cumulative number of hrs that volunteers spent searching the count circles of a given state. Data from the Christmas Bird Count were used rather than information from another national bird count (Breeding Bird Survey) because the former includes surveys of urban developments where house finches can be particularly abundant while the latter often excludes them (Badyaev et al., 2012; Sauer et al., 2012).

To assess the direct effects of bird feeding on house finch populations, we used an information theoretic approach to examine the relationship between *house finch densities* and the *density of people feeding birds* (Burnham and Anderson, 1998). For each year, we constructed three models. The first was a null model that included the intercept only and assumed no positive or negative linear relationship between the variables. The second modeled a linear relationship. The third modeled a nonlinear relationship where *finch density* increased with *feeder density* until reaching a plateau caused by density-dependent population limitation (Motulsky and Christopoulos, 2004). We used the model $y = \alpha - \alpha\beta^x$, in which α reflects the *finch density* plateau and β (which ranges from 0 to 1) determines the slope of the nonlinear

Fig. 1. Establishment of house finch populations in the eastern United States. Populations established prior to 1982 were part of this study (grey, $n = 22$ states); states with populations that were <10 years old by 1991 were too new to be included and delineated the western and southern borders of the study area (white).

curve (Ratkowsky, 1990). The model assumes the curve originates at $x = 0$, $y = 0$. We used SAS Enterprise Guide 4.3 (SAS Institute, Inc., Cary, NC) to parameterize the models. PROC GLM was used for the null and linear models and PROC NLIN was used for the nonlinear model. The latter procedure uses an iterative approach to determine parameter estimates and requires that seed values be specified (SAS Institute Inc., 2011). We specified α by plotting *finch density* against *feeder density* and estimated the plateau value based on the visualization ($\alpha_{1991} = 7$, $\alpha_{1996} = 3$, $\alpha_{2001} = 3$, $\alpha_{2006} = 3$). We arbitrarily specified β at 0.5 for all years. We ranked models by comparing AIC*c* values and assessed relative support for the models in each year using model probabilities (Burnham and Anderson, 1998). Models with AIC*c* values within four units of the top model were considered competitive (i.e., well-supported alternative models compared to the top-model). To determine the existence and type of indirect effects of bird feeding on finch populations, we tested for a linear relationship between *changes in finch density* between years to *changes in feeder density*. We constructed models for 1991 and 1996, 1996 and 2001, and 2001 and 2006. Parameter estimates are reported ± SE.

3. Results

In all four years, models in which feeder densities influenced house finch densities were supported (Fig. 2, Table 1). In 1991, the nonlinear model was superior to other models, indicating that finch density increased with the density of people feeding birds but eventually leveled off (Fig. 2). Following the spread of mycoplasmal conjunctivitis, the top model for 1996 indicated a positive linear relationship between finch and feeder densities, though the nonlinear and null models were also competitive models (i.e., <4 ΔAIC*c*). Support for the null model indicated that the relationship between finches and feeders was weak in 1996. House finch numbers were substantially reduced from 1991 to 1996; in the

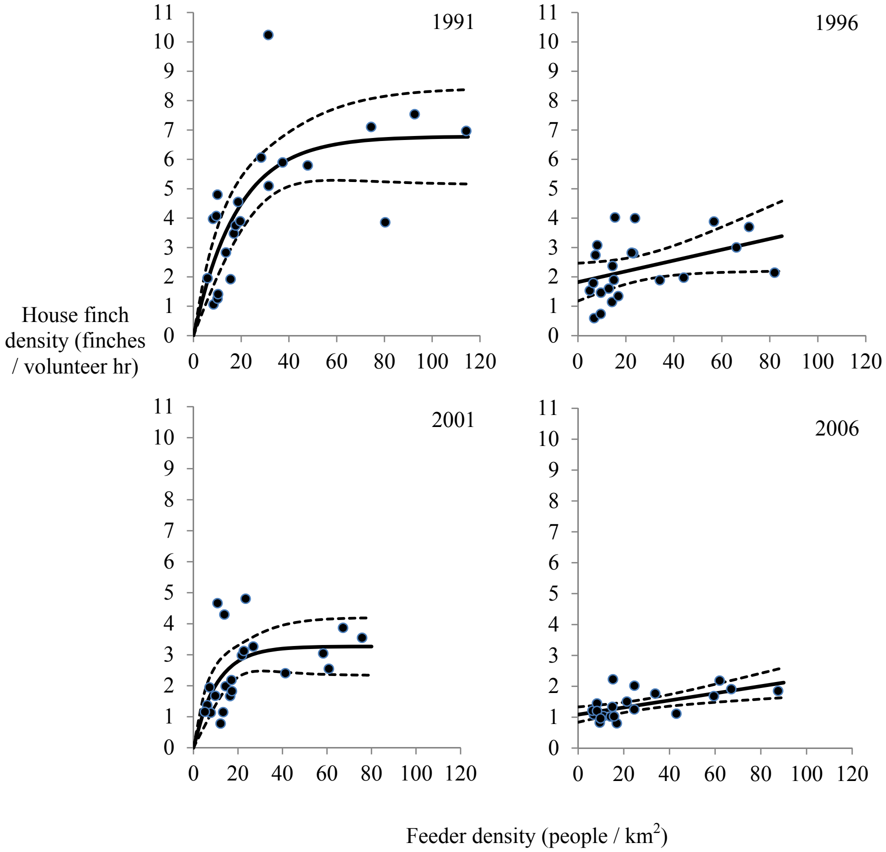

Fig. 2. Effect of feeder density on house finch density every 5 years from 1991 to 2006 in the eastern United States ($n = 22$ states). Solid lines are the best supported predictive model from a candidate set that included a null (intercept only), linear, and nonlinear model. Dashed lines are the 95% CL of the predictive line.

nonlinear model for 1996 (Table 1), the asymptote for finch densities (2.90 ± 0.37) was nearly half that of the plateau in 1991 (6.78 ± 0.79), and the confidence limits of the estimates did not overlap (Table 1). In 2001, the relationship between feeders and finches was still weak since the null model was competitive, though the null model was not as well supported as the linear and nonlinear models. The plateau for house finch density in the nonlinear model was similar to that from 1996 (3.27 ± 0.45; confidence limits overlapped; Table 1). In 2006, only the linear model was well supported (Fig. 2, Table 1), so the 2006 nonlinear model plateau could not be compared to that from previous years (maximum finch density did not exceed 2.25).

Table 1
Model comparison of the effect of feeder density (people/km^2) on house finch density (finches/volunteer hr; $n = 22$). Included are the number of parameters modeled (k; for nonlinear models, the number of parameters includes an estimate of the residual sum of squares), a comparison of the top model from each year to the other models (ΔAIC*c*), and the probability a given model is the top model for a particular year (w). A parameter estimate, SE, and 95% CL were included for the slope of the linear model and the asymptote of the nonlinear model.

	k	ΔAIC*c*	w	Estimate	SE	95% CL	
						Lower	*Upper*
1991							
Nonlinear	3	0.00	0.907	6.782	0.790	5.134	8.429
Linear	2	4.60	0.091	0.045	0.013	0.017	0.073
Null	1	11.84	0.002	–	–	–	–
1996							
Linear	2	0.00	0.509	0.018	0.009	0.000	0.037
Nonlinear	3	1.22	0.277	2.896	0.368	2.129	3.663
Null	1	1.73	0.214	–	–	–	–
2001							
Nonlinear	3	0.00	0.444	3.267	0.447	2.335	4.198
Linear	2	0.22	0.398	0.024	0.011	0.000	0.047
Null	1	2.07	0.157	–	–	–	–
2006							
Linear	2	0.00	0.908	0.011	0.003	0.004	0.019
Nonlinear	3	5.18	0.068	1.721	0.155	1.398	2.044
Null	1	7.31	0.023	–	–	–	–

The change in house finch densities was positively related to changes in feeder densities between 1991 and 1996 (Table 2, Fig. 3; linear slope $= 0.09 \frac{\Delta \text{ finches / volunteer hr}}{\Delta \text{ people / km}^2}$, $F_{22,1} = 5.35$, $P = 0.03$). Changes in finch densities were unaffected by changes in feeder densities from 1996 to 2001 ($F_{22,1} = 3.04$, $P = 0.10$) and from 2001 to 2006 ($F_{22,1} = 0.13$, $P = 0.72$).

4. Discussion

The availability of bird food appeared to have a positive direct effect on house finch populations. Prior to the outbreak of mycoplasmal conjunctivitis, the density of finches was strongly related to the density of people providing food for birds, though finch density leveled off beyond 40 feeders/km^2. This nonlinear

Table 2
Linear relationship of the change in feeder density (people/km^2) and the change in house finch density between years (finches/volunteer hr; $n = 22$).

	Parameter estimate	SE	*F*	*P*	r^2
1991–1996	0.089	0.038	5.35	0.0315	0.211
1996–2001	−0.085	0.049	3.04	0.0966	0.132
2001–2006	−0.020	0.056	0.13	0.7232	0.006

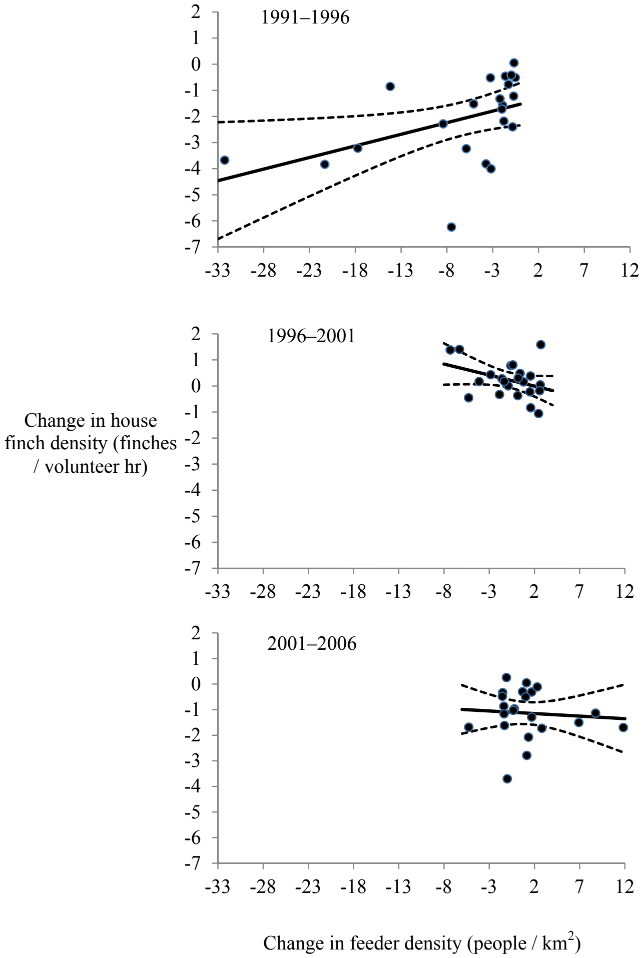

Fig. 3. Effect of changes in feeder density on changes in house finch density between time periods ($n = 22$ states). Solid lines are the predicted linear model and dashed lines are the 95% CL.

relationship suggests that bird seed is a heavily utilized resource for house finches—to the point that it limits their numbers where feeder densities are low. Where feeders are more abundant, finch densities increase until density-dependent factors such as intraspecific competition limit further population growth. Even after mycoplasmal conjunctivitis substantially reduced finch numbers, feeder density still affected finch density, particularly in 2006. These findings provide evidence for the direct effect hypothesis because our study was a conservative test—our proxy for food availability did not address the types or amount of food provided by people nor the frequency with which it was replenished, all of which could have weakened the effect of feeder density on finch density.

An alternative explanation for these patterns is that house finch densities are driven by habitat availability rather than simply the abundance of anthropogenic food. The number of people that feed birds increases with urbanization (Lepczyk et al., 2004), which suggests that the density of feeders could be a proxy for urban land cover (the preferred habitat of house finches in the eastern United States; Badyaev et al., 2012). However, if habitat availability determined house finch densities, then the relationship between finch numbers and people feeding birds should have been linear rather than nonlinear, as more habitat should support larger house finch populations.

We found limited support for indirect effects of bird feeding on disease-related mortality. The transmission hotspot hypothesis proposed that bird feeders could contribute to disease-related mortality because house finches transmit mycoplasmal conjunctivitis at bird feeders, diseased birds spend more time at bird feeders, and feeders lead to high concentrations of foraging finches (Hotchkiss et al., 2005; Dhondt et al., 2007; Hawley et al., 2007). We did not observe the predicted negative relationship between changes in finch densities and changes in feeder densities though (i.e., reductions in finch numbers were not smaller where the number of people feeding birds declined more). Instead, we found a positive relationship between changes in finch densities and changes in feeder densities between 1991 and 1996 that substantiated the crutch hypothesis. Despite the fact that feeders facilitate transmission of mycoplasmal conjunctivitis, feeders provide a predictable source of food that could reduce starvation rates (Robb et al., 2008). In addition, infections from contaminated food are less severe than infections from direct contact with diseased birds (Dhondt et al., 2007). Consequently, feeders may function as inoculation stations where birds become infected but are more likely to survive than if feeders were absent.

The positive indirect effect of feeders was not observed from 1996 to 2001 or 2001–2006. Perhaps positive indirect effects are only evident beyond a threshold of change in feeder densities, as numbers fluctuated much more from 1991 to 1996 than in other years. Alternatively, the observed pattern may have been produced in part or in whole by a direct effect rather than an indirect one. From 1991 to 1996, the number of people feeding birds nationwide dropped from 63.1 million to 52.2 million and has only increased by 1.1 million since (US Census Bureau, 2013). The cause of the decline is unknown, but the 17% decrease in number of feeders could have led to a loss of house finches due to starvation, particularly in areas where decreases in feeder numbers were greatest.

While many researchers have suggested that anthropogenic food could affect population dynamics of birds (Marzluff, 2001; Shochat et al., 2006), most studies have been conducted at spatial scales that were too small to provide unambiguous support for this assertion (Robb et al., 2008). Some have shown that the relative abundance of certain species is greater at sites where anthropogenic foods are more abundant (Wilson, 1994; Martinson and Flaspohler, 2003; Daniels and Kirkpatrick, 2006; Parsons et al., 2006), but these patterns could be explained by altered habitat use in response to the distribution of food rather than changes in population size. Other studies have found that when natural diets are supplemented, birds survive longer or have greater reproductive output, but increases in survival or fecundity may not last beyond one or two years or be counteracted by reductions in survival in different life stages (Robb et al., 2008). Nevertheless, the few studies that have been carried out at landscape scales suggest that anthropogenic food does affect population dynamics. For example, in the city of Sheffield, England, variation in the density of bird feeders throughout the city predicts the abundance of species that use feeders (Fuller et al., 2008).

Our study provides additional evidence that anthropogenic food can affect population dynamics, which could in turn have profound ramifications for community structure through interspecific interactions (Robb et al., 2008; Süld et al., 2014). For example, eastern populations of house finches that are supported by bird feeding could negatively impact other species. House finches displace American goldfinches (*Spinus tristis*) at bird feeders (Badyaev et al., 2012) and spread mycoplasmal conjunctivitis to species such as house sparrows (*Passer domesticus*) and American goldfinches (Ley et al., 1997; Hartup et al., 2001; Dhondt et al., 2013). In addition, house finches are frequently preyed upon by *Accipiter* hawks, small falcons, and cats (Dunn and Tessaglia, 1994), raising the possibility that greater numbers of house finches could support larger populations of predators that could increase predation pressure on other prey species (i.e., apparent competition; Bonsall and Hassell, 1997). Consequently, large-scale changes in bird feeding practices have the potential to affect wildlife communities by altering population sizes of some species and mediating their impacts on other species (Galbraith et al., 2015).

5. Conclusions

Our study is part of a growing body of literature that describes how collective actions of people can affect populations and communities of wildlife (Cannon, 1999; Goddard et al., 2010; Lerman and Warren, 2011). Individual decisions to allow pet cats outdoors, to landscape yards to benefit wildlife, or to provide food for wildlife are compounded across landscapes and can result in broad-scale changes in predation and resource availability (Lepczyk et al., 2004), though the motivations leading to these decisions are highly varied and remain poorly understood (Howard and Jones, 2004). In a world where the extent and rate of human development is expected to increase, the future of biodiversity and ecological functioning will clearly be influenced by the decisions of individuals (Goddard et al., 2010).

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