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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