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Nest usurpation by non-native birds and the role of people in nest box management

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Abstract
Invasive species are a threat to global biodiversity, yet the impacts of invasive birds on the native birds with which they compete are understudied. Humans have a long history of providing and managing nest boxes to support native birds; however, their management of non-native birds has received limited research attention. We surveyed people who maintain nest boxes in North America to examine the extent of interference competition for nest sites between native and non-native birds and the human behaviors intended to reduce nest site competition. Our specific objectives were to examine observations of nest usurpation of native birds by non-native birds across the United States and Canada, to ascertain whether and how people who maintain nest boxes control non-native bird species in favor of native species, and to quantify various factors correlated with the likelihood of engaging in management activities. We found that nearly one-third of the 871 respondents had observed a non-native species usurp a nest box occupied by a native species. Among respondents who reported nest usurpations, species-specific nest usurpation rates varied (range = 3–35%). We found that witnessing a nest usurpation is the most important predictor of whether or not someone will engage in management activities. Management activity was also associated with the extent to which respondents believed non-native birds to be a problem at the continental scale. Our study shows that people's observations of threats from introduced species are correlated with the environmental management actions people take, and that these actions can mitigate the threats, and potentially support the survival of native birds.

KEYWORDS
citizen science, conservation behaviors, European Starling, House Sparrow, NestWatch

1 | INTRODUCTION

Approximately 85 species of birds in North America are known to use cavities for nesting (Scott, Evans, Patton, & Stone, 1977), and bird enthusiasts and wildlife managers have long been supplementing nesting birds with artificial cavities (i.e., nest boxes) in order to attract more birds to cavity-limited areas (Froke, 1983; Jackson & Tate,
1974; Newton, 1994). Although data on private nest box ownership are limited, recent survey work in the United States and Canada suggests that 48–61% of households that feed birds may also supplement birds with nest boxes (Horn & Johansen, 2013; Martin, Mady, Dayer, & Bonter, unpublished data). If 57.2 million American households feed birds (U.S. Department of the Interior USFWS, U.S. Department of Commerce USCB, 2016), then potentially 27.4–34.9 million are supplementing nests with nest cavities, a nontrivial contribution with the potential of restructuring cavity-nesting bird communities, particularly in urban areas (Tomasevic & Marzluff, 2017). Moreover, since at least the 1960s, people providing nest boxes have been experimenting with methods to optimize breeding success by limiting predation, competition, and weather-related nest failures through modifications to nest-box designs (Bailey & Bonter, 2017; Bolen, 1967; Kibler, 1969; Raleigh, Ray, Grisham, Siegrist, & Greene, 2019). People managing nest boxes express interest in making science-based management decisions to better support nesting birds (Hvenegaard & Perkins, 2019; Larson, Cooper, & Hauber, 2016; Phillips, Ballard, Lewenstein, & Bonney, 2019; Raleigh et al., 2019). Additionally, citizen scientists—volunteers collaborating in professional scientific research—contribute substantially to the literature on nesting ecology and to the conservation of cavity-nesting birds (Cooper, Bailey, & Leech, 2015; Hvenegaard & Perkins, 2019; Phillips & Dickinson, 2009; Raleigh et al., 2019).

Nest site competition from invasive birds can reduce the opportunities for successful nesting by native cavity-nesting birds (Aitken & Martin, 2008; Strubbe & Matthysen, 2009; Weitzel, 1988). There are two widely accepted types of competitive interactions for limited resources that may also govern cavity use: interference competition, wherein one bird physically prevents another from using a nest site through acts of aggression, and exploitation competition, wherein a bird uses a cavity, thereby making it unavailable for other individuals, without necessarily interacting with others (Dhondt, 2012; Park, 1954). Two of the most widespread invasive cavity-nesters in North America are the European Starling (Sturnus vulgaris) and House Sparrow (Passer domesticus), both native to Europe, southwest Asia, and northern Africa (Cabe, 1993; Lowther & Link, 2006). Originally introduced into the United States from Europe in the mid to late 1800s, European Starlings and House Sparrows were ubiquitous breeding birds throughout most of the United States and southern Canada, and elsewhere, by the mid-20th century (Cabe, 1993; Lowther & Link, 2006). Within their native range, both House Sparrows and European Starlings are effective competitors for nest cavities, via both interference (Goldshtein, Markman, Leshem, Puchinsky, & Charter, 2018; Van Balen, Booy, Van Franeker, & Osieck, 1982) and exploitation (Charter, Leshem, & Izhaki, 2013) competition. Both species also readily nest in supplementary nest boxes and will compete with a variety of primary and secondary cavity-nesting birds for nest sites throughout the United States and Canada, particularly in urban areas (Tomasevic & Marzluff, 2017). Competition for nest sites with European Starlings and House Sparrows has been implicated in population declines of some native cavity-nesting birds in North America (Brown & Tarof, 2013; Estabrook, 1907; Linz, Homan, Gaulker, Penry, & Bleier, 2007; Zeleny, 1976) and negative impacts elsewhere in the introduced range (Burger, 1976; Pell & Tidemann, 1997).

Numerous researchers have documented competition between European Starlings and native cavity-nesting birds throughout their introduced range (Fisher & Wiebe, 2006; Kalmbach & Gabrielson, 1921; Kerpez & Smith, 1990; Pell & Tidemann, 1997; Weitzel, 1988). Likewise, local-scale studies document cases of House Sparrows interfering with the nesting of native species (Burger, 1976; Gowaty, 1984). Despite the published and anecdotal evidence of competition at the local level, studies examining population-level effects are rare (Baker, Harvey, & French, 2014). In one such study, Koenig (2003) examined large-scale census data from two sources, but failed to unambiguously connect the European Starling invasion to significant declines in populations of native cavity-nesting bird species. In short, there are insufficient documented observations of interference competition between native and non-native species to inform management action (Callaghan, Martin, Kingsford, & Brooks, 2018).

Along with meta-analyses from different studies, citizen science may be another useful tool for quantifying nest site competition at a large spatial scale (Callaghan et al., 2018). People who maintain nest boxes are well suited to record nest site competition given that as many as 85% of them may already be recording nesting observations (Hvenegaard & Perkins, 2019). NestWatch (NestWatch.org) is a citizen-science project that engages the public to submit information about the reproductive success of nestling birds (Phillips & Dickinson, 2009). Participants submit details on the nesting attempts of birds including the species, location, number of eggs, number of hatched young, egg-laying phenology, hatch dates, and outcome of the nesting attempt, among other variables. In cases where nests were lost to interference competition, monitors might note the presence of a new nest on top of a previously existing nest in an occupied box, resulting in a nest failure (evidenced by, e.g., broken eggs buried in nest material or dead nestlings on the ground
below the box). It is common for people who witness such competition between native species to try to accommodate both species by adding more nest boxes in an approach known as pairing (Gowaty & Plissner, 2015; Stanback, Niemasik, Millican, & McGovern, 2019). However, when competition for a nest box involves a non-native species and a native species, it can elicit a very different emotional response (Larson et al., 2016).

An observer's concern for the survival of native birds may drive management activities designed to limit the impact of non-native species. These activities may include a variety of active and passive management actions targeting non-native species, such as trapping and euthanasia, removing nests or eggs, shooting adults, or modifying the nest box (Larson et al., 2016). We define active management as lethal techniques such as euthanizing birds (Grarock, Tidemann, Wood, & Lindenmayer, 2014; Weitzel, 1988), removing nests or eggs, oiling or adding eggs (Fernandez-Duque, Bailey, & Bonter, 2019; Hindman, Harvey, & Conley, 2014), and we define passive management as nonlethal techniques, such as reducing entrance hole sizes to exclude unwanted species based on body size (Charter, Izhaki, Ben Mocha, & Kark, 2016). Invasive bird management is legal (i.e., no permit necessary) under the Migratory Bird Treaty Act of 1918 in the United States and the Migratory Birds Convention Act of 1994 of Canada, both of which only protect species native to North America.

To understand the potential effects of interference competition by non-native birds on native cavity-nesting species at the continental scale, we conducted a survey of people who maintained nest boxes throughout the United States and Canada. Our specific objectives were to use survey responses to examine observations of nest usurpation of native birds, to ascertain whether and how people who maintain nest boxes control non-native species, and to identify factors that may influence the management activities of people who maintain nest boxes. For our third objective, we were also interested in quantifying whether active engagement in the NestWatch citizen-science project correlated with an individual's likelihood to undertake management actions.

2 | METHODS

This study employed a pre-/post-survey design that was implemented at the beginning and the end of the 2018 nesting season (i.e., March and September). The questions presented here formed part of a larger survey of adults over the age of 18 years who maintain at least one nest box in North America for cavity-nesting birds. The study received approval from Cornell University’s Institutional Review Board (Protocol #1803007815).

2.1 | Survey instrument

We developed the survey questions to address gaps in the conservation literature, especially of the effects of invasive species on native cavity-nesting birds, conservation behaviors, and the methods by which people manage nest boxes, following best practices for internet survey design (Dillman, Smyth, & Christian, 2014). The coauthors have collective expertise in nest box monitoring, survey design, citizen science evaluation, and NestWatch. We pretested the survey questions with eight volunteers consisting of people who monitor nest boxes, birdwatchers, and ornithologists. Following their feedback, we made minor changes to improve the clarity of the questions.

The surveys were conducted online using the Qualtrics survey platform (qualtrics.com). The pre-nesting season survey contained information about the study and informed participants that their participation was voluntary and anonymous. Each respondent was required to give consent to participate in the study prior to the start of each survey. Both pre- and post-surveys asked detailed questions about observations of usurpation events by non-native species, management actions, skills at identifying non-native species, confidence in identifying cavity-nesting birds, and enjoyment of different bird species or species groups (see Supporting Information for the full survey instruments). The relevant survey items for the current study are excerpted in Table 1 and include demographics of the respondents (pre-survey Questions 21 and 22); experience in monitoring nest boxes (pre-survey Question 5a; post-survey Question 5); management actions undertaken by the respondents (post-survey Questions 15, 17, and 19); observations of non-native species displacing native species using nest boxes (post-survey Questions 13 and 16); and perception of how much of a problem non-natives are (post-survey Question 20). We determined participation in NestWatch by comparing email addresses of respondents with those who had contributed at least one nest record to the NestWatch database. We included the NestWatch participation variable because behaviors directed at invasive (or native) species may be influenced by citizen science participation, which may reflect people's level of ecological knowledge (Bonney et al., 2009; Brossard, Lewenstein, & Bonney, 2005; Larson et al., 2016). Age and gender were included because evidence suggests that participation in NestWatch and similar citizen-science projects is skewed towards females and
TABLE 1  Relevant survey questions used in the analyses are excerpted from the pre- and post-nesting season survey documents for convenience (see Supporting Information for the full survey instruments)

| Variable | Pre-survey questions |
|----------|----------------------|
| Total years of experience monitoring nest boxes | 5a. For approximately how many combined total years have you been monitoring nest boxes? |
| Gender | 21. Which gender do you identify as? |
| Age | 22. In what year were you born? |
| Post-survey questions | |
| Total number of nest boxes monitored | 5. How many nest boxes did you monitor in the 2018 nesting season? |
| People who reported a non-native species taking over a native species’ nest | 13. The remaining questions are concerned with the non-native (i.e., invasive) bird species, House Sparrow, and European Starling. Sometimes these birds compete with native birds over nest boxes. A nest that has been “taken-over” can involve the non-native species removing or harming any eggs, chicks, or adults of a native species, removing nest contents, and/or building their nest over the original nest. During the 2018 nesting season, did you have an occupied nest of a native bird taken over or destroyed by a House Sparrow or European Starling? |
| Proportion of nests usurped | “Yes” → |
| Management group (active, passive, none) | 15. During the 2018 nesting season, did you intentionally prevent any non-native (i.e., invasive) birds from nesting in your boxes? Passive management = techniques employed before a bird is seen (e.g., using a Sparrow Spooker or starling-resistant entrance hole); active management = techniques done in response to seeing the bird (e.g., trapping birds or removing nests or eggs) |
| Summary of active techniques | “Yes, actively manage” or “yes, actively and passively manage” → |
| Summary of passive techniques | “Yes, passively manage” or “yes, actively and passively manage” → |
| Perception of the invasive species problem | 20. How much of a problem do you think non-native birds are for native birds in North America? |

older adults (Dayer et al., 2019; Hvenegaard & Perkins, 2019; Larson et al., 2016).

2.2  |  Survey administration

A convenience sampling method (Bryman, 2012) was employed to recruit respondents from two groups, people who were participating in NestWatch, and people who monitor nest boxes but do not take part in the NestWatch project. Invitations to take the pre-survey were sent via email on March 14, 2018 to all electronic newsletter subscribers who opted-in to receiving email communications from NestWatch (n = 43,805). To reach people who monitor nest boxes but do not participate in NestWatch, we shared the survey on Facebook on March 15, March 28, and April 12, 2018. Two interest groups whose members engage in nest monitoring (North American Bluebird Society and The Peregrine Fund’s American Kestrel Partnership) also distributed the survey to their members.
via Facebook. We estimate that the Facebook invitations (combined) potentially reached ~61,750 people, but actual reach is unknown due to privacy protections.

We sent reminders on March 22 and April 26, 2018 via the NestWatch electronic newsletter. We included a downloadable report form at the end of the pre-survey, inviting all respondents to keep track of any non-native birds that usurped the nests of native birds in their nest boxes during the upcoming 2018 nesting season (see Supporting Information). Respondents were directed to use this form to record the nesting activity of invasive species and to assist with completing the post-survey. We closed the pre-survey on May 1, 2018. Only those respondents who completed the pre-survey received a follow-up email invitation to take the post-survey on September 27, 2018, after the nesting season was completed across most of North America. We sent three subsequent reminders to those who had not completed the post-survey. The post-survey was closed on October 26, 2018. The surveys were designed to take approximately 15 min each and were available in English only. We incentivized completion of both surveys by offering a random drawing for a Zeiss Terra ED binocular valued at $400. In order to be entered to win the prize, participants had to consent to and complete both surveys.

The pre-nesting season survey was opened by 2,604 people. It is impossible to determine a true response rate for the respondents who were recruited through the social media posts and forwarded emails since the total population size is unknown, but the maximum possible response rate of completed surveys (not including duplicates) is 5.7%. We removed 370 responses in total: 244 were incomplete, 104 were duplicates, 20 did not consent to the study, and 2 were deemed unreliable due to irregularities in their responses, resulting in a total of 2,234 useful responses. For the post-survey, 2,231 people were successfully invited (three people were dropped due to invalid email addresses). Of these, 1,051 people opened the survey link (47.1% response rate). After removing those who did not monitor at least one nest box \((n = 177)\) and three additional responses with irregularities, our final analysis file included 871 respondents who met the minimum criteria for inclusion in subsequent analyses.

2.3 Analytical methods

To examine the potential effects of non-native species on the reproductive efforts of native species, and to examine how respondents reacted to observations of non-native species in their nest boxes, we limited our analyses to those respondents who answered affirmatively that they found a nest in their nest box(es) in the 2018 nesting season and followed its progress through the nesting cycle (post-nesting season survey Question 4); in this way, monitoring a nest (as opposed to simply cleaning a box annually) is a precondition for inclusion.

In the interest of survey brevity and higher completion rates, participants who reported no native species’ nests being usurped by a non-native species in 2018 were not asked about the total number of nests of each species they monitored. Therefore, we were unable to examine true nest usurpation rates, and we instead focus on the relative impact of European Starlings and House Sparrows on different species groups. To test for differences among native species regarding nest usurpation by European Starlings and House Sparrows, we first calculated the proportion of nest attempts by the host species that were usurped by the non-native species at sites reporting at least one takeover for any nesting attempt. We then used paired \(t\) tests across all sites reporting the host species to test for differences in the incidence of total nest usurpation events by European Starlings and House Sparrows targeting each host species.

Next, we modeled the performance of seven variables in predicting a person’s decision to manage invasive species (logistic regression, binary response = manages/does not manage). Of the seven predictive variables included, three focused on engagement in the activity of monitoring nest boxes (total number of nest boxes monitored, total years of experience monitoring nest boxes, and participation in NestWatch [binary yes/no]), two were demographic (age and gender), and two were experiential (whether or not they recorded the nest of a native species being usurped by a non-native species in 2018 [binary yes/no], and their perception of invasive species’ effects on native birds [7-point scale, ranging from 1 = “Not a significant problem” to 7 = “An extremely significant problem”]). If respondents answered “unsure” with regards to whether or not they observed a nest usurpation (Question 13, Table 1), they were removed from the analysis so that only those who were confident in having witnessed a usurpation (or not) were included; this resulted in a loss of 34 respondents from the logistic regression analyses. We assessed potential multicollinearity among predictor variables by examining the variance inflation factors (VIF) and bivariate correlation coefficients using a threshold of VIF < 10 and \(|r| < .80\) (Chatterjee & Hadi, 2006). We found no strong evidence of multicollinearity (all VIF < 2; all pairwise \(|r| < .77\)). A Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 2000) was conducted and confirmed acceptable model fit \((χ^2 = 13.77, p = .088)\).

To assess whether there were differences in those who managed invasive species using either passive or
active approaches, we constructed a similar logistic regression model as above, but with the response variable limited to only those who managed actively or passively (binary response). Respondents who indicated that they engage in both active and passive management actions were classified as active managers for this analysis. We assessed potential multicollinearity among the same predictor variables by examining the VIF and bivariate correlation coefficients for this reduced sample and found no strong evidence of multicollinearity (all VIF < 2; all pairwise $|r| < .80$). A Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 2000) was again conducted to confirm appropriate model fit ($\chi^2 = 7.67, p = .467$). All analyses were conducted using SAS 9.4 (SAS Institute, Cary, NC).

3 | RESULTS

Of the 871 respondents who observed nests in boxes during the 2018 nesting season, 59% were female and 41% were male. The majority (70.5%) had not submitted data to the NestWatch citizen-science project. The average age of respondents was 61.0 years ($n = 809, SD = 12.9$). Their involvement in monitoring nest boxes was substantial, with an average of 10.4 years ($n = 807, SD = 9.4$) of experience and 15.9 nest boxes monitored ($n = 871, SD = 38.6$). Respondents ranked non-native birds as a problem for native birds in North America (mean score = 6.1 out of a possible 7, $n = 834, SD = 1.1$). Of the 845 people who answered the question about whether they managed the non-native occupants of nest boxes, 36.9% said they did not, 17.3% managed passively, 29.0% managed actively, and 16.8% managed both actively and passively. Of the 212 respondents who witnessed a non-native species usurp the nest of any of our focal native species (see Figure 1 for complete list of focal native species) and engaged in active management techniques, the majority (78.3%) managed the invasive species by removing the nest from the box. Less common management techniques included removing the eggs of the invasive species (55.1%), trapping and euthanizing the adults of the non-native species (33.4%), or adding or oiling the eggs to prevent hatching and then returning the eggs to the nest box (0.1%). Based on content analysis of open-ended responses regarding passive management techniques ($n = 246$), the three most popular passive approaches were the use of appropriately sized entrance holes to exclude starlings and sparrows (69.5%), the use of so-called “Sparrow Spooker” devices (18.7%; e.g., see www.sialis.org/sparrowspooker.htm), and monofilament (i.e., fishing) line attached to nest boxes to deter sparrows (8.1%; e.g., see www.sialis.org/hosp.htm#monofilament).

**FIGURE 1** Proportion of nest attempts by native host species usurped by non-native European Starlings and House Sparrows. Nest samples: $n = 3,156$ bluebird (Sialia sp.); $n = 1,468$ Tree Swallow (T. bicolor); $n = 412$ Purple Martin (Progne subis); $n = 81$ American Kestrel (F. sparverius); $n = 439$ House Wren (T. aedon); $n = 19$ Northern Flicker (Colaptes auratus); $n = 164$ chickadee (Poecile sp.); $n = 37$ titmouse (Baeolophus sp.); and $n = 46$ Bewick’s/Carolina Wren (Thryomanes bewickii/Thryothorus ludovicianus). Asterisks above columns indicate results of the tests for differences in the proportion of species (or species group) nests usurped by European Starlings and House Sparrows ($t$ tests, no asterisk indicates $p > .05$, * = $p < .05$, ** = $p < .01$).
3.1 Nesting impacts and management behavior

A total of 264 respondents (30.3%, \(n = 871\)) reported observing the nest of a native species of bird being usurped by the nest of either a House Sparrow or European Starling in 2018. Respondents who were unsure or failed to answer whether they had observed a nest usurpation (6.9%) were excluded from further analysis. Among these, 264 people who monitored 5,820 nests, the percentage of nest attempts usurped varied by species, ranging from 2.7 to 35.3% (Figure 1). House Sparrows were more likely than European Starlings to usurp nests of bluebirds (\(Sialia\) sp.), Tree Swallows (\(Tachycineta bicolor\)), House Wrens (\(Troglohytes aedon\)), and chickadees (\(Poecile\) sp.), while observers documented American Kestrels (\(Falco sparverius\)) experiencing more takeovers from European Starlings (paired \(t\) tests comparing usurpation rates by House Sparrows and European Starlings, all \(p \leq .05\), Figure 1).

In the logistic regression analysis of factors affecting a person’s decision to manage invasive species’ nests or not (\(n = 700\), of which 436 respondents managed), people who reported a non-native species taking over a native species’ nest were more likely to engage in either passive or active management (\(\chi^2 = 77.57, p < .001\); Figure 2). The likelihood of managing invasive species was greater for those participating in NestWatch than for people who did not participate in the citizen-science project (\(\chi^2 = 9.10, p = .003\)). People were more likely to engage in management as their perception of the invasive species problem increased (\(\chi^2 = 10.06, p = .002\)). Management action was not related to total number of nest boxes (\(\chi^2 = 1.07, p = .301\)), age (\(\chi^2 = 3.6, p = .549\)), gender (\(\chi^2 = 1.68, p = .195\)), or total years of experience monitoring nest boxes (\(\chi^2 = 3.6, p = .547\)).

In the logistic regression analysis of factors differentiating active versus passive management approaches (\(n = 436\), of which 318 respondents actively managed), people who had experienced a non-native species taking over a native species’ nest were more likely to engage in active management than passive management (\(\chi^2 = 37.01, p < .001\); Figure 3). As perception of the severity of the invasive species problem increased, respondents were more likely to actively than passively manage (\(\chi^2 = 5.16, p = .023\)). Total number of boxes (\(\chi^2 = 3.32, p = .068\)), age (\(\chi^2 = 3.29, p = .070\)), gender (\(\chi^2 = .008, p = .929\)), total years of experience (\(\chi^2 = 1.33, p = .249\)), and participation in NestWatch (\(\chi^2 = .23, p = .628\)) were not correlated with approach to management.

**FIGURE 2** Probability that a person monitoring nest boxes will undertake management actions to reduce the nesting success of non-native species. Data show predicted values (±95% confidence intervals) from the logistic regression model examining factors potentially associated with management decisions (\(n = 700\) survey respondents)

**FIGURE 3** Probability that a person monitoring nest boxes will undertake active management actions (as opposed to passive management techniques) to reduce the nesting success of non-native species. Data show predicted values (±95% confidence intervals) from the logistic regression model examining factors potentially associated with management behavior (\(n = 436\) survey respondents)
**4 | DISCUSSION**

We found that nearly one-third of respondents reported witnessing a non-native bird species usurp the nest of a native species, causing failure of the reproductive attempt. Thus, interference competition over nest sites may be a significant source of nesting failure for native cavity-nesting species in North America. While quantifying the population-level impacts of this competition is difficult, our survey highlights the need to examine competition for nest sites more closely, particularly concerning reproductive efforts in natural cavities. Because our study explicitly focused on birds nesting in nest boxes provided by people, the rates of nest usurpation may not be indicative of the pressure faced by native birds in more natural situations. Rather, passive approaches to nest box management, such as restricting the diameter of the entrance hole, may reduce competition for these cavities, particularly competition from the relatively large European Starling. Alternatively, nest boxes may be more visible, densely distributed, or closer to anthropogenic sources of food than natural cavities, making birds nesting in boxes more frequent targets for competition from non-native species. Attempts to quantify population-level effects of nest usurpation by non-native species will require standardized nest monitoring at large spatial scales. While informative, extrapolation of our survey results is limited because we do not have data on the total numbers of nests monitored by people who did not witness usurpation events. Further, it is possible that people were more likely to respond to the survey if they witnessed a nest usurpation event.

Our results demonstrate variability in the intensity of nest usurpation experienced by native species, as well as frequency of interference by the two non-native species examined. Variability in nest usurpation is probably related to a variety of factors. Potential factors may include timing of breeding, nest entrance size, and characteristics of the native species (e.g., mass, aggressive behavior, social behaviors; Merilä & Wiggins, 1995; Charter et al., 2013; Goldshtein et al., 2018). For example, chickadees are year-round residents and tend to nest earlier in the breeding season than migratory House Wrens and Purple Martins (*Progne subis*), which both tend to nest later in the season. It is possible that the latter two species suffered lower rates of nest usurpation by House Sparrows (3.9 and 3.4%, respectively, compared to 15.9% for chickadees) due to their tendency to nest later in the season, after House Sparrows have selected other cavities. We did not test these hypotheses, but future study warrants such investigation, which may be possible with data generated by citizen scientists.

Northern Flicker (*Colaptes auratus*) and American Kestrel experienced the highest total rate of usurpation (35.3 and 23.0%, respectively), an intriguing finding considering these two species are experiencing widespread population declines (Sauer et al., 2017). Given the relatively small sample sizes for these two species, however, we interpret this finding with caution. Koenig (2003) was unable to find support for the hypothesis that competition from European Starlings was driving long-term declines in flicker and kestrel populations (or any other native cavity-nesting bird population). Nevertheless, in one local study of natural nests, the most common cause of nest failure for Northern Flicker was eviction by European Starlings (Tomasevic & Marzluff, 2017). The effects of local nest site competition (both interference and exploitation) between starlings, flickers, and kestrels may be offset by the ability of American Kestrels to occasionally outcompete starlings for nest sites (Bechard & Bechard, 1996; McClure, Hilleary, & Spurling, 2015), and the ability of Northern Flickers to excavate their own cavities and renest later in the season if evicted from an initial nesting cavity (Ingold, 1994). Furthermore, as European Starlings are urban-associated species, their impacts may be constrained to urban populations of Northern Flickers and American Kestrels, which may be reflected in the high rates of usurpation presented in both our study and that of Tomasevic and Marzluff (2017).

Our results only reflect direct interference competition at the nest site in which a nest attempt failed. This study does not reflect the number of instances in which the non-native species initiated breeding first, and thereby precluded a native species from nesting (i.e., exploitation competition). In these preclusive cases, there may be indirect effects such as earlier or delayed nestling by native species, and any subsequent changes in fecundity that might result (Charter et al., 2013, 2016; Fisher & Wiebe, 2006; Ingold, 1996, 1998). Additionally, native species could be excluded from their preferred habitat and be forced to either forego breeding or nest in less optimal habitat (Ghilain & Bélisle, 2008; Kerpez & Smith, 1990). Even when the nest sites of native species are not usurped, they may need to spend more time and energy defending nests from competitors (Burger, 1976; Goldshtein et al., 2018; Krist, 2004; Pearce, Pryke, & Griffith, 2011), which could have implications for limiting offspring growth rates and survival. Both interference and exploitation competition for nest sites can act on birds within a nesting season; thus, more study is needed on these synergistic effects.

In a previous study examining the behaviors of people who monitor nest boxes, Larson et al. (2016) found that people who control House Sparrow breeding in their nest boxes were more likely to have witnessed a usurpation...
firsthand. The study also suggests a willingness of people to control invasive species nesting in boxes (69 vs. 63% in our study), as well as a preference for lethal and non-lethal management relative to taking no management action (Larson et al., 2016). Our study expands upon the previous work by quantifying specific actions taken in a nesting season by respondents rather than recording preferences or retrospective responses.

Our analysis of the decision of people to manage invasive species revealed an additional effect of active engagement in citizen science, with NestWatch participants having an increased likelihood of engaging in management activity. NestWatch participants, however, were not more experienced in nest box monitoring than nonparticipants (mean years of experience = 10.5 and 10.4 years, respectively), suggesting that participants may pay closer attention to nest boxes as a consequence of their data collection activities. Alternatively, participants may be more aware of invasive species or emotionally invested in the outcomes of the nests they monitor, or they may have different educational levels or other unmeasured factors than nonparticipants, which may affect their attitude towards controlling invasive species (Brossard et al., 2005; Phillips et al., 2019).

Installing supplemental nest boxes for birds has been recommended as a conservation practice throughout the world (e.g., Aitken & Martin, 2012; Charter et al., 2016; Libois et al., 2012; Newton, 1994). For instance, the recovery of Eastern Bluebird (*Sialia sialis*) populations over the past century is largely attributed to the installation of nest boxes by thousands of bluebird enthusiasts across their range (Gowaty & Plissner, 2015). However, the addition of artificial nest sites is only expected to aid a population under certain demographic conditions (McClure, Pauli, & Heath, 2017). While managing nests in boxes may have little effect on the continental population size of invasive species, management activities may reduce their local abundances (Grarock et al., 2014). Weitzel (1988) demonstrates that small scale (0.35 ha) culling of European Starlings can benefit local bird communities; however, unless efforts are continuous both within and between years, the benefits will likely be short-lived due to renesting and immigration (Estabrook, 1907; Grarock et al., 2014; Thomas, 1972). Bird enthusiasts in North America have been discouraging House Sparrows at local scales for at least a century (Estabrook, 1907), and yet the continental population continues to be abundant. Nevertheless, continental populations of starlings and sparrows are declining (Rosenberg et al., 2019; Sauer et al., 2017), and a coordinated effort to limit the reproductive success of these species may contribute to continued declines. Moreover, even if population-level changes of starlings and sparrows are not being influenced by nest box managers, activities to improve artificial nesting locations may still be important for a species like the Purple Martin, which is experiencing long-term population declines and largely relies upon managed housing for sustained population recruitment (Raleigh et al., 2019).

Data on the extent to which humans intentionally provide and maintain nesting sites for birds are lacking, as is information on the importance of nest boxes for avian reproduction at the population level. The convenience sampling approach (Bryman, 2012) we employed in our survey potentially reached people who are more engaged in managing and monitoring nest boxes than the general public. Nevertheless, ours is one of the largest surveys of people who monitor nest boxes in North America, and we observed among respondents a willingness and ability to manage threats to native birds, as has been documented elsewhere (Dayer et al., 2019; Hvenegaard & Perkins, 2019; Larson et al., 2016; Phillips et al., 2019; Raleigh et al., 2019). Our study adds to the growing body of literature on conservation behaviors to benefit native birds (e.g., Cooper, Larson, Dayer, Stedman, & Decker, 2015; Dayer et al., 2019; Larson et al., 2016; Lepczyk, Mertig, & Liu, 2004). We suggest that future research focus on which management techniques are most effective at reducing long-term breeding success of non-native species as well as developing messaging strategies that engage members of the public in managing their nest boxes. Finally, having established that the public can detect nest usurpations by non-native species, future efforts in citizen science could allow the public to formally report species-specific usurpation rates (e.g., via NestWatch.org), allowing researchers to evaluate the relative importance of invasive species among all other sources of nest failure. Together with controlled field experiments, such data would further reveal the population-level effects of non-native birds on native species.

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**CONFLICT OF INTEREST**

The authors declare no conflicts of interest.

**AUTHORS’ CONTRIBUTIONS**

All authors were involved in conceiving the idea, designing the study, and reviewing manuscript drafts. H.F. and
R.B. administered the survey. R.B. and D.B. analyzed the data with support from H.F. R.B. and D.B. led the writing of the manuscript.

ETHICS STATEMENT
The study received approval from Cornell University’s Institutional Review Board (Protocol #1803007815).

DATA AVAILABILITY STATEMENT
The de-identified analysis data are archived at https://data.mendeley.com/datasets/wp29ywzvvt/1. For the privacy of respondents, we have not publicly archived the open-ended responses (comments) which were used in the content analysis of passive management techniques.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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