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ORIGINAL PAPER

What are the competitive effects of invasive species? Forty years of the Eurasian collared-dove in North America

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Abstract Eurasian collared-doves (*Streptopelia decaocto*; hereafter 'collared-doves') have spread throughout North America since they first colonized Florida in the early 1980s. Here I test for adverse effects of this introduced species on four confamilial potential competitor dove and pigeon species using data from the breeding season (North American Breeding Bird Survey; BBS) and the winter (Audubon Christmas Bird Count; CBC). Within sites of both sets of surveys, correlations between populations of collared-doves and all four potential competitor species have generally been either nonsignificant or positive, indicating a lack of adverse competitive effects due to collared-doves. Similarly, there were no significant differences in population trends of any of the four species in sites where collared-doves were present compared to those where they were not, and there have been no significant declines in population trends of the four species driven by differences in collared-dove abundance in areas where the latter were present. Overall, analyses revealed no negative effects of collared-doves on populations of these potential competitors. Evidence thus far supports a 'passenger' rather than a 'driver' role for collared-doves in North America, although future monitoring of potential competitor species is warranted, especially if collared-dove populations continue to increase.

Keywords Band-tailed pigeon · Competition · Eurasian collared-dove · Exotics · Invasive species · Mourning dove · Rock pigeon · White-winged dove

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Introduction

North American bird populations have been greatly altered since colonization by Europeans due to both human-induced extinctions—perhaps most notably the passenger pigeon (*Ectopistes migratorius*) (Schorger 1955; Bucher 1992) but including at least half a dozen other species—and, conversely, through species introductions. The latter include a host of species, most successfully the house sparrow (*Passer domesticus*), European starling (*Sturnus vulgaris*), and rock pigeon (*Columba livia*). The effects of these alterations are often poorly understood and controversial in part because of the many confounding factors that concurrently affect native populations, but also because the overall impact of an exotic species can be on multiple levels, including not only individuals, populations, and the communities of which they are a part but also on genetic processes such as hybridization (Huxel 1999; Parker et al. 1999; Gurevitch and Padilla 2004). Yet another issue is whether species introductions are likely to be exacerbated by climate change (Dukes 2000). These questions make the investigation of the ecological impacts of exotic species challenging, yet timely and important.

One relatively recent avian invader in North America that is ripe for examination is that of the Eurasian collared-dove (*Streptopelia decaocto*). This species, native to warm temperate and subtropical Asia, was introduced to North America in 1974 when a small population escaped captivity in the Bahamas (Hengeveld 1993). It subsequently colonized Florida by 1982 (Smith 1987; Romagosa and Labisky 2000) and has since spread throughout most of North America, reaching California as early as 1992 and coastal British Columbia by the mid 2000s (Romagosa and McEnearney 2000; Romagosa 2020).

Several recent studies have focused on the dynamics of this range expansion, concluding that populations tend to advance best in moderate to warmer regions in human-altered habitats, preferentially occupying large suburban landscapes from which they later expand into surrounding agricultural areas and other sites highly modified by human activity where grain is available (Bonter et al. 2010; Fujisaki et al. 2010; Bled et al. 2011; Rocha-Camarero and DeTrucios 2002; Scheidt and Hurlbert 2014). With the exception of the Bonter et al.'s (2010) study restricted to Florida using data from bird feeders, however, there has been scant attention given to the potential effects of this invader on previously established populations of related species. Given the recent continental-wide expansion of collared-doves, along with its potential as both a competitor with native species (Poling and Hayslette 2006) and as a disease vector (Schuler et al. 2012; Panella et al. 2013), it is timely to examine its effects as a case study addressing the extent to which invasive birds can have negative impacts on populations of native species.

Methods

Data on the relative numbers of Eurasian collared-doves (hereafter 'collared-doves') and four common North American related species (hereafter 'competing species') were gathered from two sources: the North American Breeding Bird Survey (BBS) and the Audubon Christmas Bird Counts (CBC). Species considered as potential competitors included the mourning dove (*Zenaida macroura*), rock pigeon (*Columba livia*), band-tailed pigeon (*Patagioenas fasciata*), and white-winged dove (*Zenaida asiatica*). These species were chosen because they all feed on seeds and agricultural grain crops, and as members of the family Columbidae, they are the most likely to share diseases as well as compete for food with collared-doves (Webb et al. 2002; Strauss et al. 2006). Furthermore, they are the four species in this family that are sufficiently common and widespread, both during the breeding season and winter, that analyses could be conducted on a large number of sites on a continental or subcontinental scale.

BBS data consist of 3-min censuses at a series of 50 stops 0.8 km apart along a road transect (Bystrack 1981), whereas CBC data consist of one-day surveys conducted within a two-week period around Christmas (25 December) restricted to a 24-km-diameter circle (Sauer and Link 2002). In all analyses, CBC values were standardized for effort by dividing the number of birds counted by the number of independent groups of individuals participating in the survey ('party-hours'), and, unless otherwise stated, BBS and CBC values were *ln*-transformed to help normalize their distributions (Koenig 2003).

Both surveys are conducted annually, and provide estimates of relative populations of birds during the breeding season (BBS) and winter (CBC). Surveys between 1980 and 2017 (winter 2017–2018 for the CBC data) conducted within the continental United States and Canada were gathered and further restricted as detailed below.

In order to investigate whether collared-dove populations have had a significant effect on the competing species, I conducted two sets of analyses focusing on different levels of potential interactions between them. Key to both tests was how numbers of the competing species changed through time with respect to the colonization or abundance of collared-doves; these changes are referred to as 'population trends'.

The first set ('correlational analyses') was designed to test whether increasing populations of collared-doves resulted in declines in the competing species within sites. Analyses were performed at the site-by-site level using only sites that collared-doves had colonized. For each set of surveys, I calculated

Pearson correlations between the (*ln*-transformed) number of individuals of each species counted and year ('species by year'), and between the number of collared-doves ('ECD') counted and the number of each competing species ('ECD by competitor species').

In order to restrict analyses to the time period during which collared-doves were colonizing an area and before they potentially achieved an equilibrium with competing species, analyses started with surveys conducted the year collared-doves were first detected at a site and ended either in 2017 (2018 for the CBC data) or 20 years later, whichever came first. Only sites for which at least 10 years of data were included and, for correlations between collared-doves and the competing species, analyses were restricted to sites where collared-dove population trends had increased over time ('ECD by year' correlation was positive); this eliminated 150 of 479 (31.3%) BBS and 159 of 760 (20.9%) CBC sites. This latter restriction ensured that analyses focused on sites where increasing populations of collared-doves were most likely to exhibit an effect on the competing species.

Binomial tests were used for this first set of analyses, from which I present the proportion of sites for which correlations were positive. The expected null proportion of sites increasing (that is, positive) in these tests was 0.5. 'Species by time' values significantly above 0.5 indicated increasing population trends through time, while 'ECD by competitor species' values above 0.5 denoted species increasing concomitantly with increasing collared-dove populations. Conversely, values significantly below 0.5 indicated decreasing population trends through time and competitor species decreasing as collared-dove populations increased; this latter result was assumed to indicate adverse effects of competition from increasing populations of collared-doves.

The second set of tests ('regression analyses') were aimed at testing whether there was a difference in the average population trends of the competing species between sites that were and were not colonized by collared-doves, and then, among the colonized sites, whether the overall density of collared-doves affected the population trends of the competing species. First I divided sites into those colonized by collared-doves (type = 1) and those at which no collared-doves had as yet been recorded (type = 0). I then performed linear regressions where the dependent variable was the 'species by year' correlation coefficient for the competing species at that site while 'type' and an inverse distance-weighted autocovariance term (controlling for spatial autocorrelation; Augustin et al. 1996; Wintle and Bardos 2006; Bonter et al. 2010) were the independent variables. Next I performed a second regression using only 'type 1' sites colonized by collared-doves. The 'species by year' correlation for the competing species was again the dependent variable while the independent variables were the mean number of collared-doves counted over all years included in the sample at that site and the inverse distance-weighted autocovariance term.

In order to take into consideration the differing length of time that collared-doves invaded different regions and limit the analyses to when collared-doves were likely to be increasing (and thus have the greatest effect on competing species), the regression analyses (second set of tests) started the year collared-doves were first detected in the BBS/CBC surveys in that state (rather than at the particular site) and extended through to the end of the period covered by the surveys (2017 for BBS; 2018 for CBC) or 20 years, whichever came first. Surveys in states where collared-doves had not yet colonized were excluded. As in the correlational analyses, sites where collared-doves were present but did not increase over the time period (46 of 1050 BBS sites [4.4%] and117 of 1261 CBC sites [9.3%]) were excluded. These proportions differed from those of the correlational analyses because of the different criterion used to determine the starting year of samples at individual sites.

All analyses were conducted in R 3.5.1 (R Development Core Team 2018).

Results

The population trends based on both BBS and CBC surveys (Fig. 1) indicated that populations of collared-doves overall increased exponentially starting from when they were first detected in the surveys in 1986 (BBS: $ln(\text{BBS}) = 0.207 * \text{YEAR}—417.8$, $R^2 = 0.96$, $P < 0.001$; CBC: $ln(\text{CBC}) = 0.198 * \text{YEAR}—398.8$, $R^2 = 0.90$, $P < 0.001$). Dramatic increases in collared-dove populations were also evident from the correlations through time at the individual sites, a highly significant 68–79% of which were positive (Table 1). Significantly increasing populations through time were also evident for white-winged doves (73–78% of sites increasing) but not for mourning doves or rock pigeons. Band-tailed pigeons increased somewhat in the CBC routes but exhibited no significant changes overall based on the BBS data.

Despite the generally increasing collared-dove populations, analyses revealed no evidence of adverse effects of collared-doves on any of the competing species; that is, none of the 'ECD by competitor species' values (reporting the proportion of sites for which the correlation between the two species was positive) was significantly below 0.5 (Table 1). On the contrary, a significant proportion of correlations between collared-doves and the competing species were positive using the CBC data and for two of the four species using the BBS data. The remaining two species in the BBS analyses exhibited no significant differences in the proportion of sites with a positive or negative relationship between collared-doves and the competing species.

Table 2 further investigates the effects of collared-doves on populations of the competing species. BBS surveys failed to reveal any significant negative effects of either presence/absence of collared-doves or mean numbers of collared-doves on the population trends of any of the competing species. CBC analyses also revealed no significant relationships between population trends of the competing species and collared-doves, although there was a highly significant *positive* relationship between numbers of collared-doves and population trends of rock pigeons.

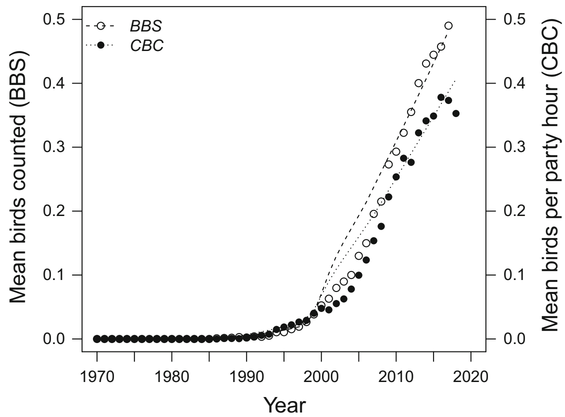

Fig. 1 Mean numbers of Eurasian collared-doves reported by all BBS and CBC surveys in North America (north of Mexico) by year. Lines drawn by locally weighted scatterplot smoothing (R procedure *lowess*)

Table 1 Mean correlations between survey numbers (*ln*-transformed) of all five columbid species and year, and between survey numbers of Eurasian collared-doves and the other four competing species

Variables	BBS		CBC	
	Pearson correlation ± SE (*N*)	Proportion of sites positive[a]	Pearson correlation ± SE (*N*)	Proportion of sites positive[a]
ECD by year	0.218 ± 0.022 (479)	0.68***	0.377 ± 0.016 (760)	0.79***
MD by year	− 0.063 ± 0.010 (1882)	0.44***	− 0.153 ± 0.009 (1560)	0.33***
RP by year	− 0.128 ± 0.010 (1433)	0.36***	− 0.018 ± 0.009 (1574)	0.44***
BTP by year	− 0.049 ± 0.047 (75)	0.40	0.063 ± 0.034 (99)	0.63*
WWD by year	0.204 ± 0.030 (158)	0.73***	0.258 ± 0.019 (314)	0.78***
ECD by MD	0.079 ± 0.019 (328)	0.58**	0.066 ± 0.013 (585)	0.60***
ECD by RP	− 0.009 ± 0.021 (254)	0.48	0.132 ± 0.014 (589)	0.65***
ECD by BTP	− 0.147 ± 0.177 (7)	0.29	0.091 ± 0.034 (92)	0.66**
ECD by WWD	0.167 ± 0.029 (118)	0.70***	0.257 ± 0.019 (254)	0.81***

ECD Eurasian collared-dove; *MD* mourning dove; *RP* rock pigeon; *BTP* band-tailed pigeon; *WWD* white-winged dove. Years included start with the first year ECDs were recorded at each site and extend to the end of the period covered by the surveys (2017 for BBS; 2018 for CBC) or the next 20 years, whichever was less (see text). Excludes sites with less than 10 years of data, and only sites at which ECDs increased during the time period were included in the correlations with the competing species

[a]Significance based on binomial tests where the expected null proportion is 0.5; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; other $P > 0.05$

Table 2 Linear regressions testing the effects of Eurasian collared-doves (ECD) on the correlations through time of four competing species

	Mean ± SE effect size on change through time of competing species (*N* sites)			
Competing species	Presence [1]/absence [0] of collared-doves	*P* value	Mean numbers of collared-doves where present	*P* value
BBS				
Mourning dove	− 0.004 ± 0.023 (1483)	0.86	− 0.006 ± 0.026 (992)	0.82
Rock pigeon	− 0.013 ± 0.024 (1056)	0.60	− 0.021 ± 0.025 (761)	0.41
Band-tailed pigeon	0.035 ± 0.083 (105)	0.67	− 0.095 ± 0.086 (75)	0.27
White-winged dove	− 0.146 ± 0.107 (228)	0.18	0.044 ± 0.044 (217)	0.33
CBC				
Mourning dove	0.030 ± 0.020 (1399)	0.14	− 0.007 ± 0.023 (913)	0.75
Rock pigeon	− 0.001 ± 0.020 (1442)	0.95	0.088 ± 0.022 (948)	< 0.001
Band-tailed pigeon	0.050 ± 0.112 (180)	0.66	0.077 ± 0.087 (172)	0.38
White-winged dove	0.106 ± 0.179 (307)	0.56	0.054 ± 0.034 (304)	0.12

Each row summarizes results from two models; in both the dependent variable is the correlation (*r* value) of the number of competing species (*ln*-transformed) through time while the explanatory variables are (for the first model) the presence/absence of ECDs and an inverse distance-weighted autocovariance term, and (for the second model) the mean (*ln*-transformed) number of ECDs counted when present and the inverse distance-weighted autocovariance term. (The autocovariance term not included in the table.) All analyses included data starting in the year ECDs first showed up in surveys in that state and extend to the end of the period covered by the surveys (2017 for BBS; 2018 for CBC) or the next 20 years, whichever was less, and, for sites with ECDs, exclude sites where ECDs declined during the period covered by the survey (see text). Excludes sites with less than 10 years of data

Discussion

Analyses of two different continental-wide bird survey schemes, one of which focused on the breeding season while the other focused on wintering birds, failed to reveal evidence for negative effects of collared-doves on populations of any of four species of confamilial, potential competitor species in North America. This was despite limiting analyses to sites where collared-doves were increasing, and thus where adverse effects due to competition or spread of disease were most likely to occur. On the contrary, in many cases analyses indicated that populations of the potential competitor species increased concommittantly with those of collared-doves, suggesting that the conditions favoring the increasing population trends of collared-doves were similarly favorable for the potential competitors.

Results thus support those of an earlier analysis that detected no negative effects of collared-doves on native populations of doves and pigeons in the state of Florida based on data from bird feeders (Project FeederWatch; Wells et al. 1998) that, like the CBC data, was collected during the winter (Bonter et al. 2010). In one case, lack of adverse effects were to some extent expected given a previous study that found differences in seed-size selection by collared-doves and mourning doves that limited foraging competition between them (Hayslette 2006). Also a likely contributor to the lack of competitive effects is the catholic diets of the species, all of which feed on a wide range of plant material, often focused on seeds and agricultural grains (Keppie and Braun 2020; Lowther and Johnson 2020; Romagosa 2020; Schwertner et al. 2020). To the extent that adverse effects of collared-doves on other species—columbids or non-Columbiformes—are eventually detected, they are likely to be limited to highly-modified landscapes where collared-doves are most likely to occur (Bonter et al. 2010; Fujisaki et al. 2010).

That invasive species can have dramatic effects on native communities is widely recognized (Simberloff 1996; Vitousek et al. 1997). The effects of introduced birds on other native bird species, however, is generally less clear. A review of 16 invasive bird species in Southeast Asia concluded that they "may have some negative impacts on the native biodiversity" primarily due to the potential for the common myna (*Acridotheres tristis*) to displace native cavity-nesting species (Pell and Tidemann 1997; Yap and Sodhi 2004). European starlings in the United States pose a similar threat due to their ability to aggressively displace native cavity-nesting species, although a study focusing on the demographic effects of this species found scant evidence that starlings have resulted in population declines in any native bird species (Koenig 2003).

Kumschick and Nentwig (2010) looked at introduced European species of birds and concluded that four of them posed potential threats to native bird species. The threat of one of these, the ruddy duck (*Oxyura jamaicensis*), was primarily due to hybridization with the native white-headed duck (*Oxyura leucocephala*) (Hughes et al. 2006; Muñoz-Fuentes et al. 2007), while a second, the ring-necked parakeet (*Psittacula krameri*), was due to potential nest-hole competition with native species (Gebhardt 1996). The remaining two species (sacred ibis *Threskiornis aethiopicus* and Canada goose *Branta canadensis*) were both considered potential threats although no serious impacts had been detected thus far (Watola and Feare 1996; Yésou and Clergeau 2005).

The best examples of invasive birds resulting in declines of other bird populations of which I am aware involve range expansions of avian brood parasites, often assisted by human habitat modification. Cases include the well-documented negative effects of the brown-headed cowbird (*Molothrus ater*) on North American forest passerines as cowbirds expanded their pre-European settlement range (Mayfield 1961; Brittingham and Temple 1983; Cox et al. 2012), and adverse effects of the shiny cowbird (*Molothrus bonariensis*) on native populations of yellow-shouldered blackbirds (*Agelaius xanthomus*) as the former has spread through the Caribbean (Cruz et al. 2005). The African pin-tailed whydah (*Vidua macroura*), common escapees from the pet trade currently established in several semi-tropical localities in North America, is a recent example of generalist brood parasite considered to be a potential threat (Crystal-Ornelas et al. 2017). Overall, however, it would appear that few invasive bird species have unambiguously led to a severe decline, much less extinction, of a population of native birds with the exception of brood parasites expanding their range and adversely affecting bird populations that have not evolved effective defenses and, more rarely, closely related invasive species that hybridize with a native conspecific, compromising the latter's genetic distinctness (Huxel 1999; Muñoz-Fuentes et al. 2007).

Results presented here support the conclusion that the Eurasian collared-dove in North America is an invasive bird species that has thus far had little or no significant impact on populations of native (or, in the case of rock pigeon, previously introduced) species. Of course, the absence of any obvious negative effects on previously established populations of related species does not guarantee that collared-doves will not have adverse effects in the future, particularly if populations continue to increase. Any such future effects are unlikely to be the result of hybridization, since the genus *Streptopelia* is primarily distributed in Africa and Southeast Asia and no congeneric species are native to North America, although several congeners have been either introduced or recorded as accidentals. Two such species include the spotted dove (*Streptopelia chinensis*), established in southern California (Garrett and Walker 2020), and the European turtle-dove (*Streptopelia turtur*), which has been recorded accidentally in Massachusetts (Veit 2006), possibly originating as an escapee of the pet trade (as was the Eurasian collared-dove [Smith 1987]).

There is, perhaps, greater potential for collared-doves to harm native species through disease transmission (Romagosa and Labisky 2000). Collared-doves have been found to harbor antibodies to West Nile virus (Rappole et al. 2000) and concerns have been raised over the potential spread of pathogens through expanding populations of other species of doves (Conti and Forrester 1981; Schuler et al. 2012; Panella et al. 2013). No such effects have been attributed to collared-doves thus far, however.

In summary, evidence supports the conclusion that, like most non-parasitic invasive bird species, Eurasian collared-doves are a 'passenger' rather than a 'driver' of change in the medium- to largely-degraded North American ecosystems that they have thus far invaded (MacDougall and Turkington 2005). If collared-dove populations maintain their rate of increase, they will continue to offer outstanding opportunities to test the potential ecological effects of an ongoing avian invasion, contributing to our further understanding of the role of introduced birds as agents of ecological change (Simberloff 1996; Didham et al. 2005).

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