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The rapid spread of invasive Eurasian Collared Doves *Streptopelia decaocto* in the continental USA follows human-altered habitats

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Understanding factors related to the range expansion trajectory of a successful invasive species may provide insights into environmental variables that favour additional expansion or guide monitoring and survey efforts for this and other invasive species. We examined the relationship of presence and abundance of Eurasian Collared Doves *Streptopelia decaocto* to environmental factors using recent data from the North American Breeding Bird Survey to understand factors influencing its expansion into the continental USA. A zero-inflated Poisson (ZIP) model was used to account for excess zero observations because this species was not observed on the majority of survey routes, despite its large geographical range. Model fit was improved when we included environmental covariates as compared with the null model, which only included distance from the route where this species was first observed. Probability of zero count was positively related to the distance from the first route and road density and was inversely related to minimum temperature and distance to coast. Abundance of the species was positively related to road density and was inversely related to annual precipitation and distance to coast. Random intercept by land-cover type also improved model fit. Model fit was improved with the ZIP model over the standard Poisson model, suggesting that presence and abundance of this species are characterized by different environmental factors. However, overall low accuracy of model-predicted presence/absence and abundance with the independent validation dataset may indicate either that there are other explanatory factors or that there is great uncertainty in the species' colonization process. Our large-scale study provides additional evidence that the range expansion of this species tends to follow human-altered landscapes such as road and agricultural areas as well as responding to general geographical features such as coastlines or thermal clines. Such patterns may hold true for other invasive species and may provide guidelines for monitoring and assessment activities in other invasive taxa.

Keywords: exotic species, invasive species, North American Breeding Bird Survey, occurrence, zero-inflated Poisson.

Human activities have been reshaping ecological processes by facilitating introduction and establishment of exotic species (Blackburn *et al.* 2008). While numerous introductions of exotic species have occurred on a global scale, successful establishment varies by species (Long 1981, Williamson 1996, Duncan *et al.* 2003). The Eurasian Collared Dove *Streptopelia decaocto* is one of the most successful terrestrial invaders and its spread and colonization are closely related to human activities (Romagosa & Labisky 2000). The Eurasian population, now established throughout most of Europe, was believed to have originated in India, Sri Lanka

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and Myanmar, and spread to Turkey and the Balkans in the 16th century via natural dispersal or human introduction (Smith 1987, Gorski 1993, Romagosa & McEneaney 1999). It was not until the early 1900s that this species rapidly colonized much of Europe and northwest Africa, establishing itself throughout most of the area within about 50 years (Crooks & Soule 1999, Rocha-Camerero & Hidalgo de Trucios 2002, Eraud *et al.* 2007). Reasons for this rapid expansion after a long lag time may include increasing urbanization and/or climate change allowing for longer breeding seasons (Crooks & Soule 1999). The dispersal pattern progressed in a generally northwest direction and has been shown to encompass small foci lying ahead of colonized regions. These foci then fill in as the local populations grow (jump dispersal) (Hudson 1972, Romagosa & Labisky 2000). The Iberian Peninsula has been one of the most recent areas to be colonized and shows a typical pattern for Europe. The first individuals were from France and appeared in the Asturias area in 1960. They spread rapidly towards the west along the northern coastal fringe and appeared sometime later along the Mediterranean coast, moving south and inland more slowly (Rocha-Camerero & Hidalgo de Trucios 2002).

Collared Dove habitat preferences are well studied throughout Europe. High human commensalism is a unique attribute of this species. In Britain, its distribution is associated with human settlements such as suburban gardens and town parks with a mixture of shrub and tree cover, including human-made structures (Coombs *et al.* 1981, Hengeveld 1988). They are also abundant on or near the coast in a mosaic landscape that includes small fields, mixed livestock pasture land, horticulture, grain farming, and marginal scrublands, but they tend to avoid areas of intensive farming and woodland (Hudson 1972). As an example of mosaic landscapes used in Europe, they seem to prefer 'dehesas', or parklands of the Iberian Peninsula that have *Quercus* sp. intermixed with cropland and Mediterranean woodland (Rocha-Camerero & Hidalgo de Trucios 2002). In France, low detection probability and occupancy rate of the species occurred in regions with a large proportion of wooded and mountainous areas (Eraud *et al.* 2007). The species' climatic limit is uncertain. Although they originated in and initially colonized tropical, subtropical, temperate and arid regions, Collared Doves have successfully colonized countries within various climatic zones (Romagosa & McEneaney 1999). In Europe, the distribution of this species is generally restricted to relatively warmer regions, but it may also occur at low-temperature areas such as western Siberia (Hengeveld 1988). In their original range in India, they occur at elevations of up to 2500 m and are occasionally present over 3000 m (Cramp 1985, Hengeveld 1988). Occurrence is mainly below 300 m in the UK (Hengeveld 1988) and initially below 650 m and later up to 1000 m in Switzerland (Schifferli *et al.* 1980).

Since first being observed in the early 1980s, probably through escape from captivity in the Bahamas (Smith 1987), Collared Doves rapidly expanded their range throughout the USA, as predicted by Hudson (1972). Romagosa and Labisky (2000) reported that relative abundance of the species increased in Florida from 1986 to 1996 based on National Audubon Society Christmas Bird Count (CBC) data. Initial observations of this species may have been confounded by its similarity with the Ringed Turtle Dove *Streptopelia risoria*. Hooten *et al.* (2007) and Hooten and Wikle (2008) showed rapid population growth of the species in the USA using North American Breeding Bird Survey (BBS) data. Several local monitoring efforts also confirmed this species' presence in locations throughout the USA (Bohlen 1997, Drennen 1997, Beckett *et al.* 2007). Some similarity in habitat preference and dispersal pattern in the USA to that in Europe has been reported. In northern Colorado, Collared Doves inhabit rural farming landscapes similar to breeding habitat in Europe (Beckett *et al.* 2007). Occurrence and abundance of this species are associated with human-modified landscapes within Florida (Bonter *et al.* in press). Range expansion in Florida was most prevalent along the coast (Romagosa & Labisky 2000), agreeing with observations in Britain where the bird is abundant around the coastal belt (Hudson 1972). Romagosa and Labisky (2000) also reported possible dispersal pattern along rivers in Florida.

Although these studies suggest that range expansion of Eurasian Collared Dove is related to environmental and human factors, most studies of its habitat characterization are based on local observations or within relatively small geographical ranges. Current availability of spatially explicit environmental data of large geographical coverage, such as climate and land-cover type, and large-scale population monitoring data allow us to examine factors responsible for its range expansion. This study examines how presence and abundance of Eurasian Collared Dove are related to environmental and human-influenced landscape features to provide a better understanding of the range expansion trajectory and potential for future expansion and population growth.

METHODS

Data

We used 2007 BBS data on Collared Doves from surveys within the continental USA (Robbins *et al.* 1986). BBS volunteers record counts of each bird species observed or heard during 3 min at locations at 0.8-km intervals along a 39.4-km route. We used route-level data because complete coordinate information on the individual stop locations was not available at the time of our data retrieval. The data for each year at each survey route were classified as either 'acceptable' or 'unacceptable' for use based on criteria such as weather conditions, time of day, and completeness of route coverage. We excluded data classified as 'unacceptable' and routes where the coordinates were not released due to uncertainty of location accuracy.

Environmental covariates for each survey route were derived from public sources. We created 4-km resolution raster data of average annual minimum temperature and annual total precipitation for 10 years using raster data of annual minimum temperature and annual total precipitation 1998–2007 in the USA created by Oregon State University PRISM group (Daly *et al.* 2000, DiLuzio *et al.* 2008) (Fig. 1a,b). To quantify association of this species with human settlements, we initially considered using human population as a covariate, as used by Hooten and Wikle (2008); however, available population data were at state, county, and city levels, not fine enough to characterize each survey route (state- and county-level data) or scattered in rural areas (city-level data).We felt that rural areas, including agricultural areas where roads are present but human density is low, may be an important habitat feature and that the presence of roads might address this human-altered landscape pattern better than population alone. As an alternative, we created a 1-km resolution raster layer of road density by the kernel density method using the TIGER® database developed at the United States Census Bureau (http://www.census.gov/geo/www/tiger/), because a number of studies used road density as an indicator of anthropogenic effects on wildlife habitat (Findlay & Houlahan 1997, Shriver *et al.* 2004) (Fig. 1c). This raster layer was used as an indicator of human disturbance. We used 1-km resolution MODIS/Terra land-cover type I, the finest classification scheme among all five MODIS/Terra land-cover type products, to examine association of the distribution of Collared Dove with each land-cover type (Friedl *et al.* 2002). The land-cover data in 2004 were the most up to date at the time of data collection. We calculated raster-based numerical covariates (annual minimum temperature, annual total precipitation and road density) at each BBS route as an average weighted by route length intersect with each grid of the raster data. Land-cover type of each BBS route was defined as the type in which the largest segment of each route fell. We calculated distance from the centre of each survey route to nearest coast and river, and used ESRI's shapefiles of continental boundary and major river lines to derive these distances. We also calculated distance from all BBS routes to the BBS routes in Plantation Key in Florida, where Collared Doves were first observed in the survey in the USA in 1986.

Analysis

A large number of absences or zero counts (zero inflation) are a common feature in ecological data possibly related to population parameters of interest. However, the data may not fit standard distributions if the number of zeros is too large (Martin *et al.* 2005). We applied a zero-inflated model to account for excess zero values through Bayesian inference using Markov Chain Monte Carlo simulation following earlier studies (Martin *et al.* 2005). Bayesian inference depends on simulated probability density of model parameters (posterior) given data values (Congdon 2003). Count response variables in a zero-inflated Poisson (ZIP) model are assumed to have a distribution that is a mixture of one with binary outcome with probability p and another with Poisson distribution with event occurrence rate of λ with probability of $1-p$,

$$\begin{cases} P(y_i = 0) = p \\ P(y_i \sim \text{Poisson}(\lambda)) = 1 - p, \end{cases}$$

where y_i is an ith count response. We modelled p in a logit function and λ in a log-linear function.

(a) Minimum temperature

(b) Annual total precipitation

(c) Road density

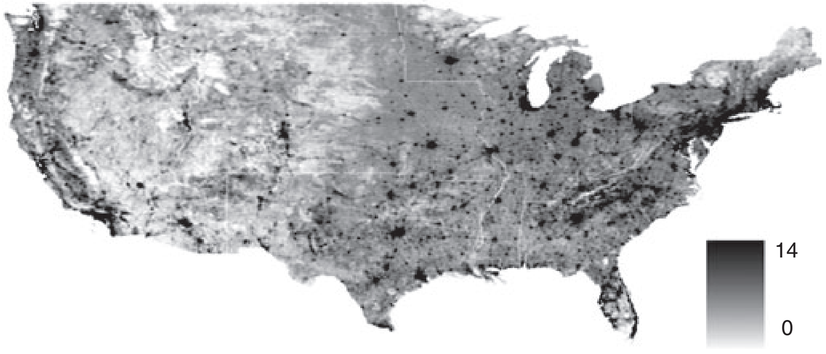

Figure 1. Raster layers used to derive minimum temperature (a), annual total precipitation (b) and road density (c) of each survey route.

We first compared null and full models in forms of ZIP. The null model assumes that presence/absence and abundance depend only on distance to the location of initial introduction, and includes only one covariate, distance to the first route,

$$\begin{cases} \operatorname{logit}(p_i) = \alpha_0 + \alpha_1 D_i \\ \log(\lambda_i) = \beta_0 + \beta_1 D_i, \end{cases}$$

where p_i is probability of the species present at the ith route, α_0 is an intercept, α_i is a coefficient for the distance to the first route from ith route (D_i)

in the logit function, λ_i is the Poisson rate, β_0 is an intercept, and β_i is a coefficient for D_i in the log-linear function. The full model has all environmental covariates in addition to D_i in both logit and log-linear parts,

$$\begin{cases} \operatorname{logit}(p_i) = \alpha_1 D_i + \alpha_2 T_i + \alpha_3 P_i + \alpha_4 R_i \\ \qquad + \alpha_5 C_i + \alpha_6 V_i + \alpha_{7,i} \\ \log(\lambda_i) = \beta_1 D_i + \beta_2 T_i + \beta_3 P_i + \beta_4 R_i \\ \qquad + \beta_5 C_i + \beta_6 V_i + \beta_{7,i} \end{cases}$$

where α_1–α_6 and β_1–β_6 are coefficients for D_i, mean minimum temperature (T_i), mean annual total precipitation (P_i), road density (R_i), distance to coast (C_i), and distance to river (V_i) in logit and log-linear models, and α_7 and β_7 are effects of land-cover type. This essentially is a two-part (logit and Poisson) ZIP model with fixed environmental effects and intercepts centred at each land-cover type (Martin *et al.* 2005).

The full models were reduced by removing covariates that have 95% credible interval (CI) of coefficients neither clearly positive nor negative (Congdon 2003). We compared full and reduced models with an approximate deviance information criterion (DIC) which was derived as the sum of the posterior mean of the deviance and effective number of parameters defined as half the posterior variance of the deviance (Sturtz *et al.* 2005). We also compared ZIP models with Poisson null and full models, which have the same covariates as null and full models described above. We considered that a model fit is substantially improved if the DIC was minimized at over 5 (Spiegelhalter *et al.* 2002).

We randomly took 300 observations (20% of the dataset) to use for model validation before estimating model parameters. We first calculated the probability of zero-count with the logit function of the final model and predicted the number of birds with the Poisson function of the final model if the probability of zero-count was < 0.5.

We used flat priors for all parameters. We referred to Ghosh *et al.* (2006) for coding and estimated parameters from 100 000 iterations after 10 000 burn-in using WINBUGS 1.4 (Spiegelhalter *et al.* 2003). Convergence was assessed with scale reduction factor (SRF) Gelman–Rubin diagnostics using the CODA package considering that parameters were converged if SRF is < 1.1 (Brooks & Gelman 1998).

RESULTS

Collared Doves have dispersed in a wide geographical area in the continental USA, extending to the Pacific coast and near the Canadian border by 2007, but there were large gaps where the species was not observed on BBS survey routes (Fig. 2). The species was not observed in the majority of survey routes (81.4% of 1716 routes) included in our analysis. The posterior of α_i

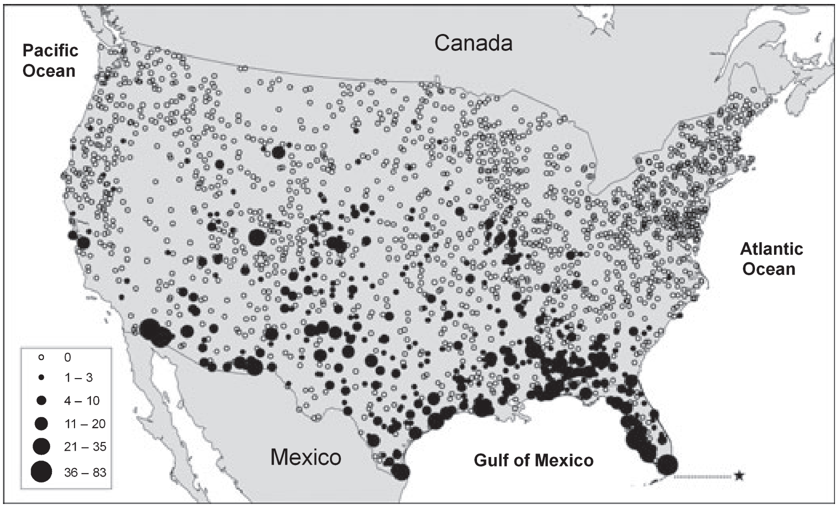

Figure 2. Centre location of BBS routes of 2007 survey in which points were scaled by number of observed Eurasian Collared Doves. Open circles are routes where the species was not observed. The star indicates the location of the survey route where the bird was observed for the first time in a BBS survey in 1986.

(coefficient for distance to the first route in the logit function) for the null model ($\hat{\alpha}_1 = 0.0007$) implied that the further a survey route is from the first route on which the species was observed in the USA, the lower the chance of observing Collared Doves (Table 1). However, there was uncertainty regarding the importance of posterior β_1 (coefficient for distance to the first route in the log-linear function) because the effect of this covariate was not clear (95% CI: −5.9E–5 to 4.6E–5), suggesting that proximity to the first route explains presence but not abundance of Collared Doves. The DIC was largely reduced (Δ = −237.1) when we used the full model that included all environmental covariates in both logit and Poisson functions, suggesting improved fit with the full model (DIC = 2549.7) over the null model (DIC = 2786.8).

There were several covariates whose effects were not clear (95% CI was neither positive nor negative) and uncertainty of their importance existed, including annual total precipitation (95% CI: −0.0001 to 0.0017) and distance to river (95% CI: −0.0011 to 0.0043) in the logit function, and annual minimum temperature (95% CI: −0.0118 to 0.0396) and distance to river (95% CI: −0.0008 to 0.0009) in the log-linear function. We removed these variables from the model and the reduced model included four variables in the logit function (distance to the first route, annual minimum temperature, road density and distance to coast) and three variables in the log-linear function (annual total precipitation, road density and distance to coast). There was an increment in DIC from the full model to the reduced model, but the change was marginal (Δ = 2.2), implying that the model fit of the two models was not substantially different.

With the reduced model, the probability for a zero-count of Collared Doves was positively related to the distance to the first route ($\hat{\alpha}_1 = 0.0006$) and road density ($\hat{\alpha}_4 = 0.3135$) and was inversely related to annual minimum temperature ($\hat{\alpha}_4 = -0.2759$) and distance to the coast ($\hat{\alpha}_5 = -0.0009$). A positive coefficient of road density in the Poisson function suggested that this species was abundant in areas with high road density while holding all other variables in the model constant. Conversely, negative coefficients of annual precipitation and distance to the coast in the Poisson function suggest this species is abundant in areas with lower rainfall and near to the coast if other factors in the model are held constant.

Overall, the percentage of routes where the species was observed and abundance of the species varied largely by land-cover type (Fig. 3). The DIC largely increased (Δ = 354.6) when we removed the random intercept for each of the MODIS land-cover types, implying importance of this variable to improve the model fit. In the logit function, all posterior CIs of the intercepts for land-cover types overlap each other (Fig. 3). In the Poisson function, the posterior of the intercept associated with cropland is relatively high and has a narrow CI, and is distinctly higher than that of mixed forest,

Table 1. Summary of posterior (simulated density) of model parameters for null, full and reduced zero-inflated Poisson model. Posteriors were left blank if the parameter was not included in the reduced model.

	Logit				Poisson				
Model term	Estimate	sd	2.5%	97.5%	Estimate	sd	2.5%	97.5%	DIC
Null model									
Distance to 1st route	0.0007	8.00E-5	0.0006	0.0009	−0.68E-6	2.67E-5	−5.91E-5	4.59E-5	2786.84
Full model									
Distance to 1st route	0.0008	0.0002	0.0004	0.0012	−2.90E-5	6.46E-5	−1.58E-4	9.63E-5	2549.70
Min. temperature	−0.2751	0.0331	−0.3422	−0.2119	0.0139	0.0130	−0.0118	0.0396	
Precipitation	0.0008	0.0005	−0.0001	0.0017	−0.0009	0.0001	−0.0012	−0.0007	
Road density	0.3051	0.1498	0.0196	0.6047	0.2848	0.0443	0.1983	0.3722	
Distance to coast	−0.0011	0.0003	−0.0018	0.0005	−0.0008	0.0001	−0.0011	−0.0005	
Distance to river	0.0016	0.0014	−0.0011	0.0043	0.0004	0.0005	−0.0008	0.0009	
Reduced model									
Distance to 1st route	0.0006	0.0002	0.0003	0.0010	–	–	–	–	2551.90
Min. temperature	−0.2759	0.0328	−0.3419	−0.2140	–	–	–	–	
Precipitation	–	–	–	–	−0.0009	8.27E-5	−0.0010	−0.0007	
Road density	0.3135	0.1503	0.0289	0.6157	0.2985	0.0419	0.2172	0.3807	
Distance to coast	−0.0014	0.0003	−0.0019	−0.0007	−0.0009	7.84E-5	−0.0011	−0.0008	

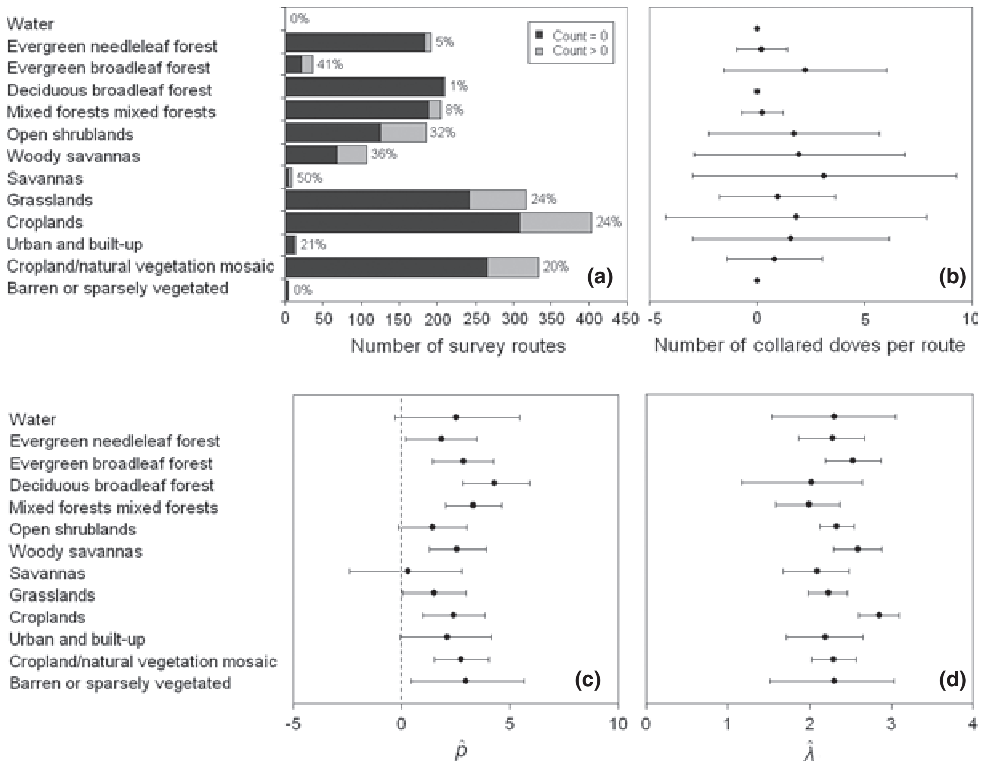

Figure 3. Histogram of number of survey routes in which presence⁄absence of Collared Doves was indicated by MODIS land-cover types (a). Percentage associated with each land-cover type is percentage of survey routes where Collared Doves were observed. Zero per cent indicates that no individual was observed. Land-cover types in which no surveys were conducted were not included. Mean and standard deviation of number of Collared Doves observed per survey route by MODIS land-cover types (b). Posterior and 95% credible intervals of intercepts associated with 13 MODIS land-cover types in logit (p) and Poisson (λ) components for the reduced model (c, d).

savannas, grasslands, and cropland⁄natural vegetation mosaic (Fig. 3).

Compared with ZIP models, Poisson models resulted in larger DIC. When we fit the data with the null Poisson model with distance to the first route as the covariate, the DIC increased by 5080 (DIC = 7867.0) compared with the null ZIP model. With the full Poisson model that included all environmental covariates, the DIC was higher than the full ZIP model by 3159.8 (DIC = 5709.5). These results suggest that ZIP models fit better than the Poisson models.

We used posteriors of the reduced ZIP model to predict bird counts of 300 routes in the independent validation data. Overall, correlation between the observed and predicted count of Collared Dove was not strong ($r = 0.46$). Of 232 routes with actual zero-counts, 221 (95.3%) were correctly classified but 46 routes of 68 routes (67.6%) where Collared Dove was observed were predicted to have zero-counts.

DISCUSSION

The current distribution (presence⁄absence) and abundance of Collared Doves in the USA are characterized by environmental factors similar to those in Europe (Coombs *et al.* 1981, Hengeveld 1988, Beckett *et al.* 2007). Compared with the null model, which contained only distance to the site of initial introduction, models with environmental information, including minimum temperature, precipitation, human disturbance and distance to coast, greatly improved model fit, supporting the influence of environmental parameters on range expansion and growth. In our reduced model, logit and Poisson components included different subsets of environmental covariates, implying that the presence⁄absence and abundance is characterized by different environmental factors.

The distance from the first route was an important explanatory variable for the species presence, but not for abundance; the greater the distance from the first route, the more likely the species was absent. Collared Doves are common in captivity, so multiple releases might have contributed to their range expansion. However, our results indicate that current distribution is still a function of the proximity to the first introduction site.

Minimum temperature was a strong explanatory variable of species occurrence; Collared Doves tend to be absent in areas of low minimum temperature. The species was observed in only 3% of survey routes (eight of 288 routes) where the mean minimum temperature over the past 10 years was below 0 °C. This was consistent with the report of Hengeveld (1988) that in Europe the species occurrence was locally restricted to relatively warm areas. The relationship between Collared Dove occurrence and precipitation has not been well documented. Our results imply that a survey route with higher annual precipitation is more likely to have a zero-count if other factors are held constant, but that annual precipitation does not explain bird abundance. We had confounding results for the estimated coefficients for distance to the coast. Distance to the coast was inversely related to absence of the Collared Dove (i.e. it tends to be present inland), whereas it was positively related to abundance (i.e. it is more abundant near the coast). Notably, Collared Doves dispersed and the population increased more westward along the Gulf Coast than northward along the Atlantic Coast (Fig. 2). These suggest that coastlines might be suitable for population growth if Collared Doves colonize, but there might be other limiting factors affecting presence in coastal habitat. We also cannot ignore the effect of time since colonization on population growth. With data from 1986 to 1996, Romagosa and Labisky (2000) reported a primary dispersal pattern along coasts in Florida. An inverse relationship between distance to the coast and population abundance might result from presence in coastal areas for a longer period. Collared Dove abundance was positively related to road density, which was used as an indicator of human disturbance. This result agreed with observations in Europe, where the species is abundant in human-altered landscapes (Coombs *et al.* 1981, Hengeveld 1988). In contrast to this association of abundance with road density, we had the unexpected result that the species was more likely to be absent when road density increased. These results may imply that Collared Doves are generally more likely to be present in undisturbed areas, but when they do colonize around human settlements they become more abundant. However, we should also note that our sample is potentially biased toward areas where Collared Doves are less abundant, as the BBS tends to avoid areas with the greatest abundance of this species, i.e. large urban areas.

This result was not consistent with the study by Hooten and Wikle (2008), in which human population did not turn out to be a significant covariate in modelling Collared Dove counts. It might be due to differences in indices, as we used road density as an index of human presence instead of population size. It also might be due to the model structure. In our study, human index was a significant factor in the Poisson function that modelled abundance but not in the logit function that modelled zero-count.

An excess number of zeros is a common feature of ecological data and is often related to ecological effects of interest (Martin *et al.* 2005). In spatially attributed data collected in a large geographical range, zero count (i.e. species absence) may be due to demographic processes in a species or environmental factors such as habitat type and other biotic and abiotic factors associated with sampled sites. Accounting for such zero inflation in a model to avoid violation of basic assumptions implicit in the use of standard distributions is important to make appropriate model-based inferences (Martin *et al.* 2005). Zero-inflated models have been used in various ecological studies (Welsh *et al.* 1996, 2000, Barry & Welsh 2002, Podlich *et al.* 2002, Kuhnert *et al.* 2005) and our results also showed that the ZIP model improved model fit compared with a Poisson model, providing additional insight on population inferences.

On the other hand, we should note that we interpreted a zero count as absence and that our analysis did not account for false zero counts. A true zero count signifies actual absence of the species from the location because of ecological effects, whereas a false zero count occurs when the species was not present during the survey period or was not detected. There are two possibilities for how false zero counts could have occurred in the data. First, BBS data may under-represent certain populations of this species, which is most abundant in urban areas; thus zero counts on survey routes do not necessarily denote absence of the species from an area. Secondly, detection probability (the probability of detecting an individual of a species that is known to be present) is influenced by multiple factors such as land-cover type and timing of survey (Harris & Haskell 2007). In our study, we did not address detection probability, but it could be confounded with land-cover type.

In this study, we selected environmental covariates by reviewing literature mainly from studies in Europe, but there are untested factors. Elevation is a factor that potentially affects Collared Dove range, as it was observed that the species is rarely present over 3000 m in its native range in India (Hengeveld 1988). We did not include elevation in our analysis because there were only a small number of BBS survey routes in high-elevation sites where occurrence of this species might be constrained (Hengeveld 1988). Presence of specific landscape features such as parks, gardens and animal food mills may also affect abundance of the species, as association of the species with these features was reported in Britain (Coombs *et al.* 1981); however, including such local information in a large-scale analysis is difficult because of a lack of data. Directional effect is another factor that we did not test in our study. In Europe, there was a tendency for the species to expand its range in a northwesterly arc (Coombs *et al.* 1981). There appeared to be a similar directional trend in range expansion in the USA, as illustrated by yearly maps reported by Hooten *et al.* (2007) and Hooten and Wikle (2008). However, we did not include this potential directional tendency in our model because the Collared Dove was introduced at the southeastern edge of the USA (i.e. northwestward was the natural direction for range expansion). Omission of these environmental factors might explain some of the overall poor prediction accuracy of our model.

The Collared Dove is known to disperse long distances, so-called jump dispersal, and then fill in the gaps (Hudson 1972, Romagosa & Labisky 2000). The bird has currently expanded both westward and northward in North America, but it appears that there are still many gaps where it was not observed (Fig. 2; Hooten *et al.* 2007, Hooten & Wikle 2008). The Common Starling *Sturnus vulgaris*, another common exotic bird in the USA, was purposely introduced from Europe to the east coast. After about a decade, expansion occurred rapidly and was characterized by advance records of winter stragglers, followed later by establishment of breeding birds (Wing 1943, Cabe 1993). Like the Collared Dove, spread was faster across the south and south-central states and followed towns (Wing 1943). The introduction and spread of the House Sparrow *Passer domesticus*, however, exhibited a more uniform front of expansion but it also followed towns and especially railroads (Robbins 1973, Lowther & Cink 2006). What may appear to be jump dispersal in this species is more likely to be purposeful introductions throughout North America (Robbins 1973).

Exotic invasions impact native species and alter biodiversity (Pimentel *et al.* 2000). Studies of the environmental factors related to exotic invasions can assist in predicting invasion trajectories and potential impacts on native communities. Whereas relatively little attention has been paid to the impacts of Collared Dove invasions on native species, potentially negative interactions have been reported (Poling & Hayslette 2006). Further studies are required to understand the ecological impacts of this successful invader on native species. Studies of invasion processes may also provide a framework for understanding the evolutionary process (Duncan *et al.* 2003), or they may demonstrate genetic and life-history differentiation of introduced species (Baker 1922, Selander & Johnston 1967, Baker & Moeed 1987). Moreover, in the context of a changing global climate, inferences about factors contributing to exotic invasions, such as a species' physical tolerance and habitat preferences, can be extended to predict responses of species to climate change (Blackburn & Duncan 2001). In this study, we identified environmental factors that relate to the current distribution and abundance of the Collared Dove more than two - decades after its introduction into North America. On a continental scale, habitat preferences of this species tend to follow human-altered landscapes such as roads and agricultural areas, and may also be influenced by general geographical features such as coastlines and climatic factors such as temperature and precipitation. Our results provide further understanding of habitat selection and potential physiological tolerance of this species and may be useful to predict future range expansions. Also, the observed pattern of range expansion and population abundance may hold true for other invasive species and our results may be useful as a guideline for monitoring and assessment of other invasive taxa.

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figures. The dataset we used for this study was the North American Breeding Bird Survey ftp dataset, version 2009.0, retrieved from the ftp site of the USGS Patuxent Wildlife Research Center (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/datafiles/).

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