



The effect of habitat on the range expansion of a native and an introduced bird species

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ABSTRACT

Aim Range expansion across a heterogeneous landscape may depend on the habitat selected and used by the expanding species. If habitat selection influences range expansion then localities colonized by a species should contain a greater proportion of favoured habitat (and less non-habitat) than other nearby localities not colonized. White-winged doves (*Zenaida asiatica*) and Eurasian collared doves (*Streptopelia decaocto*) are two bird species that provide an excellent opportunity to test this hypothesis, because the geographic ranges of both species have been expanding in North America for more than two decades.

Location Continental USA.

Methods We used distribution data from the North American Breeding Bird Survey to test whether the landscapes occupied by each species contained a greater proportion of favoured habitat (urban land, grassland/pasture, shrub land and cropland) and a lower proportion of non-habitat (forest land) than landscapes where doves were not found. We tested each species separately in each of three broad expansion areas, namely East, Central and West. We also compared rates of spatial spread between expansion areas and between the two species.

Results As predicted, both species tended to occupy landscapes with greater proportions of urban land, shrub land and cropland but with less forest land compared with landscapes without doves, in all three expansion areas. Contrary to prediction, occupied landscapes tended to have slightly less grassland/pasture than unoccupied landscapes. Rates of spread differed between the two species and among expansion areas.

Main conclusions Range expansion and the extent to which a species fills or saturates its range are influenced by the habitat ecology of the expanding species. Species colonize localities based on the availability of suitable habitat. However, the role of habitat in a species' range expansion does depend somewhat on the greater geographical setting. Over large regional and geographical scales, range expansion (rate of spread and saturation) may proceed unevenly, suggesting that range expansion is a very dynamic and context-specific process.

Keywords

Breeding Bird Survey, habitat ecology, invasive species, landscape heterogeneity, North America, range expansion, spatial spread, *Streptopelia decaocto*, USA, *Zenaida asiatica*.

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INTRODUCTION

Our current understanding of range expansion and the spatial spread of invasive species has emerged, to a large extent, from theory and mathematical modelling. As discussed by Hastings *et al.* (2005), the study of spatial spread in species dates back to the diffusion model of Fisher (1937), although Fisher was mostly interested in the spread of an advantageous mutant gene within a species' range and not in range expansion *per se*. Nonetheless, Fisher's model and Skellam's (1951) addition to it became the early foundations for studying range expansion, possibly because of their relative simplicity. Neither model has many parameters: rate of spread is predicted from dispersal (displacement) distance of individuals per unit time and a function describing spatially dependent population increase. A later model (van den Bosch *et al.*, 1990, 1992), proposed as an 'alternative' to the general Fisher–Skellam model, also placed an emphasis on dispersal distances and population growth.

It makes sense that range expansion would be modelled based on dispersal and population growth. Long-distance permanent dispersal of individuals each generation (or time step of a model) effectively puts individuals in new locations, particularly when dispersing individuals are moving away from the current range boundary or 'wave front'. Positive population growth produces 'excess' individuals that are available to disperse. More recently, researchers have recognized that range expansion is a much more complicated process than just modelling dispersal and population increase (i.e. reproduction) as simple mathematical parameters (Liebhold *et al.*, 1992; Hill *et al.*, 2001; Hastings *et al.*, 2005; Hughes *et al.*, 2007; Urban *et al.*, 2008; Duckworth & Badyaev, 2009; Melbourne & Hastings, 2009; Wilson *et al.*, 2009). For example, range expansion might be influenced by environmental heterogeneity within the landscape or region being invaded, by interactions between the invading species and indigenous ones, by density-dependent reproductive success (Allee effects), and by conspecific attraction. All these factors point towards dispersal being non-random, in contrast to the Fisher–Skellam model. Even the actual spatial pattern of range expansion may take several forms other than the classic 'advancing wave' or 'leading edge' (Wilson *et al.*, 2009).

Within spatially heterogeneous landscapes, habitat availability (and habitat preferences of the expanding species) may have a crucial role in the expansion process. A species will colonize and occupy certain types of habitat that facilitate reproduction and hence establishment of new populations while less suitable habitats are not colonized (e.g. Gammon & Maurer, 2002; Balbontin *et al.*, 2008; Bonter *et al.*, 2010). If habitat selection is involved in range expansions, then we should observe a pattern in which colonized sites differ in habitat composition from other nearby locales (i.e. involving no physical dispersal limitation) not colonized. We tested for this pattern in white-winged doves, *Zenaida asiatica* (Linnaeus, 1758) and Eurasian collared doves, *Streptopelia decaocto* (Frivaldszky, 1838), both currently undergoing range expansions in North America. Moreover, the former species is

indigenous to North America whereas the latter is not. Therefore, our study is also a comparison between a native and a non-indigenous species in their patterns and rates of range expansion.

MATERIALS AND METHODS

Habitat of white-winged and Eurasian collared doves

White-winged doves (WWD) and Eurasian collared doves (ECD) are neither ubiquitous generalists nor habitat-specific specialists. Both species seem to prefer and are more common in woodland, shrub land and mid-successional habitats that do not have complete canopy closure (Romagosa, 2002; Schwertner *et al.*, 2002). In the south-western USA and northern Mexico, WWD inhabit thorny woodlands, sometimes in riparian areas, and areas of palo-verde and tall cactus (Schwertner *et al.*, 2002). In Europe and Asia, ECD have historically occupied relatively open habitat with some vertical structure (e.g. scattered tall trees), similar to habitats used in North America (Romagosa, 2002). Being granivorous, both species (particularly collared doves) utilize urban and agricultural areas for food and will also nest in urban/suburban habitats. Both species nest in a variety of tree and shrub species and on some anthropogenic structures (Romagosa, 2002; Schwertner *et al.*, 2002).

Dove occurrence data

We retrieved data on the occurrence of both dove species from the North American Breeding Bird Survey (BBS) by downloading raw data files directly from the BBS website (<http://www.pwrc.usgs.gov/bbs>) (Sauer *et al.*, 2008). The BBS is an annual survey of birds recorded on c. 4000 survey routes located throughout North America. The routes are surveyed by well-trained volunteers (observers) once per year, usually between early May and mid-June. Each route is c. 39.2 km in length and most follow secondary highways and rural roads. Breeding bird surveys have been conducted since 1966, although some routes have been added and some eliminated since the first year. A route is typically (and ideally) surveyed by the same observer each year to minimize any potential 'observer effect' in the data (Sauer *et al.*, 1994; Veech, 2006a). An observer effect occurs when there is a difference in the number of birds counted in successive years simply because different observers counted birds each year; that is, the difference does not represent a real biological effect.

We used all routes in which either WWD or ECD had been recorded in at least 1 year, with the requirement that the routes had been surveyed for at least 5 years (between 1966 and 2008) and the last year of the survey was post-1990. Most routes had more than 10 years of data (the mean number of survey years per route was 20). Only 17% of the routes had data limited to 10 or fewer years, and these were mostly 'new' routes initiated within the last 10 years. About 80% of the routes were currently active (latest survey year = 2008) and

98% had been surveyed since 2000. We did not use routes that were discontinued prior to 1990 because we did not have land cover data for these routes (see next section). Further details on the design and sampling protocol of the BBS can be obtained from Sauer *et al.* (1994, 2003).

For each route, we calculated the number of years for which the route had been surveyed, the first and last years the route was surveyed, the first year that either WWD or ECD were recorded on the route, the number of survey years before each species was recorded, the number of survey years since each species was first recorded, the number of survey years in which each species was recorded, the number of individuals recorded per year for those years that each species was recorded, and whether or not the first year each species was recorded on a route corresponded to a new observer for the route. This correspondence occurred for only about 15% of the routes. WWD and ECD are visually distinctive from one another and from other sympatric doves [mourning dove (*Zenaida macroura*), rock pigeon (*Columba livia*)] and hence we believe that observers probably did not mis-record these species when they existed on a route.

To test whether land cover types might be facilitating range expansion, we needed to statistically compare routes with doves to those without. Therefore, we compiled a group of routes without either dove species. We selected all BBS routes (surveyed since 1990 and with at least five surveyed years) within 60 km of any route with doves. This distance is probably short enough to include routes that could be colonized by doves but have not been (i.e. there is no dispersal limitation) and long enough to give us adequate sample sizes for comparison with the set of routes with doves. In this study, we also assumed that detection probabilities (for each species) were similar among the different routes (where the species actually did occur) and not dependent on the particular land cover composition of the routes or the observer. This is not a critical assumption in that the stipulations (above) for classifying a route as either having or not having a species substantially reduce the chance of misclassifying the route.

We further subdivided the sets of routes with and without doves into three geographic range-expansion areas for each species (Fig. 1). For WWD, range expansion has originated from three sources (in south Florida, south Texas, and the arid south-west of the USA). Expansion has proceeded mostly northwards into what we refer to here as the 'East', 'Central' and 'West' expansion areas; to some extent these three sources might also represent subspecies (Pruett *et al.*, 2000). In the central and western areas, range expansion has been from indigenous sources, in that expansion represents an extension of the species' native range, whereas range expansion in the East has occurred from a single 'point source' representing an anthropogenic introduction (Saunders, 1980; Aldrich, 1981; Stevenson & Anderson, 1994) (Fig. 1). Spread of ECD in North America began in the mid-1980s; it does not represent range expansion by an indigenous species in that the ECD is not native to North America. Because ECD have spread so rapidly and across a very heterogeneous continent, we

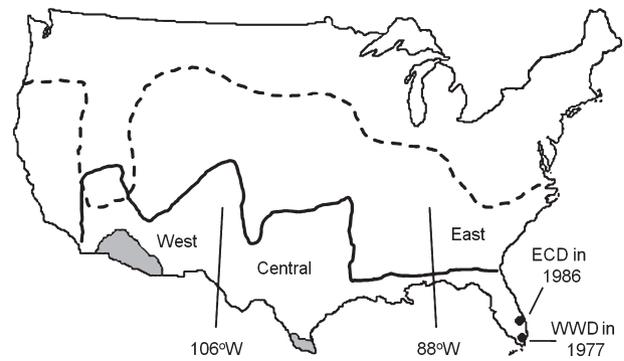


Figure 1 Map of the range expansion areas and sources for white-winged doves (WWD, *Zenaida asiatica*) and Eurasian collared doves (ECD, *Streptopelia decaocto*). For WWD, the range-expansion areas correspond to the three sources of expansion. In the eastern USA, spread of WWD has occurred from a point source, which is depicted as the North American Breeding Bird Survey (BBS) route where WWD were first recorded in Florida in 1977. In the central and western USA, expansion has occurred from parts of the historical range (shown in grey). The eastern expansion area extends from the east coast to latitude 88° W, the central expansion area extends from 88.1° to 105.9° W, and the western expansion area extends from 106° W to the west coast (these longitudinal boundaries correspond to discontinuities in the current distribution of WWD on BBS routes, not shown). The discontinuous range for WWD depicted on the map (grey areas) represents the occurrence of WWD on BBS routes in the initial years of the survey prior to 1970. However, note that the historical range of WWD includes a large area of Mexico, parts of southern New Mexico, and a continuous area along the Rio Grande of Texas (not shown). The solid heavy line represents the current northern range limit for WWD. The entire expansion of ECD has occurred from a single source area in Florida, depicted in the figure as the BBS route where ECD were first recorded in 1986. Since then, ECD has spread into the central and western expansion areas. The dashed line represents the current northern range limit for ECD.

subdivided the ECD expansion into the same three geographic areas as for WWD (Fig. 1). This also facilitated a direct comparison of range expansion between the two dove species.

Land cover data

Land cover data for each BBS route were obtained from the 1992 and 2001 versions of the National Land Cover Database (NLCD). The NLCD is compiled by the Multi-Resolution Land Characteristics Consortium (<http://www.mrlc.gov>), a group of multiple USA federal government agencies. Briefly, the NLCD consists of remote sensing imagery data classified into 20–30 distinct land cover types on a 30 × 30 m pixel grid and formatted as GIS files (Homer *et al.*, 2004). The 1992 and 2001 versions of the NLCD differ in classification of some land cover types. Therefore, in order to use both datasets, we combined land cover types from the 1992 and 2001 versions into five broad categories: urban, forest, shrub, grassland/pasture and cropland. Each category consisted of the following

original land cover types (given as the numeric codes used by the NLCD) from the 1992 and 2001 NLCD: urban (1992: cover types 21–23, 85; 2001: cover types 21–24), forest (1992: 41–43; 2001: 41–43), shrub (1992: 51; 2001: 52), grassland/pasture (1992: 71, 81, 83; 2001: 71, 81) and cropland (1992: 61, 82; 2001: 82). Urban is composed of land developed for industrial, retail, residential, transportation and city park uses. The typical backyard in most neighbourhoods (and entire neighbourhoods) falls within this cover type; again this cover type could supply an important food source inasmuch as residents have bird feeders. Shrub is land covered by natural or semi-natural woody vegetation < 6 m in height over an extent of 25–100% where shrubs and small trees are the dominant plant forms. Forest is land covered by vegetation > 6 m in height at an extent of 25–100% with trees being the dominant plant form. Grassland/pasture is land covered to an extent of 25–100% by herbaceous vegetation that may or may not be grazed. Cropland includes land covered by row crops, cover crops, fallow fields, and orchards. These five broad land categories were also created because they represent cover types that may affect the range expansion of doves. The five categories are not exhaustive, as there are other minor NLCD cover types (barren land, wetlands, open water) that were not included in the categories or analysed in this study. See Bonter *et al.* (2010) for use of NLCD in a similar study.

For each BBS route, we imported NLCD files from the 1992 and 2001 databases into GIS software ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to quantify proportions of each land cover type (category) within a 0.4-km buffer around the route. For each cover type on each route, we then calculated the mean of the 1992 and 2001 estimates. Thus, the land cover composition of each route was categorized into five broad cover types averaged over a period from about the early 1990s to about 2004 (Homer *et al.*, 2004).

We predicted that the urban, shrub, grassland/pasture and cropland cover types should have a positive effect on range expansion; that is, BBS routes with doves should have a greater proportion of these cover types within their 0.4-km buffers than do routes without doves. Shrub, grassland/pasture and cropland are representative of the semi-open habitat of these dove species. In addition, cropland provides food resources in the form of grain and other seed crops. Urban areas also provide food resources in the form of backyard feeders, as well as microclimates that ameliorate the effects of harsh temperatures. We predicted that the forest cover type, in contrast to the foregoing cover types, should not have a positive effect given that forest represents a habitat that is not often utilized by WWD and ECD in North America.

Statistical analysis

We first conducted a one-factor MANOVA testing for differences in land cover composition among the BBS routes, each route assigned to one of four groups: WWD only, ECD only, WWD and ECD co-occurring, and neither species. A separate MANOVA was applied to each range-expansion

area because of differences among the three areas in dominant land cover types. Being a multivariate test, the MANOVA used all five land cover response variables simultaneously in a comparison among the different groups of BBS routes, and thus accounted for any spurious correlation among variables.

We then used logistic regression to test for the predicted effects of each land cover type on dove occurrence on BBS routes. We tested models for each species separately in each expansion area, for a total of six regression models. Each regression model included the five land cover types as independent variables, an estimated non-zero constant, and dove occurrence (coded as '0' for absence and '1' for presence) as the response variable. Our primary interest was to test for the predicted effects of each land cover type; therefore, we used the full regression model (all five land cover variables) and limited our inference to the regression coefficients for each cover type. That is, we were not interested in the overall fit of the models to the data or in finding the exact model with the best fit. Another benefit of using the full models is that a regression coefficient for a given cover type represents the effect of that cover type when the four others are statistically controlled (Sokal & Rohlf, 1995; Gotelli & Ellison, 2004). The logistic regression models allowed us to test whether each land cover type was associated with the occurrence of doves on the BBS routes. In the full regression models a positive coefficient usually represents a greater proportion of the given land cover type on routes with doves than on those without. However, a positive coefficient also indicates that the presence of doves is positively associated with (or predicted by) the given land cover type regardless of whether the land cover type is, on average, greater on the routes with doves than on those without. Revealing these 'hidden' effects is another benefit of the full regression models. We predicted positive coefficients for those cover types presumed to function as 'habitat' for doves (urban, shrub, grassland/pasture and cropland) and a negative coefficient for the cover type (forest) that represents non-habitat. Sample sizes (number of BBS routes with and without doves) for each regression model were as follows: WWD – East: 33, 48; WWD – Central: 114, 72; WWD – West: 76, 36; ECD – East: 200, 163; ECD – Central: 364, 332; ECD – West: 112, 231. Prior to analysis, all response variables (percentage of each cover type) were log-transformed. For each combination of species and expansion area, the untransformed percentages were typically distributed such that there were many small values (< 10%) and only a few large values (> 50%). For these raw data, the log-transformation performed better in creating a normal distribution than the arcsine transformation often used for percentage data.

We calculated the mean rate of latitudinal and longitudinal range expansion for each species in each expansion area. Rate of range expansion was determined from a linear regression of latitude (or longitude) of BBS route (dependent variable) versus year of colonization (independent variable). The slope of the relationship provides an estimate of the mean latitudinal (or longitudinal) expansion in decimal degrees per year. Decimal degrees were converted

into kilometres using the Haversine formula to obtain the following conversion factors: 1 latitudinal degree = 111.2 km and 1 longitudinal degree = 95.8 km. We only included routes where WWD or ECD had not been recorded for at least three years prior to being recorded for the first time on the route. Thus, the year of colonization was defined as the first year the species was recorded on the route (we assumed that three consecutive years of no recorded occurrence was sufficient to indicate the absence of the species). For WWD, sample sizes were 29, 73 and 22 routes in the East, Central and West expansion areas. For ECD, sample sizes were 196, 379 and 113 routes in the East, Central and West expansion areas.

Finally, we also tested for significant co-occurrence between WWD and ECD in each expansion area using the probability-based test of Veech (2006b). The probability of occurrence of each species was calculated as the number of routes where the species was recorded divided by the total number of routes (total = routes where doves were recorded and routes within 60 km of those routes). The probability of co-occurrence was calculated as the joint probability of each species probability of occurrence, or $P(\text{WWD}, \text{ECD}) = P(\text{WWD}) \times P(\text{ECD})$. We then obtained the expected number of routes representing co-occurrence as $P(\text{WWD}, \text{ECD}) \times M$, where M equals the number of routes within the range of WWD (those routes where WWD was recorded and routes within 60 km). The observed and expected numbers of co-occurrences were then compared with a chi-square test. This test determines whether two species are randomly, positively, or negatively associated (Veech, 2006b). All statistical analyses were performed using either SPSS 17.0 or EXCEL.

RESULTS

The MANOVAs revealed many significant differences among the four groups of routes classified as either WWD only, ECD only, WWD and ECD, or neither species. In each of the three expansion areas (three separate MANOVAs) the mean proportion of each cover type was significantly different among the groups ($P < 0.0001$), except for cropland in the East expansion area ($F_{3,359} = 1.58$, $P = 0.193$), and forest ($F_{3,761} = 1.72$, $P = 0.161$) and grassland/pasture ($F_{3,761} =$

0.63, $P = 0.594$) in the Central expansion area. These results indicate that, for both species, differences existed between landscapes (0.4-km buffers) of routes with and without doves when analysed simultaneously with a multivariate test. Given these differences, we then used the logistic regression models to test more precisely for effects of each land cover type on each species.

For both species in all three expansion areas, the logistic regression models revealed many significant differences ($P < 0.05$) among routes with and without doves (Table 1). In accordance with our predictions, urban, shrub and cropland cover had positive regression coefficients (except for urban for WWD in the West expansion area), and forest cover had negative coefficients (except for WWD in the Central expansion area) (Table 1). In addition, urban, shrub and cropland cover tended to be greater on routes with doves whereas forest cover was lower on those routes (Fig. 2). Typically, the differences in grassland/pasture were either non-significant or in the opposite direction to our prediction; that is, the percentage of grassland/pasture cover was greater on routes without doves (Fig. 2) and/or the regression coefficients were negative (Table 1).

The most striking difference regarding rates of expansion was the much greater rate for ECD than for WWD in all of the expansion areas (Table 2). The rate in both a latitudinal and a longitudinal direction was generally 5–27 times greater for ECD than for WWD in all expansion areas, except for the low and equal rates of longitudinal expansion in the East. Expansion rates for WWD were relatively low in all expansion areas, between 3 and 13 km year⁻¹, whereas ECD expansion rates were greatest in the West (Table 2). The 95% confidence intervals (CIs) for the estimated rates are large, particularly for larger estimates (e.g. longitudinal expansion of ECD in the West). This is attributable, in part, to the way in which rate was measured as a central tendency in a regression and not as a maximum rate.

Percentage occupancy of each species' range in each expansion area varied between species and among expansion areas [$P(\text{occur})$ in Table 2]. The co-occurrence analysis based on the individual species' probabilities of occurrence [$P(\text{WWD})$ and $P(\text{ECD})$] and the joint probability [$P(\text{WWD}, \text{ECD})$] revealed significant positive associations between

Table 1 Coefficients from the logistic regression models testing for the effect of each land cover type on the presence of white-winged doves (WWD, *Zenaidura macroura*) and Eurasian collared doves (ECD, *Streptopelia decaocto*) in each of the three expansion areas in the USA. The sign of the coefficient indicates whether the land cover type had a positive or negative effect in predicting the presence of doves on the BBS routes. P -values are given in parentheses; significant ($P < 0.05$) values are given in bold.

	Urban	Forest	Shrub	Grassland/Pasture	Cropland
WWD – East	2.89 (< 0.001)	-3.58 (< 0.001)	2.44 (0.003)	-1.75 (0.020)	0.23 (0.665)
WWD – Cent.	2.09 (< 0.001)	0.16 (0.471)	2.40 (< 0.001)	0.54 (0.133)	0.28 (0.285)
WWD – West	-0.22 (0.655)	-0.81 (0.002)	1.58 (0.006)	-1.03 (0.006)	1.31 (0.001)
ECD – East	2.11 (< 0.001)	-1.07 (0.003)	2.20 (< 0.001)	-0.17 (0.662)	0.45 (0.097)
ECD – Cent.	1.38 (< 0.001)	-0.19 (0.154)	0.40 (0.005)	0.21 (0.29)	0.34 (0.025)
ECD – West	0.76 (0.066)	-0.02 (0.925)	1.05 (0.004)	0.39 (0.251)	1.39 (< 0.001)

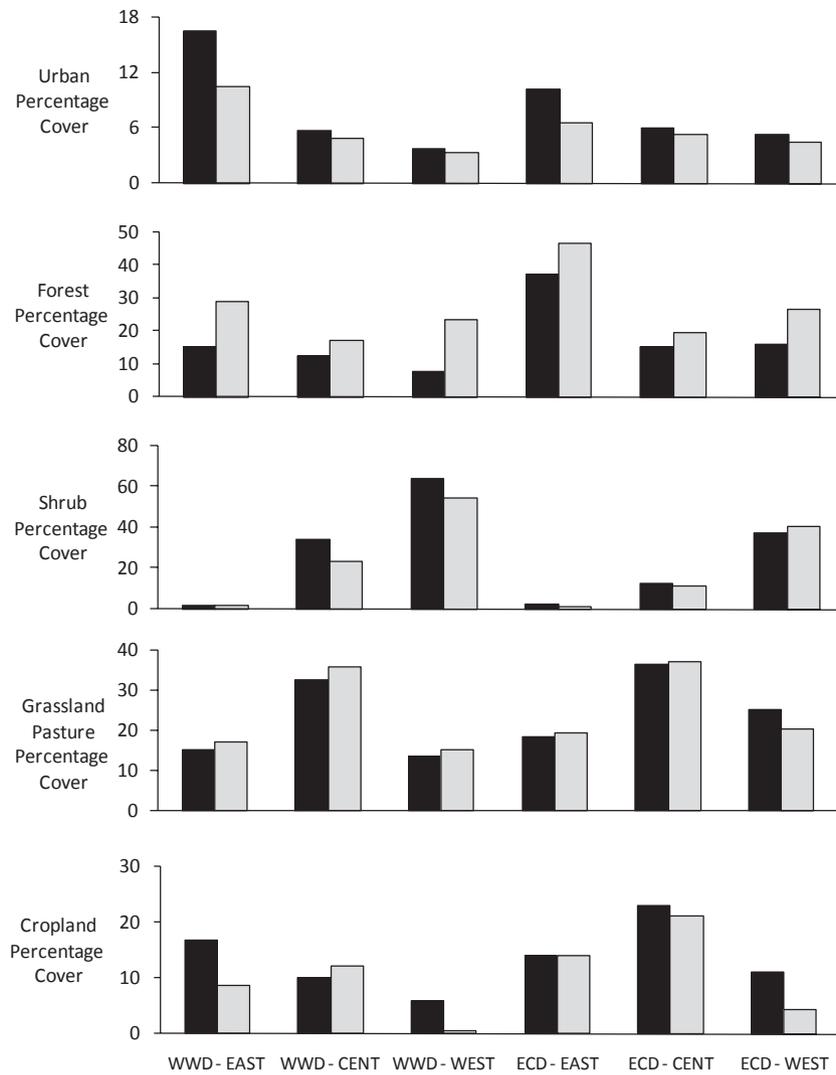


Figure 2 Mean percentage cover of each land cover type for North American Breeding Bird Survey (BBS) routes with doves (black bars) and without doves (light grey bars). Results are shown for each species, white-winged doves (WWD, *Zenaida asiatica*) and Eurasian collared doves (ECD, *Streptopelia decaocto*), in each expansion area of the USA (East, Central and West).

Table 2 Mean rate of expansion (km year⁻¹) for white-winged doves (WWD, *Zenaida asiatica*) and Eurasian collared doves (ECD, *Streptopelia decaocto*) in each of three expansion areas of the USA. All latitudinal expansion is northwards; longitudinal expansion is either eastwards (e) or westwards (w). Values in parentheses are 95% confidence intervals. *P*(occur) is the probability of occurrence, either *P*(WWD) or *P*(ECD), calculated as the number of North American Breeding Bird Survey (BBS) routes with doves as a proportion of the total number of routes (with doves and those routes within 60 km) in the expansion area.

Species	Expansion area	Latitude	Longitude	<i>P</i> (occur)
WWD	East	8.8 (0–17.3)	9.6w (2.1e–21.4w)	0.385
WWD	Central	12.8 (7.3–18.2)	4.2e (12.5e–4.2w)	0.599
WWD	West	5.6 (0–11.2)	2.7e (17.6e–12.4e)	0.661
ECD	East	44.7 (35.3–54.2)	6.6w (2.0e–13.8w)	0.517
ECD	Central	60.1 (40.8–79.4)	58.0w (38.3w–77.7w)	0.517
ECD	West	155.7 (100.4–211.1)	73.4w (13.5w–133.2w)	0.312

WWD and ECD in the East (observed co-occurrence = 33 routes, expected = 19, $\chi^2 = 10.05$, $P = 0.0015$) and Central (observed co-occurrence = 81 routes, expected = 59, $\chi^2 =$

7.77, $P = 0.0053$) but a non-significant or random association in the West (observed co-occurrence = 31 routes, expected = 24, $\chi^2 = 2.23$, $P = 0.14$).

DISCUSSION

Our study revealed that habitat ecology does influence the process of range expansion. Both dove species colonized sites (i.e. BBS routes) that had greater proportions of urban, shrub and cropland cover and less forest cover. Another recent study also found positive associations of white-winged and collared doves with urban and agricultural land and a negative association with forest land, although in a limited geographic area (Bonter *et al.*, 2010). Urban land, shrub land and cropland represent habitat that is relatively open (structurally) and likely to provide year-round food resources. Individuals of both species are primarily granivores and forage on the ground (Romagosa, 2002; Schwertner *et al.*, 2002). Open habitat allows for predator vigilance and for unhindered escape when taking flight from the ground. In addition, doves prefer to nest and roost in scattered trees and even on anthropogenic structures such as utility wires (Romagosa, 2002). Therefore, locales providing these resources will tend to be colonized, and populations will tend to establish more rapidly than in locales lacking these resources. Interestingly, range expansion in these two dove species did not appear to be facilitated by grassland and pasture habitat, perhaps because it is too open and lacks roosting and nesting sites. At some level, habitat 'selection' was likely to be occurring in both species as there were many uncolonized areas (i.e. unoccupied BBS routes) near to each colonized site; percentage occupancy was 31–66% (Table 2). All of the uncolonized areas used in this study were within 60 km of a colonized site, well within the daily foraging flight distance of each species (Small *et al.*, 2006), and scattered throughout each species' expanding range. In addition, both species are prolific breeders (Cottam & Trefethen, 1968; Romagosa, 2002). Thus, dispersal and propagule limitation are probably not involved in preventing colonization.

In theory, potential competition with other species already established in an area could prevent colonization by the two dove species. Although we did not examine this possibility, we do not believe it has much influence on the range expansion of either species. There is no reason to believe that any of the cover types or entire BBS routes are more (or less) saturated with potential competitors than any other cover type or route. In addition, Bonter *et al.* (2010) found that white-winged dove and Eurasian collared dove abundances were positively correlated at different survey sites throughout Florida, USA.

To our knowledge, this is the first study to estimate a rate of spread in white-winged doves, although rates have been estimated for Eurasian collared doves in Europe. Collared doves are thought to have originally been endemic to India, having spread to Turkey during the four centuries prior to 1900 (Fisher, 1953). They began spreading in a north-westerly direction out of Turkey around 1900 (Fisher, 1953) and by the 1980s they had colonized most of Europe (Hengeveld, 1988, 1992). By regressing the square root of the expanding range size against time, van den Bosch *et al.* (1992) estimated a mean rate of spread of 43.7 km year⁻¹ for collared doves expanding throughout Europe between 1900 and 1980. This estimate is

similar to what we found for collared doves in the eastern and central expansion areas but slightly lower than the estimate for the western expansion area (Table 2). In the early 1990s, collared dove distribution in North America was still limited to Florida, but Hengeveld (1993) correctly predicted that the species would quickly colonize most of the USA. He recognized that environmental variation and the spatial distribution of favourable habitat could affect the rate of spread. Fisher (1953) also commented on distinct habitat preferences (for urban and agricultural areas) influencing the spread of collared doves in Europe.

In our study, the role of habitat in each species' range expansion differed somewhat among the three expansion areas. Most notably, cropland facilitated expansion more in the western USA than in the central or eastern portions (Table 1, Fig. 2). Cropland is least abundant in the west: perhaps the food and water resources associated with cropland are relatively more beneficial to doves in the arid west than in the central or eastern portions of the USA, where these resources are more widely available. Urban land was more important to expansion in the eastern USA than in the West (Table 1, Fig. 2). This may be attributable to urban land (more specifically, residential areas and parks) in the east providing the vertical structure necessary for nesting. Preferred breeding habitat in the form of shrub land is scarce in the east. It is also interesting that the cover type most closely resembling the 'natural habitat' of both species (shrubs) is the only one for which there was a positive association in all three expansion areas (Table 1).

Spatial aspects of the range expansions also differed among the three geographic regions. White-winged doves colonized a greater proportion of available sites in the central and western regions (0.60 and 0.66, respectively) of the USA than in the eastern region (0.39). Eurasian collared doves colonized a greater proportion in the eastern and central regions (0.52 for both) than in the western region (0.31). Both species seemed to be more efficient colonizers within the central USA than in the East or West, based on a combination of a relatively high proportion of colonized sites and rapid latitudinal and longitudinal rates of spread within the central USA (Table 2). Again, the ubiquity of agriculture and relative lack of expansive forests in the central USA (i.e. Great Plains and Midwest) probably facilitate range expansion in this region. Differences among broad geographic regions in the dynamics of range expansion in both dove species highlight the general variability of the process. Even within a region, the rate of expansion could vary considerably both spatially and temporally depending on local geographic factors (e.g. habitat availability, dispersal barriers) and short-duration temporal factors (e.g. unusually beneficial or detrimental weather). Owing to data constraints, these details were not examined in this study. In nature, range expansion is multifaceted. It does not proceed as a constantly advancing wave of colonists that saturates all locales on an environmentally homogenous surface.

Although the range expansions of both species are likely to be affected by habitat availability, climate has been indicated as the

driving force in the range expansions of some species (Parmesan *et al.*, 1999; Hickling *et al.*, 2006). A few other bird species, in addition to white-winged doves, have extended their ranges northwards by tens to hundreds of kilometres from southernmost Texas (USA) over the past few decades (Rappole *et al.*, 2007). These range expansions may result from an increase in mean annual temperature over this time period (Rappole *et al.*, 2007), in essence an ameliorating winter climate allowing the species to exist further north. The spread of Eurasian collared doves within the United States has been so thorough and rapid that local climate may not be important to its range expansion. In addition, Eurasian collared doves may have broader physiological tolerances to harsh climate than do the semi-tropical bird species expanding out of southern Texas.

The greatest difference between the two dove species was in their estimated mean rates of expansion. Eurasian collared doves, the non-native invasive species, expanded much more rapidly than white-winged doves in all three geographic regions (Table 2). The two dove species were very similar in the land cover types that facilitated expansion (namely urban land, shrub land and cropland). These shared habitat 'preferences' were also reflected in the two species having positive patterns of co-occurrence; that is, they co-occurred more often than expected by chance. Thus, our study illustrates a case in which a non-indigenous species is spreading much more rapidly (and over a greater area) than an indigenous species, even though both colonize sites based on the amount of shared habitat. Because the two species do not differ in habitat, by default some other factors (e.g. differences in vagility, physiological tolerances to climatic extremes) must be responsible for the greater rate of spread in Eurasian collared doves. The comparatively faster rates of spread in non-native invasive species may be more a function of species traits than the environment. For good reason, the study of range expansion and the spatial spread of organisms has moved beyond mathematical models that include individual dispersal rates and population growth rates as the sole parameters. As discussed by Hastings *et al.* (2005), there has always been a productive interplay between theory and data in this area of ecology, even though the early models of Fisher and Skellam may be too concise to truly describe actual patterns in nature. Temporally and spatially, range expansion is a complicated process. As illustrated by two previous studies (Gammon & Maurer, 2002; Balbontin *et al.*, 2008), it is informative to study the potential role of habitat selection in the process of range expansion. At the very least, the possibility of habitat selection occurring on a heterogeneous landscape forces us to recognize that dispersal is probably best modelled as a non-random process. Our understanding of the process of range expansion may be improved by greater recognition that habitat (and habitat selection by species) can greatly influence colonization patterns and hence range expansion.

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BIOSKETCHES

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