

Article type: Original Article

Spatial and temporal variation an expanding columbid: white-winged doves in North America

Jerrold A. Butcher<sup>1,2,3</sup>, Texas A&M University, Department of Wildlife and Fisheries, 2258 TAMU, College Station, TX, 77843-2258, USA

Bret A. Collier, Texas A&M Institute of Renewable Natural Resources, 2260 TAMU, College Station, TX, 77843-2260, USA

Jay A. Roberson, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA

Nova J. Silvy, Texas A&M University, Department of Wildlife and Fisheries, 2258 TAMU, College Station, TX, 77843-2258, USA

Markus J. Peterson, Texas A&M University, Department of Wildlife and Fisheries, 2258 TAMU, College Station, TX, 77843-2258, USA

<sup>1</sup>Corresponding author

<sup>2</sup>Current address: Alvin Community College, Biological Sciences, 3110 Mustang Road, Alvin, TX, 77511, USA

<sup>3</sup>[jbutcher@alvincollege.edu](mailto:jbutcher@alvincollege.edu)

Spatial and temporal variations in the dispersal rates of white-winged doves

Word count: abstract = 298, body = 3,307

## ABSTRACT

AIM: We examined spatial and temporal patterns of range expansion of white-winged doves along the northern edge of their geographical range from 1979 to 2007, while accounting for imperfect detection. We developed a model that aided us in predicting when and where white-winged doves would be found in the future.

**LOCATION:** Our study covered the southern half of the United States.

**METHODS:** We developed spatial expansion models of white-winged doves using data from North American Breeding Bird Surveys (BBS). Variables used to model spatial variation in expansion included distance from initial population center, area of urban land cover, and ecoregion. We used robust design occupancy analysis to predict expansion of white-winged doves, Akaike's Information Criterion to rank potential models, and compared and estimated parameters using PRESENCE 4.2. We evaluated models by comparing predictions to actual observations in 1991 and 2007 using the area under the curve (AUC) of a receiver-operating characteristic (ROC) plot.

**RESULTS:** The best model from our set estimated occupancy on distance from initial population; held colonization constant between 1979 and 1991; estimated colonization from 1993 to 2007 on distance from initial population, ecoregion, and urban land cover; estimated local extinction on distance from initial population; and estimated probability of detection on ecoregion and urban land cover. In 1991, our model was an excellent predictor for detecting white-winged doves (AUC = 0.979). In 2007, our model was a useful predictor (AUC = 0.824).

**MAIN CONCLUSIONS:** Predicting occurrence of white-winged doves can be completed effectively using BBS data when one accounts for imperfect detection. Accounting for imperfect detection allowed us to use a nationwide, readily-available, long-term survey to accurately model spatial expansion of white-winged doves. Our novel approach of treating each BBS route as independent secondary survey within the primary sample periods allowed us to account for imperfect detection.

**KEYWORDS:** introduced, invasive, dispersal rate, population, range expansion, spatial, velocity of spread, white-winged doves, *Zenaida asiatica*

Over the past 60 years, white-winged doves (*Zenaida asiatica* Linnaeus, 1758) have expanded their geographical range considerably in North America (George *et al.*, 1994; Schwertner *et al.*, 2002; Veech *et al.*, 2011). As recently as 1987, the northern extent of the geographic range of white-winged doves was southern Texas. However, by 2001 breeding colonies were recorded >800 km north in Kansas (Moore, 2001). In 1959, humans introduced white-winged doves into southern Florida; the species then expanded its range northward into Georgia and southern North Carolina (Aldrich, 1981; Schwertner *et al.*, 2002). Expansion of white-winged dove ranges has attracted the attention of biologists and hunters; however, data on factors driving the spatial spread of the species are lacking (Veech *et al.*, 2011). In fact, a majority of the current knowledge on white-winged doves continues to focus on their historic geographical ranges such as Arizona and southern Texas (Schwertner *et al.*, 2002; Rabe & Sanders, 2010).

Spatial spread of species (i.e., expansion of geographic range) has long interested biologists (Fisher, 1937; Skellam, 1951; reviewed in Hasting *et al.*, 2005) based in part on their desire to predict when and where a species will be in the future (Hastings *et al.*, 2005). Predicting expansion rates and locations of spread could provide opportunities for biologists to experimentally vary processes that potentially influence the ecology of species (Cassey, 2005) and permit optimal impact study designs (Green, 1979). Accurate expansion predictions also would provide opportunities to assess potential risks to native biota (Johnson *et al.*, 2001; Wittenberg & Cock, 2001; Arriaga *et al.*, 2004) and devise alternative biosecurity procedures before invasive species arrive (Williamson, 1999; Hooten & Wikle, 2008).

As empirical and theoretical understanding of spatial dynamics increased, modeling frameworks for describing expansion patterns included reaction-diffusion and integro-difference equations, among others (Kinlan & Hastings, 2005). Variations of these modeling frameworks have a variety of assumptions, ranging from those that assume a continuous space and time and deterministic dynamics at the level of the population (Fisher, 1937; Skellam, 1951) to models that include spatial heterogeneity, competitors, mutualists, and natural enemies (Shigesada *et al.*, 1986; Obuko *et al.*, 1989; Richardson *et al.*, 2000; Mandon-Dalger *et al.*, 2004). Underlying both types of models is the implicit assumption that empirical data upon which the models are calibrated is correct; more specifically, that if the species was present it was perfectly detected and recorded as present—an assumption not likely satisfied for most species (MacKenzie *et al.*, 2003).

Failure to account for imperfect detection leads to biased estimates of occurrence and colonization rates of new locations (MacKenzie *et al.*, 2003). With reaction-diffusion and integro-difference equations, dispersal estimates are generally developed from empirical data. Examples of empirical data include spatial databases of species collection locations, field mapping of a spreading species, and species lists across a region. Predicted rates of spread based on such empirical data are often much lower than observed (Hastings *et al.*, 2005).

Modeling approaches which account for imperfect detection in models of spatial spread are available (MacKenzie *et al.*, 2003), with the primary form being a robust design occupancy approach. Robust design occupancy assesses spatial and temporal variations in occupancy rate, colonization, and local extinction probabilities relative to spatial dynamics of species (MacKenzie *et al.*, 2003; Royle & Nichols, 2003; Eraud *et al.*, 2007). It also allows for the inclusion of long distance dispersal, interactions with other species, and spatial heterogeneity—

three of the five types of biological information that were suggested by Hastings *et al.* (2005) as attributing to progress in understanding dynamics of spread. Long distance dispersal can be included in the models for colonization given survey effort includes all areas where the species could have spread. Although survey efforts often are restricted by factors other than biology (e.g., funding limitations, political borders), there are situations when including all areas is possible.

Factors driving spatial and temporal variation in expansion of white-winged doves are uncertain across the species range. However, two general patterns have emerged. First, since the 1970s, breeding populations of white-winged doves in Texas have increased in urban areas (George *et al.*, 1994; Hayslette & Hayslette, 1999; Small & Waggerman, 1999). The largest populations of white-winged doves in central Texas are now found in urban habitats (West *et al.*, 1993; Small & Waggerman, 1999; Small *et al.*, 2005; Small *et al.*, 2007). Second, expansion differs across the geographic range (George *et al.*, 1994). Little expansion has been reported in the western extent of the range (George *et al.*, 1994), moderate northward expansion has been recorded in western Texas (Small *et al.*, 1989), rapid expansion has occurred in central Texas (Hayslette & Hayslette, 1999; Small *et al.*, 2007), and rapid expansion has occurred in the Florida population (Aldrich, 1981; Schwertner *et al.*, 2002). There are two recognized subspecies of white-winged dove breeding in the United States: *Z. a. asiatica* and *Z. a. mearnsi* (Integrated Taxonomic Information System, 2009). *Z. a. asiatica* breeds in eastern Mexico, Texas, and southeastern United States and includes the introduced population in Florida. *Z. a. mearnsi* breeds in west-central Mexico, Baja California, and southwestern United States, including western Texas (Schwertner *et al.*, 2002).

Our objectives were to (1) examine spatial and temporal expansion of white-winged doves along the northern edge of their geographical range in North America from 1979 to 2007 while accounting for imperfect detection and (2) develop a model that would aid us in predicting when and where white-winged doves would be found in the future. We envision our work leading to increased knowledge of the timing and locations where white-winged doves occur and, therefore, opportunities to use optimal impact designs to examining processes influencing distribution and abundance of white-winged doves across their range.

## **Methods**

### **Data for modeling**

#### *Species movement data*

We developed spatial expansion models of white-winged doves using data from North American Breeding Bird Surveys (BBS). Breeding Bird Surveys are conducted annually during the height of the avian breeding season (i.e., June) along secondary roads. Each route along a road includes 50 stops (approximately 0.8 km apart) over 39.4 km. Since the inception of BBS, Patuxent Wildlife Research Center has added new routes while discontinuing others. At present, approximately 4,100 routes are surveyed across the United States and Canada annually (Sauer *et al.*, 2008).

A preliminary analysis of BBS routes indicated that white-winged doves have been detected at routes in Texas and Arizona since 1968. White-winged doves were first detected at a BBS route in Florida in 1979, 20 years after introduction. Our analysis of the spatial expansion of white-winged doves began with BBS data collected in 1979 to allow for comparisons among

the white-winged dove populations introduced in Florida and elsewhere. We included in our study every other year from 1979 through 2007.

We placed 150-km diameter hexagons (19,485 km<sup>2</sup> each) across a map of the southern United States using ArcGIS 9.3 (ESRI, 2008). We considered each hexagon to be a sample unit. We chose this diameter of hexagons to ensure that most, if not all, doves breeding in one hexagon would not be counted in neighboring hexagons. The mean estimated daily movement of white-winged doves is 20 km, or about 10 km one direction and 10 km back (George *et al.*, 1994). Two BBS routes within a hexagon would cover <80 km. Doves flying 10 km away from either end of the routes would likely remain within the hexagon.

#### *Environmental data*

We used ArcGIS to calculate explanatory variables for each sample unit. Variables used to model spatial variation in expansion included distance from initial population center, area of urban land cover within the sample unit, and ecoregion. We identified the initial population as those hexagons where white-winged doves were detected in 1979. We included area of urban land cover within each hexagon because urban areas are known centers of high concentration of white-winged doves (Schwertner *et al.*, 2002). Area of urban land cover was calculated as the total area defined as urban by U.S. Geological Survey (2001). We included ecoregions (U.S. Environmental Protection Agency, 2005), because white-winged doves are more likely to colonize an area if it contains environmental conditions that provide for positive fitness outcomes (Begon *et al.*, 2006). We included a temporal variable that separated years into two time periods: 1979–1991 and 1993–2007. Based on a preliminary analysis of BBS data we observed a distinct inflection at the year 1991 in a graph showing the number of routes where white-winged doves were detected (Fig. 1).

## Modeling Method

### *Robust design occupancy analysis*

We used robust design occupancy analysis to predict expansion of white-winged doves across the United States. Robust design occupancy modeling requires sample units be surveyed independently on multiple occasions per season (MacKenzie *et al.*, 2003). We treated each hexagon surveyed within a season as the primary sampling period and surveys of routes within the hexagon as secondary sampling periods within a season (Mackenzie *et al.* 2006). We assumed BBS routes within a hexagon that were surveyed during a single season were independent of one another. We assumed no change in occupancy of a hexagon within each season: a reasonable assumption given that white-winged doves are site-faithful (Schwertner *et al.*, 2002, Collier *et al.*, *in press*). Detection histories within the hexagons were used to estimate site occupancy at time  $t$  ( $\psi_t$ ), colonization at time  $t$  ( $\gamma_t$ ), and detection at time  $t$  ( $p_t$ ). Estimates of site extinction at time  $t$  ( $\varepsilon_t$ ) were derived (MacKenzie *et al.*, 2006).

### *Model comparison, calibration, and evaluation*

We developed a set of potential models that we hypothesized explained the observed spatial spread of white-winged doves. We modeled colonization as a function of the two time periods (1979–1991 and 1993–2007), amount of urban area within each hexagon ( $u$ ), distance from initial population ( $d$ ), and ecoregion ( $e$ ). We modeled the probability of detection as a function  $u$  and  $e$ . We had no expectations for local extinction processes; however, to improve model precision we modeled extinction as a function of  $d$ . We used Akaike's Information Criterion ( $AIC_c$ ) to rank potential models, and compared and estimated parameters using PRESENCE 4.2 (Hines, 2006).



To evaluate quality of predictions of models we randomly split survey data into two sets. The first set consisted of 70% of the total data, and was used to calibrate the models. The second set, the remaining 30% of the total data, was used to evaluate the models. We evaluated the models by comparing predictions to actual observations in 1991 and 2007 using the area under the curve (AUC) of a receiver-operating characteristic (ROC) plot (Fielding & Bell, 1997). We used Swets' scale (Swets, 1988) to determine whether predictions differed significantly from actual observations. Swets's scale classifies models whose AUC range from 0.5 to 0.7 as poor predictors, AUC range from 0.7 to 0.9 as useful predictors, and AUC that are greater than 0.9 as good to excellent predictors. AUC values below 0.5 reveal that the model has a higher rate of omissions and commissions than correct predictions.

## Results

The number of hexagons (area) surveyed per year ranged from 114 (2,221,290 km<sup>2</sup>) in 1983 to 151 (2,942,235 km<sup>2</sup>) in 2005 and 2007. A total of 158 hexagons were surveyed during at least one year. In 1979, survey crews detected white-winged doves at 12% of hexagons. By 2007, white-winged doves were detected at 41% of hexagons. The proportion of hexagons where white-winged doves were detected increased slightly between 1979 and 1991 (0.12 to 0.15, respectively). Between 1979 and 2007 the proportion of hexagons where white-winged doves were detected increased more quickly (0.21 to 0.41, respectively) (Table 1).

Models holding colonization constant between 1979 and 1991 consistently outperformed those that did not (Table 2). Models including ecoregion to modeling colonization outperformed those that did not. Generally, models that used only urban land cover to model probability of detection outperformed those that used only ecoregion.

The best model from our set estimated occupancy on distance from initial population; held colonization constant between 1979 and 1991; estimated colonization from 1993 to 2007 on distance from initial population, ecoregion, and urban land cover; estimated local extinction on distance from initial population; and estimated probability of detection on ecoregion and urban land cover (Table 2). Our evaluation of the model for predictions made in 1991 revealed that the model was an excellent predictor for detecting white-winged doves throughout the southern part of the United States (AUC = 0.979). An evaluation for predictions made in 2007 showed that the predictive power of the model decreased, but could still be considered a useful predictor (AUC = 0.824).

Colonization depended on time, distance from initial population, ecoregion, and urban land cover. Probability of colonization was greater between 1993 and 2007 than between 1979 and 1991 (Table 3). Probability of colonization decreased as the distance from initial population increased, but the decrease varied according to the ecoregion and the area of urban land cover (Figs 2–4). The Great Plains had the highest probability of colonization, followed by the North American Deserts, and then other ecoregions, which were dominated by the Eastern Temperate Forest. In all cases, probability of colonization was greatest in areas with the highest amount of urban land cover. Probability of extinction increased as distance from initial population increased (Fig. 5).

Probability of detection was influenced by urban land cover and ecoregion. In all ecoregions, the probability of detection decreased as urban land cover increased (Fig. 6). Probability of detection was greatest in the North American Deserts and lowest in the Great Plains.

Probability of occupancy decreased with distance from the initial population (Fig. 7). From 1979 to 1991, the probability of occupancy decreased slightly each year at locations between 100 and 600 km from the initial population. At sites within 100 km of from the initial population probability of occupancy held steady (range: 0.75–0.82). At sites further than 600 km away from the initial population, probability of occupancy remained low (range: 0.03–0.04) (Fig. 7). After 1991, the probability of occupancy varied among ecoregions, with distance from the initial population, and with area of urban land cover. Probability of occupancy in 2007 was greatest in the Great Plains and least in the Eastern Temperate Forest when comparing areas with equal urban land cover (Figs 8–10). In all ecoregions, urban land cover was positively related to probability of occupancy. The influence on probability of occupancy of large urban areas (those >1000 km<sup>2</sup>) increased at locations >450 km from the initial population. In the Great Plains, probability of occupancy decreased until at all levels of urban land cover until a site was 500 km from the initial population (Fig. 8). Between 500 and 650 km from the initial population the probability of occupancy increased in areas with >1,200 km<sup>2</sup> urban land cover.

## **Discussion**

Predicting the occurrence of white-winged doves can be completed effectively when one accounts for imperfect detection. We found that urban land cover, ecoregion, and distance from initial population were valuable at predicting occurrence of white-winged doves across the southern half of the United States. Colonization of new areas by white-winged doves depends on area of urban land cover, ecoregion, and distance birds must travel. Imperfect detection could be accounted for by urban land cover and ecoregion.

White-winged doves were more likely to colonize and, therefore, occupy urban areas. Historically, the largest nesting colonies of white-winged doves were found in densely vegetated rural scrub- and woodlands (Cottam & Trefethen, 1968). At present, the largest nesting colonies are found in urban environments. White-winged doves have colonized many of the large urban areas in the southern United States (Schwertner *et al.*, 2002).

Although white-winged doves were more likely to occupy urban areas, they were less likely to be detected there. We maintain this relationship between occupancy and detection is due to the distribution of white-winged doves within urban environments. White-winged doves nest in large colonies in a clumped distribution across a landscape (Small *et al.*, 2005). Colonies of breeding doves are larger in urban environments than in open habitats, such as their historical breeding ranges in southern Arizona and southern Texas (Schwertner *et al.*, 2002). In southern Arizona, white-winged doves form colonies along waterways (e.g., arroyos, rivers), which are long and linear (Cottam & Trefethen, 1968; Schwertner *et al.*, 2002). In southern Texas, white-winged doves nest in scrub-oak forests and in orchards (George *et al.*, 1994; Schwertner *et al.*, 2002).

We found that white-winged dove colonization was most rapid in the Great Plains, followed by the North American Deserts, and the Temperate Forest. Causes for the northward colonization of white-winged doves in any ecoregion are uncertain (Schwertner *et al.*, 2002). Two hypotheses accounting for this northward expansion are a food availability and a warmth. The food available hypothesis suggests that breeding seasons can be longer in urban areas because food is available for a longer period of time due to human-established bird feeding (Schwertner *et al.*, 2002). The warmth hypothesis suggests that breeding season is longer because the ambient temperature in urban environments remains higher and more stable in cold

weather (Hayslette & Hayslette, 1999). Although, the validity of these hypotheses is uncertain, we expect that colonization may be more rapid in the Great Plains than in the North American Deserts and the Temperate Forest because natural barriers to colonization, such as mountains ranges, are not found in the Great Plains.

From 1993 through 2007, white-winged doves expanded their geographic range the furthest in the Great Plains, followed by the North American Deserts, and then the other ecoregions, where Temperate Forest predominated. We suggest that occupancy, like colonization in the Great Plains, was not inhibited by mountains ranges as was likely in the North American Deserts and the Temperate Forest. Higher elevations may inhibit white-winged dove occupancy. White-winged doves spend summers as high as 2,100 m above mean sea level, but most remain at lower elevations (USFWS, 2010).

Although the BBS may not be the most effective tool for monitoring trends of urban-dwelling birds, if models account for imperfect detections, BBS data can be valuable for urban areas. The BBS first detected white-winged doves in Florida in 1979, twenty years after they were introduced to southern Florida (Aldrich, 1981). By accounting for imperfect detections, we estimated that in 1979 the probability of occupancy was at 0.6 between the southern tip of peninsular Florida to Tampa on the west coast, and to Cape Canaveral, Florida, on the east coast. Similarly, in 2001, a white-winged dove pair nested in Atchison County, Kansas (Anderson, 2001), which is about 1,200 km north of our initial population and 900 km north of the nearest route where white-winged doves were detected in 2001. Our model estimated that in 2001, the probability that Atchison, Kansas, was occupied was between a 0.1 and 0.3.

Accounting for imperfect detection allowed us to use a nationwide, readily available, long-term survey to accurately model the spatial expansion of white-winged doves in the United

States. Our novel approach of treating each BBS route as independent secondary surveys within the primary sample periods allowed us to estimate and account for imperfect detection, thereby, eliminating the assumption that the empirical data that our model was developed on perfectly accurate surveys (MacKenzie *et al.*, 2003). We were also able to include key types of biological information that has been shown to be important in modeling spatial spread: long distance dispersal, interactions with other species, and spatial heterogeneity (Hastings *et al.*, 2005).

Estimated predictions of when and where white-winged doves are likely to be found can be determined with our model. Knowing when and where to survey for white-winged doves could allow biologists to efficiently survey white-winged doves, use optimal impact design studies to determine the effects of the encroachment of a white-winged doves into an area (Green, 1979; Cassey, 2005), and assess potential risks to native biota (Johnson *et al.*, 2001; Wittenberg & Cock, 2001; Arriaga *et al.*, 2004).

## REFERENCES

- Aldrich, J. W. (1981) Geographic variation in white-winged doves with reference to possible sources of new Florida population. *Proceeding of the Biological Society of Washington*, **94**, 641–651.
- Arriaga, L., Castellanos, A. E., Moreno, V. E. & Alarcón, J. (2004) Potential ecological distribution of alien invasive species and risk assessment: a case study of buffel grass in arid regions of Mexico. *Conservation Biology*, **18**, 1504–1514.
- Begon, M., Townsend, C. R. & Harper, J. L. (2006) Conditions. *Ecology: from individuals to ecosystems*, 4th edn, pp. 30–57. Blackwell Publishing, Malden, MA.

- Cassey, P. (2005) Insights into ecology. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D. F. Sax, J. J. Stachowicz and S. D. Gaines), pp. 9–12. Sinauer Associates, Sunderland, MA.
- Collier, B. A., Skow, K. L., Kremer, S. R., Mason, C. D., & Snelgrove, R. T. (2012) Distribution and derivation of white-winged dove harvests in Texas. *Wildlife Society Bulletin*, In Press.
- Cottam, C. & Trefethen, J. B. (1968) *Whitewings: the life history, status, and management of the white-winged dove*. D. Van Nostrand Company, Princeton, NJ.
- Eraud, C., Boutin, J., Roux, D. & Faivre, B. (2007) Spatial dynamics of an invasive bird species assessed using robust design occupancy analysis: the case of the Eurasian collared dove (*Streptopelia decaocto*) in France. *Journal of Biogeography*, **34**, 1077–1086.
- ESRI (2008) *ArcGIS, version 9.3*. Environmental Systems Research Institute, Redlands, CA.
- Fielding, A. H. & Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49
- Fisher, R. A. (1937) The wave of advance of advantageous genes. *Annals of Eugenics (London)*, **7**, 355–69.
- George, R. R., Tomlinson, R. E., Engel-Wilson, R. W., Waggenerman, G. L. & Spratt, A. G. (1994) White-winged dove. *Migratory shore and upland game bird management in North America* (ed. by T. C. Tacha and C. E. Braun), pp. 29–50, Allen Press, Lawrence, KS.
- Green, R.H. (1979) *Sampling design and statistical methods for environmental biology*. Wiley, New York.
- Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B. A., Moore, K.,

- Taylor, C. & Thomson, D. (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, **8**, 91–101.
- Hayslette, S. E. & Hayslette, B. A. (1999) Late and early season reproduction of urban White-winged Doves in southern Texas. *The Texas Journal of Science*, **51**, 183–180.
- Hines, J. E. (2006) PRESENCE2- Software to estimate patch occupancy and related parameters. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>.
- Hooten, M. B. & Wikle, C. K. (2008) A hierarchical Bayesian non-linear spatio-temporal model for the spread of invasive species with application to the Eurasian collared-dove. *Environmental and Ecological Statistics*, **15**, 59–70.
- Integrated Taxonomic Information System. (2009) *Zenaida asiatica* (Linnaeus 1758). Available at: <http://www.itis.gov/> (last accessed 3 March 2009).
- Johnson, L. E., Ricciardo, A. & Carlton, J. T. (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecological Applications*, **11**, 1789–1799.
- Kinlan, B. P. & Hastings, A. (2005) Rates of population spread and geographic range expansion: what exotic species tell us. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D. F. Sax, J. J. Stachowicz and S. D. Gaines), pp. 381–419. Sinauer Associates, Sunderland, MA.
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. & Franklin, A. B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.



- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L. & Hines, J. E. (2006) Occupancy Estimation Modeling: Inferring Patterns and Dynamics of Species Occurrence, Amsterdam.
- Mandon-Dalger, I., Clergeau, P., Tassin, J., Riviere, J. & Gatti, S. (2004) Relationship between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, **20**, 635–642.
- Moore, L. (2001) Spring season roundup: March 1, 2001 through May 31, 2001. *Horned Lark*, **28**, 12.
- Okubo, A., Maini, P. K., Williamson, M. H. & Murray, J. D. (1989) On the spatial spread of the gray squirrel in Britain. *Proceedings of the Royal Society of London B*, **238**, 113–125.
- Rabe, M. J. & Sanders, T. A. (2010) *White-winged dove population status, 2010*. U.S. Department of the Interior, Fish and Wildlife Service, Division of Migratory Bird Management. Washington, D.C.
- Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J. & Rejmanek, M. (2000) Plant invasions — the role of mutualisms. *Biological Reviews*, **75**, 65–93.
- Royle, J. A. & Nichols, J. D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Sauer, J. R., Hines, J. E. & Fallon, J. (2008) *The North American breeding bird survey, results and analysis 1966–2007*. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- Schwertner, T. W., Mathewson, H. A., Roberson, J. A., Small, M. & Waggenerman, G. L. (2002) White-winged dove (*Zenaida asiatica*). *The birds of North America online* (ed. by A.

- Poole) Cornell Lab of Ornithology. Available at:  
<http://bna.birds.cornell.edu/bna/species/710> (last accessed 4 January 2009).
- Shigesada, N., Kawasaki, K. & Teramoto, E. (1986) Traveling periodic waves in heterogeneous environments. *Theoretical Population Biology*, **30**, 143–160.
- Skellam, J. G. (1951) Random dispersal in theoretical populations. *Biometrika*, **35**, 196–218.
- Small, M. F., Hilsenbeck, R. A. & Scudday, J. F. (1989) Resource utilization and nesting ecology of the White-winged Dove (*Zenaida asiatica*) in central Trans-Pecos, Texas. *Texas Journal of Agriculture and Natural Resources*, **3**, 37–38.
- Small, M. F. & Wagberman, G. L. (1999) Geographic redistribution of breeding white-winged doves in the Lower Rio Grande Valley of Texas: 1976–1997. *Texas Journal of Science*, **51**, 15–19.
- Small, M. F., Schaefer, C.L., Baccus, J. T. & Roberson, J. A. (2005) Breeding ecology of white-winged doves in a recently colonized urban environment. *The Wilson Bulletin*, **117**, 172–176.
- Small, M. F., Taylor, E. S., Baccus, J. T., Schaefer, C.L., Simpson, T. R. & Roberson, J. A. (2007) Nesting home range and movements of an urban white-winged dove population. *The Wilson Journal of Ornithology*, **119**, 467–471.
- Swets, J. A. (1988) Measuring accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- U.S. Environmental Protection Agency (2005) *Omernik's Level III Ecoregions of the Continental United States*. National Atlas of the United States. Reston, Virginia.  
<<http://nationalatlas.gov/mld/ecoomrp.html>>
- U.S. Geological Survey (2001) *Urban Areas of the United States*. National Atlas of the United States. Reston, Virginia. <http://nationalatlas.gov/mld/urbanap.html>

Veech, J. A., Small, M. F. & Baccus, J. T. (2011) The effect of habitat on the range expansion of a native and an introduced bird species. *Journal of Biogeography*, **38**, 69–77.

West, L. M., Smith, L. M., & Lutz, R. M. (1993) Ecology of urban white-winged doves. *Transactions of the North American Wildlife and Natural Resources Conference*, **58**, 70–77.

Williamson, M. (1999) Invasions. *Ecography*, **22**, 5–12.

Wittenberg, R. & Cock, M. J. W. (2001) *Invasive Alien Species: a toolkit of best prevention and management practices*. CAB International, Oxford.

Table 1. The numbers of hexagons (150-km diameter) in the southern half of the United States where Breeding Bird Surveys occurred each year, number of those hexagons where white-winged doves (*Zenaida asiatica*) were detected, and the proportion of hexagons where white-winged doves were detected.

Year	No. of hexagons where white-winged doves were detected	No. of hexagons surveyed	Proportion of hexagons where white-winged doves were detected
1979	16	133	0.12
1981	15	121	0.12
1983	15	114	0.13
1985	17	116	0.15
1987	19	133	0.14
1989	20	131	0.15
1991	20	135	0.15
1993	32	149	0.21
1995	33	150	0.22
1997	37	147	0.25
1999	42	147	0.29
2001	44	148	0.30
2003	46	149	0.31
2005	52	151	0.34
2007	62	151	0.41
Totals	470	2075	0.23

Model was developed on 111 hexagons and evaluated on 47 hexagons

Table 2. Model selection results for 18 potential models used to estimate occupancy ( $\psi$ ), colonization rates ( $\gamma$ ), extinction rates ( $\varepsilon$ ), and detection probability ( $p$ ) of white-winged doves (*Zenaida asiatica*) in the southern half of the United States where  $d$  is distance from initial population in 1979,  $c_{79}$  is a constant for colonization rate from 1979 to 1991,  $d_{93}$  is a variable the models colonization on distance from initial population from 1993 to 2007,  $e_{93}$  is a variable the models colonization on ecoregion from 1993 to 2007,  $u_{93}$  is a variable the models colonization on urban land cover from 1993 to 2007,  $e$  is ecoregion, and  $u$  is urban land cover.

Model	AIC	$\Delta$ AIC	AIC weight	Model Likelihood	No. of Parameters	-2*Log Likelihood
$\psi(d), \gamma(c_{79}+d_{93}+e_{93}+u_{93}), \varepsilon(d), p(e+u)$	2038	0	1	1	10	2018
$\psi(d), \gamma(c_{79}+d_{93}+u_{93}), \varepsilon(d), p(u)$	2183	145	0	0	6	2171
$\psi(d), \gamma(c_{79}+d_{93}+e_{93}), \varepsilon(d), p(u)$	2190	152	0	0	7	2176
$\psi(d), \gamma(c_{79}+d_{93}+e_{93}), \varepsilon(d), p(e)$	2211	173	0	0	8	2195
$\psi(d), \gamma(d_{79}+e_{79}+u_{79}+d_{93}+e_{93}+u_{93}), \varepsilon(d), p(e+u)$	2266	228	0	0	13	2240
$\psi(d), \gamma(c_{79}+d_{93}+u_{93}), \varepsilon(d), p(e)$	2315	277	0	0	7	2301
$\psi(d), \gamma(d_{79}+e_{79}+d_{93}+e_{93}), \varepsilon(d), p(e)$	2342	304	0	0	10	2322
$\psi(d), \gamma(d_{79}+e_{79}+d_{93}+e_{93}), \varepsilon(d), p(u)$	2344	305	0	0	9	2326
$\psi(d), \gamma(d_{79}+u_{79}+d_{93}+u_{93}), \varepsilon(d), p(u)$	2370	332	0	0	7	2356
$\psi(d), \gamma(d+u), \varepsilon(d), p(u)$	2380	342	0	0	5	2370
$\psi(d), \gamma(d+e+u), \varepsilon(d), p(e)$	2383	345	0	0	8	2367
$\psi(d), \gamma(d_{79}+d_{93}), \varepsilon(d), p(u)$	2386	348	0	0	5	2376
$\psi(d), \gamma(d_{79}+d_{93}), \varepsilon(d), p(e)$	2406	368	0	0	6	2394
$\psi(d), \gamma(d_{79}+u_{79}+d_{93}+u_{93}), \varepsilon(d), p(e)$	2600	561	0	0	8	2584
$\psi(d), \gamma(d+u), \varepsilon(d), p(e)$	2607	569	0	0	6	2595
$\psi(d), \gamma(d_{79}+d_{93}), \varepsilon(d), p(e)$	2677	638	0	0	6	2665
$\psi(d), \gamma(d), \varepsilon(d), p(e)$	2693	655	0	0	5	2683
$\psi(d), \gamma(d_{79}+d_{93}), \varepsilon(d), p(u)$	2694	656	0	0	5	2684

Table 3. Parameter estimates for the top model,  $\psi(d), \gamma(c_{79}+d_{93}+e_{93}+u_{93}), \varepsilon(d), p(e+u)$ , used to estimate ( $\psi$ ), colonization rates ( $\gamma$ ), extinction rates ( $\varepsilon$ ), and detection probability ( $p$ ) of white-winged doves (*Zenaida asiatica*) in the southern half of the United States where  $d$  is distance from initial population in 1979,  $c_{79}$  is a constant for colonization rate from 1979 to 1991,  $d_{93}$  is a variable the models colonization on distance from initial population from 1993 to 2007,  $e_{93}$  is a variable the models colonization on ecoregion from 1993 to 2007,  $u_{93}$  is a variable the models colonization on urban land cover from 1993 to 2007,  $e$  is ecoregion, and  $u$  is urban land cover.

Parameter	$\beta$ Estimate	Standard Error
$\psi$ distance from BBS routes occupied in 1979	-0.997364	0.299973
$\gamma$ constant (1979–1991)	-3.528748	0.260879
$\gamma$ distance from BBS routes occupied in 1979 (1993–2007)	-1.664497	0.392120
$\gamma$ Great Plains (1993–2007)	1.480975	0.427895
$\gamma$ North American Deserts (1993–2007)	0.631135	0.580376
$\gamma$ urban land cover (1993–2007)	1.235634	0.466605
$\varepsilon$ distance from BBS routes occupied in 1979	3.861284	0.577552
$p$ Great Plains	0.294667	0.135522
$p$ North American Deserts	0.392080	0.144318
$p$ urban land cover	-0.856405	0.134704

Figure 1. Proportion of Breeding Bird Survey routes in the southern half of the United States where white-winged doves were detected.

Figure 2. Probability of colonization after 1993 for the Great Plains in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

Figure 3. Probability of colonization after 1993 for the North American Deserts in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

Figure 4. Probability of colonization after 1993 for “other” ecoregions in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

Figure 5. Probability of extinction in relation to distance from Breeding Bird Survey routes occupied in 1979.

Figure 6. Probability of detection in three ecoregions in relation to amount of urban land cover. Ecoregions include the Great Plains (solid line), North American Deserts (dashed line), and “other” ecoregions predominantly covered by Temperate Forest (dotted line).

Figure 7. Probability of occupancy from 1979 to 1991 in relation to distance from Breeding Bird Survey routes occupied in 1979. Four years are graphed: 1979 (dotted line), 1983 (dashed line), 1987 (dot-dashed line), and 1991 (solid line).

Figure 8. Probability of occupancy in 2007 in the Great Plains in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

Figure 9. Probability of occupancy in 2007 in the North American Deserts in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

Figure 10. Probability of occupancy in 2007 in “other” ecoregions in relation to distance from Breeding Bird Survey routes occupied in 1979 and amount of urban land cover classified as none (dotted line), 300 km<sup>2</sup> (short-dashed line), 600 km<sup>2</sup> (medium-dashed line), 900 km<sup>2</sup> (dot-dashed line), and 1,200 km<sup>2</sup> (long-dashed line).

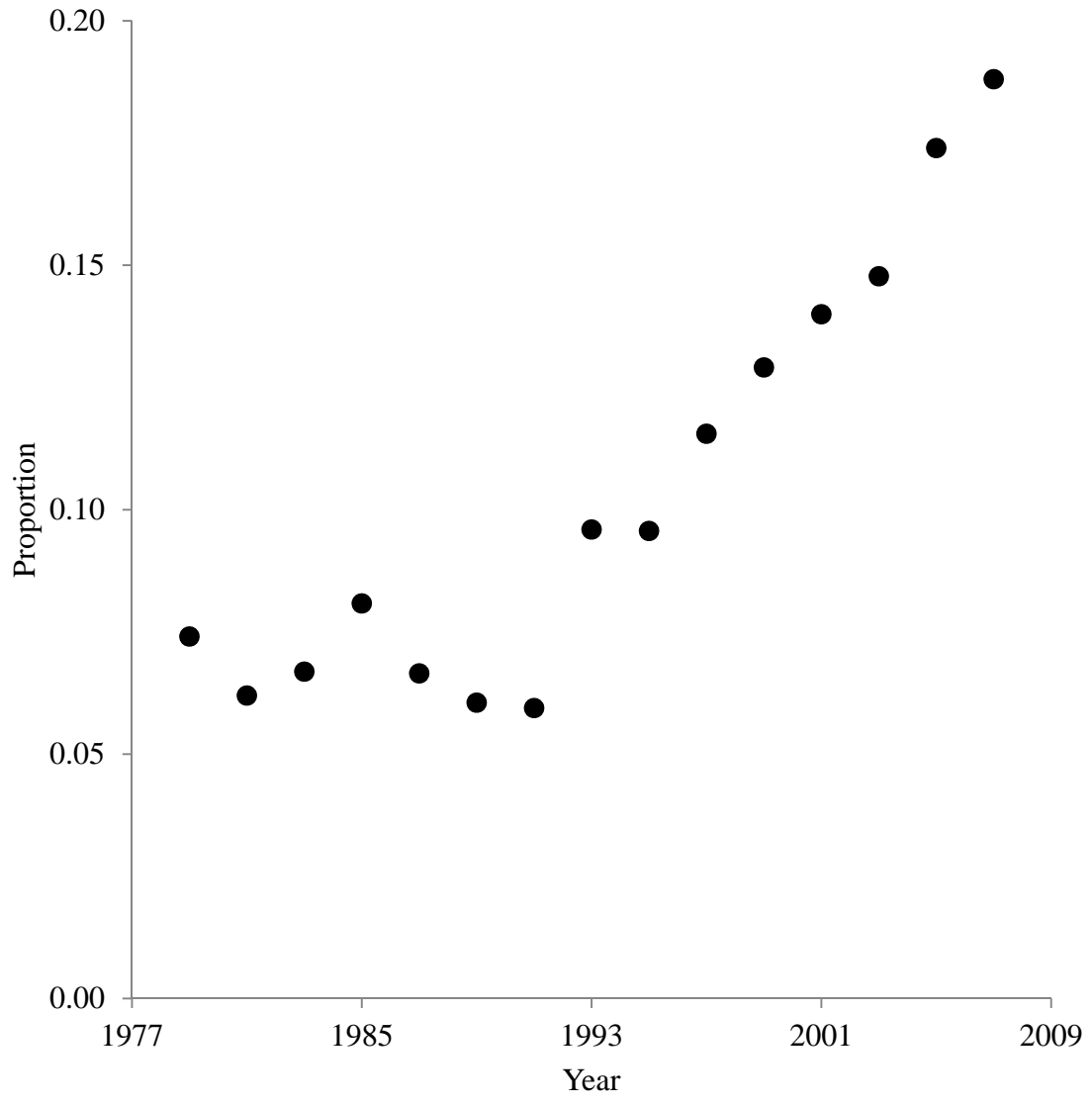


Fig1



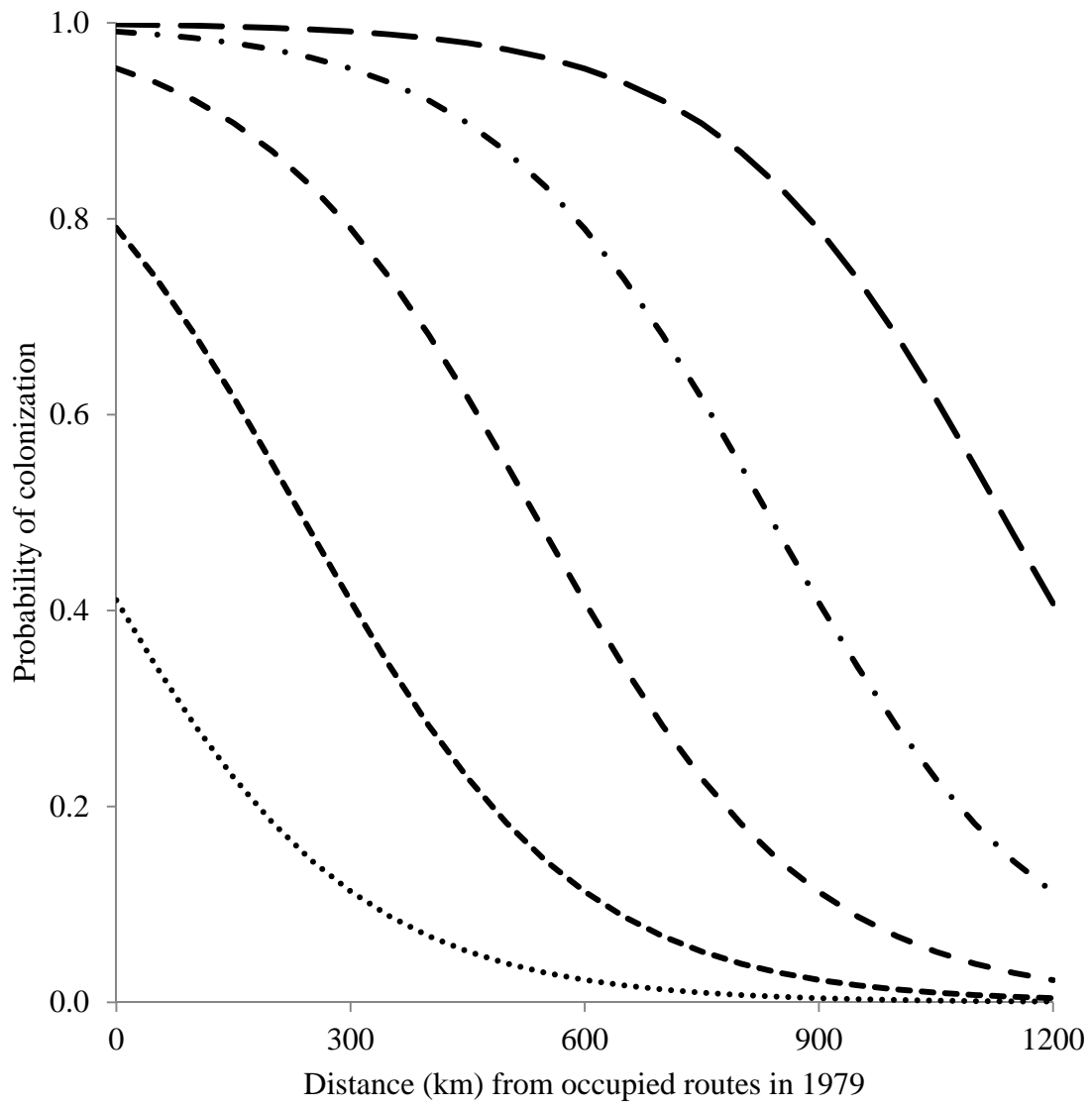


Fig2

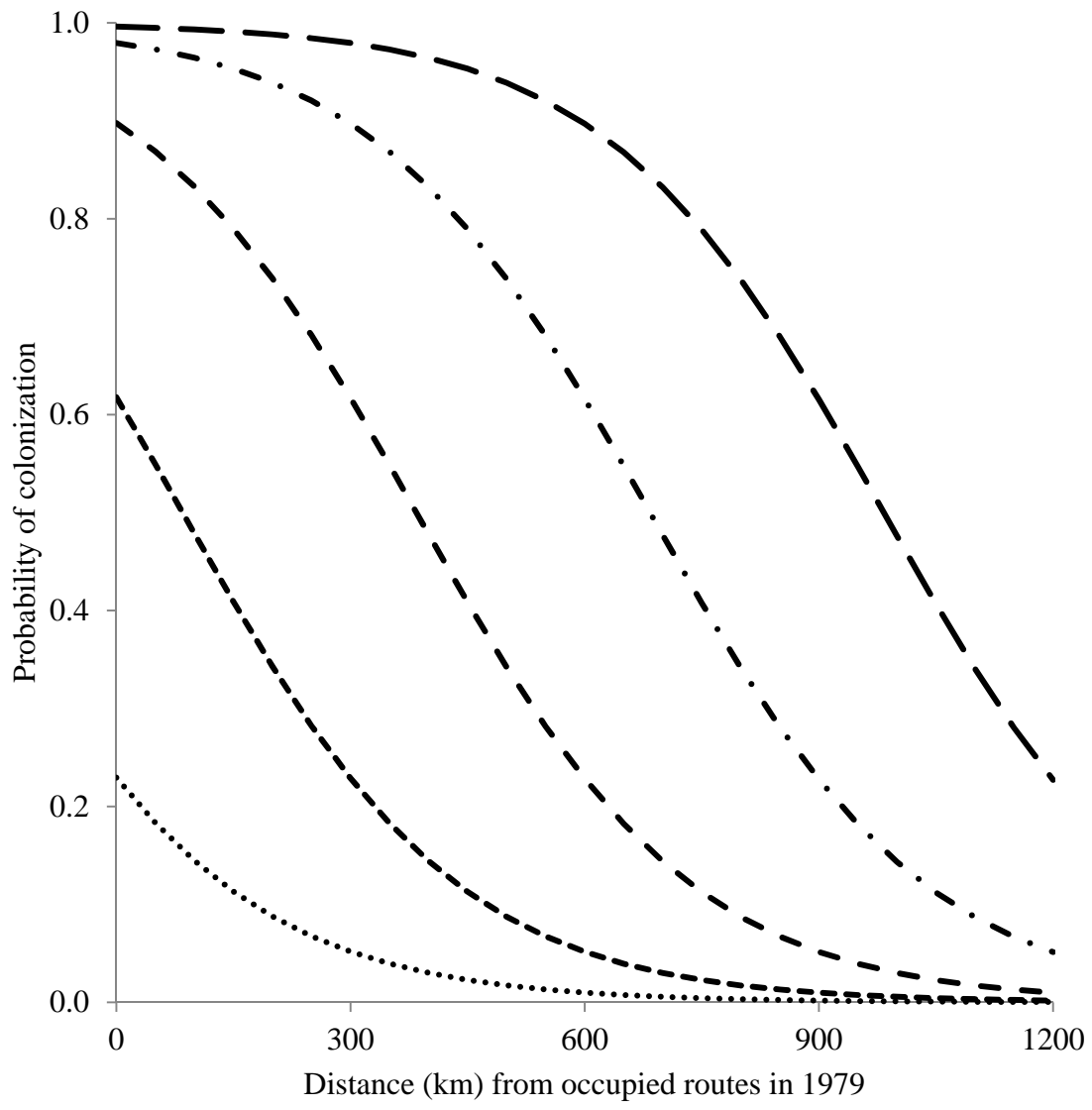


Fig3

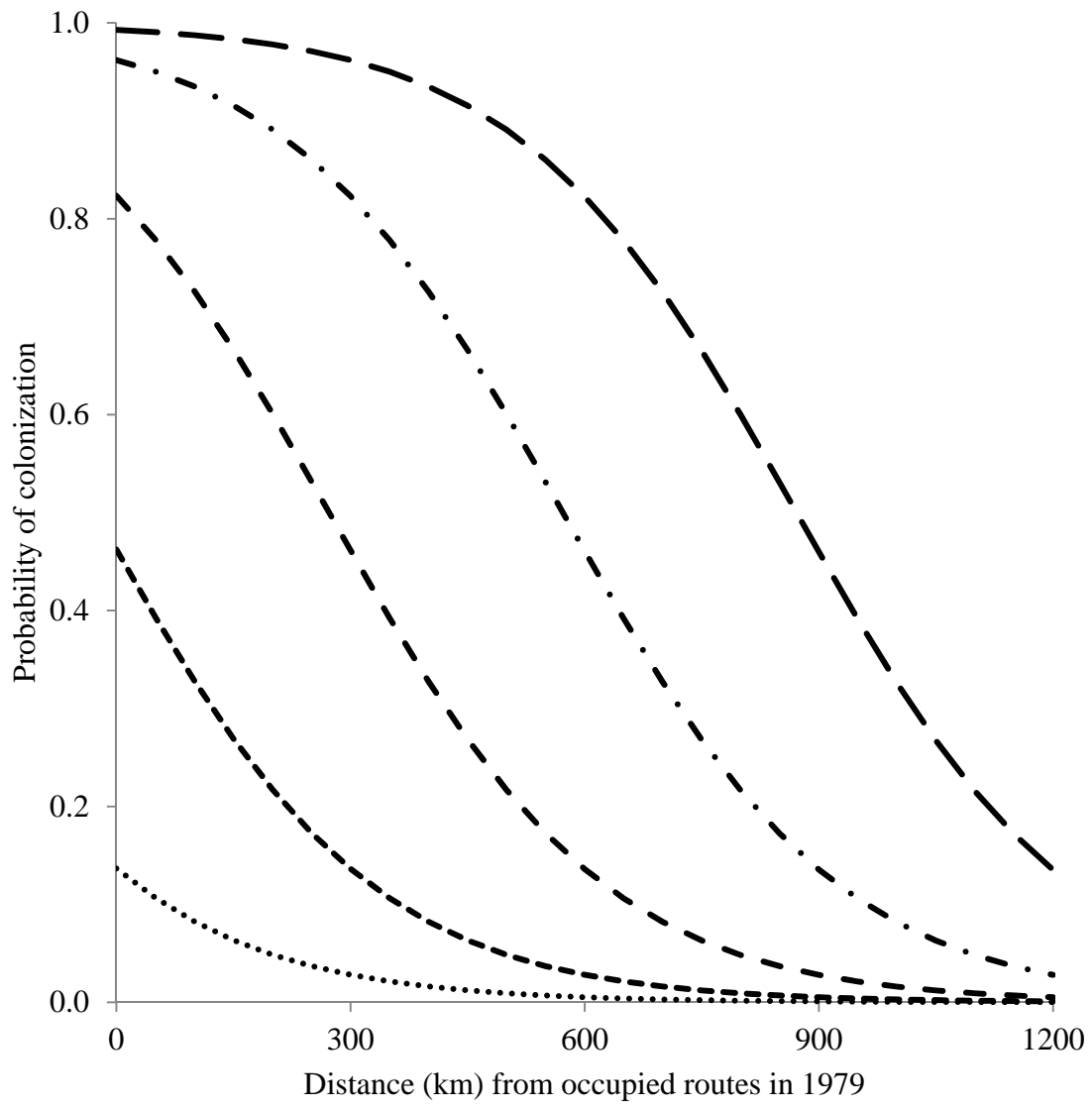


Fig4

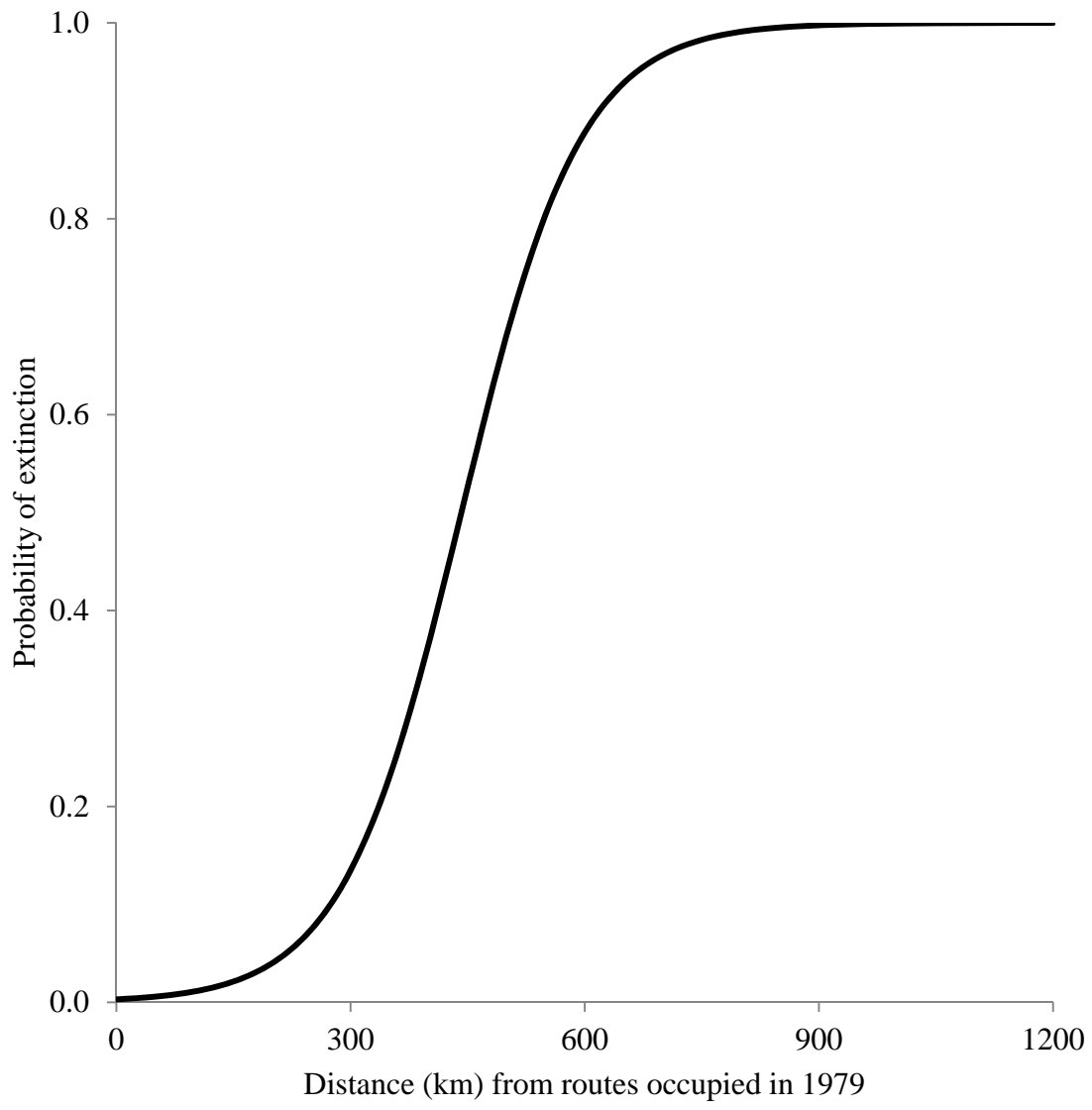


Fig5

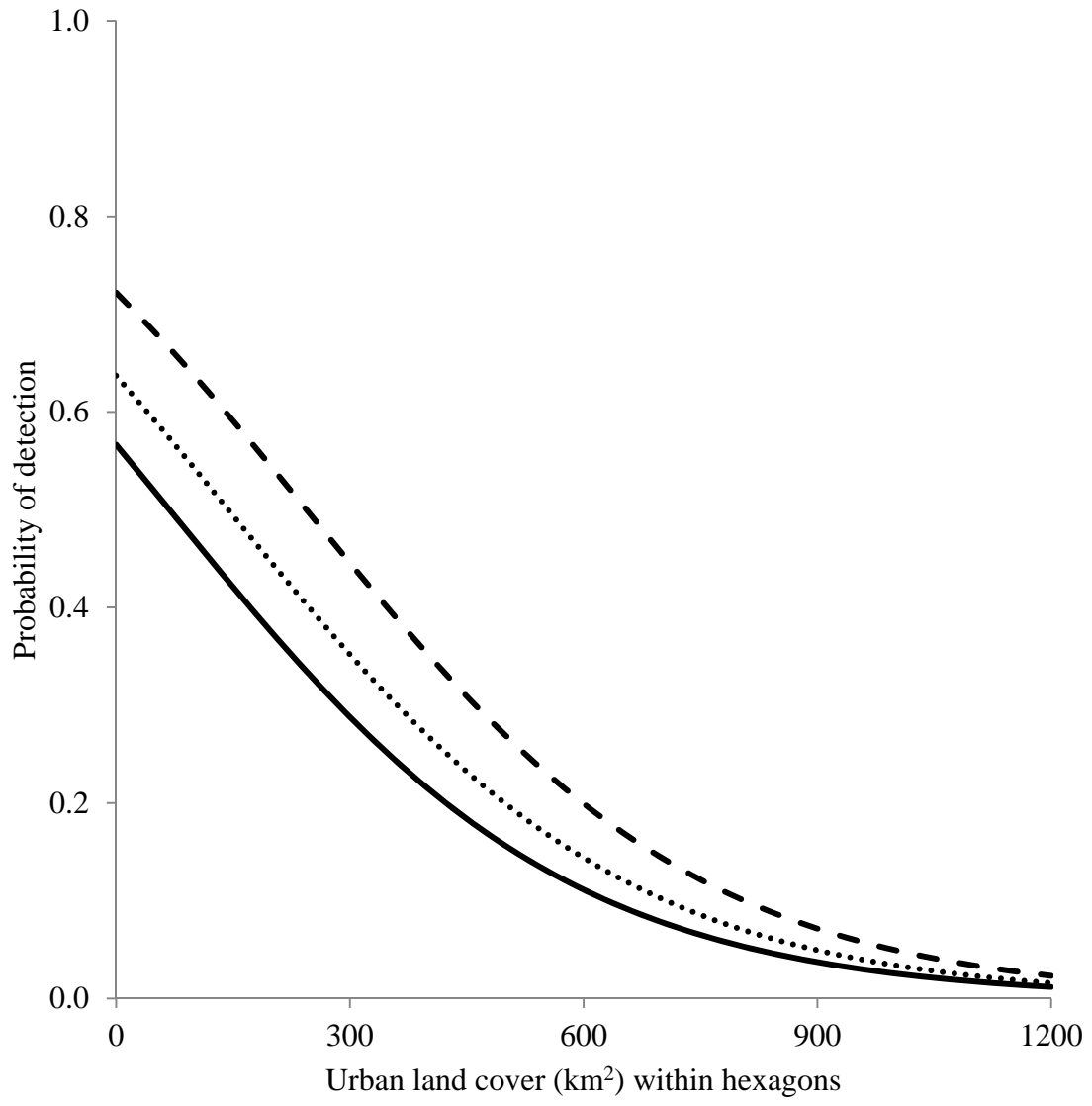


Fig6

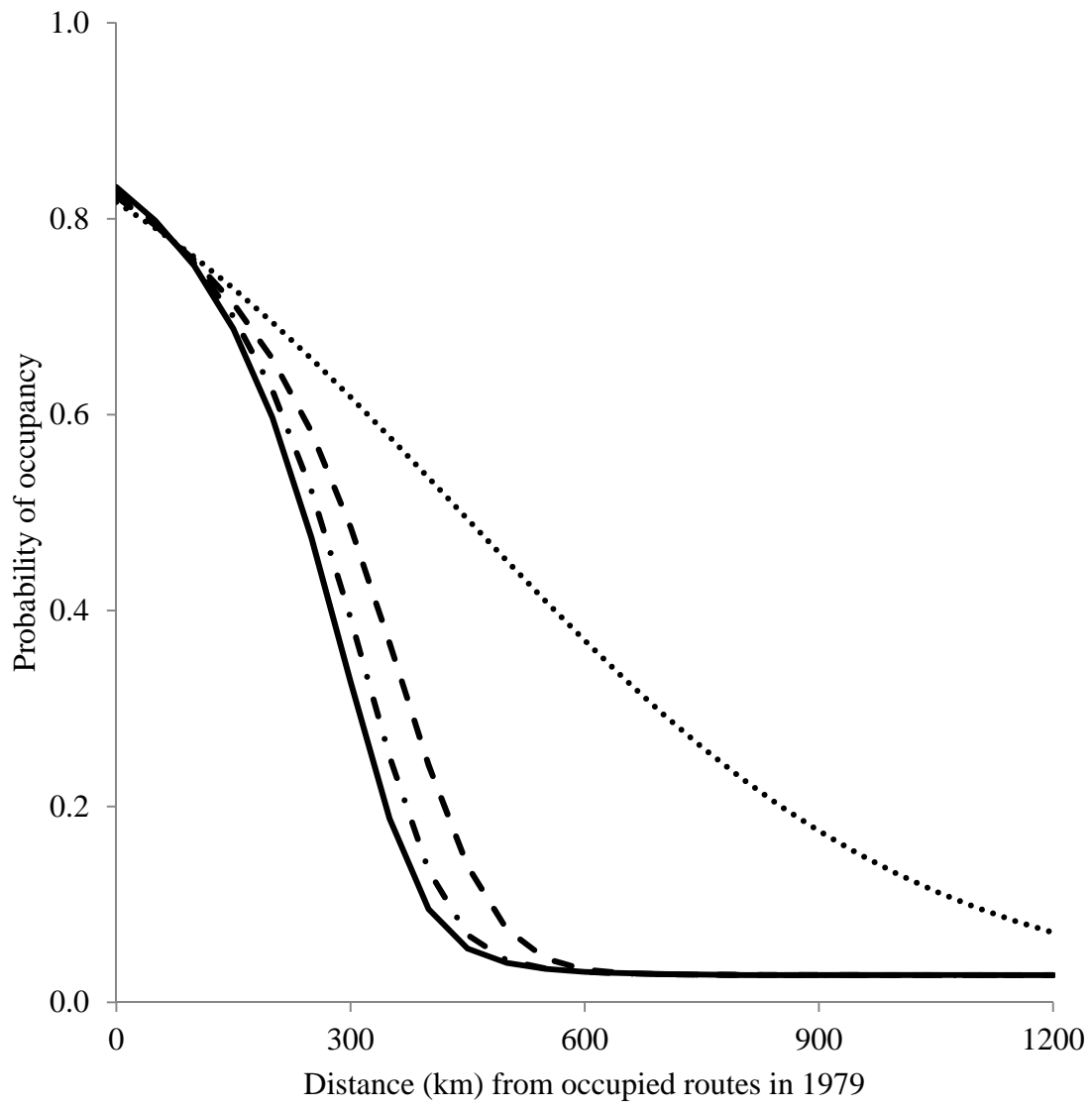


Fig7

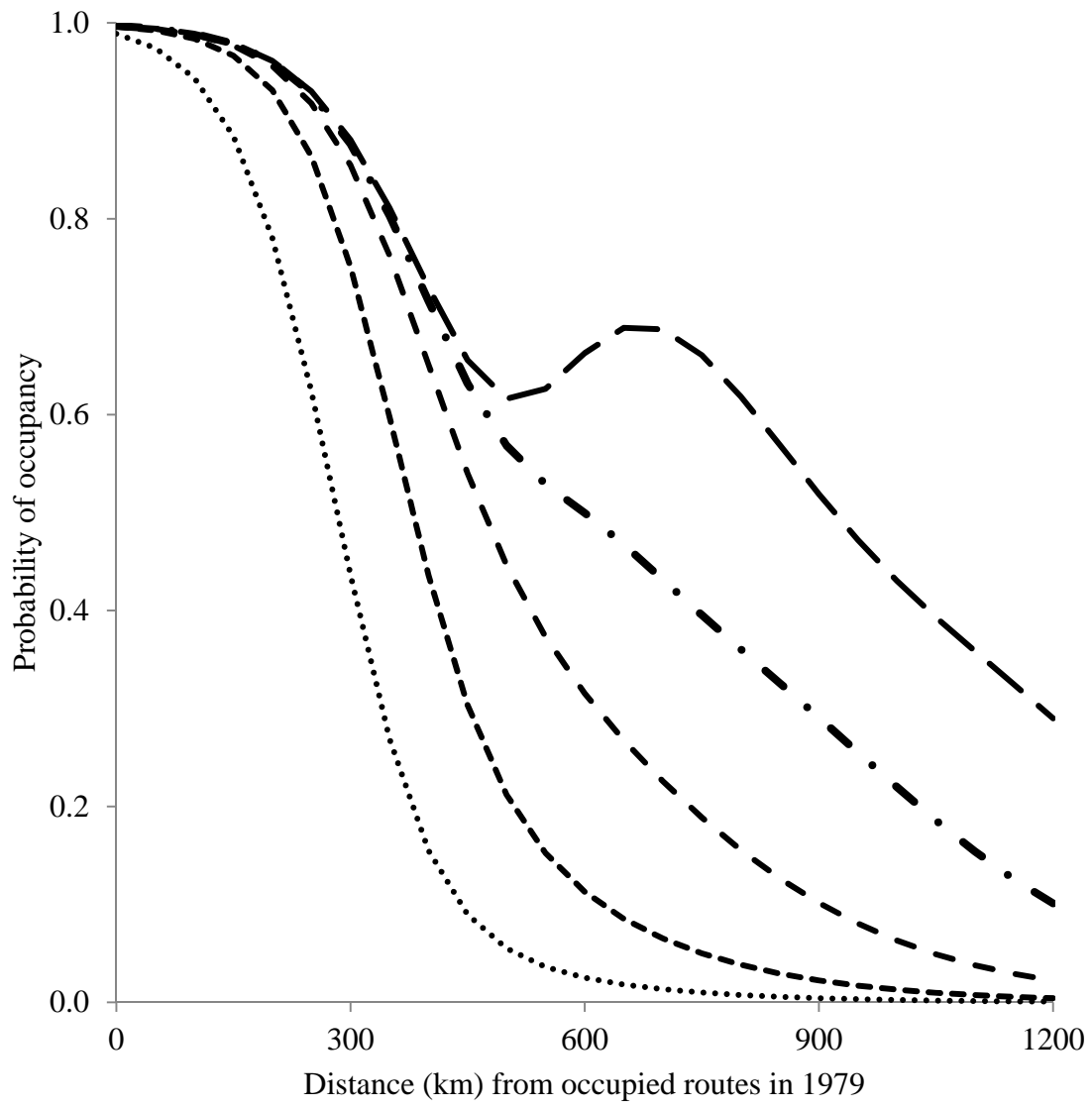


Fig8

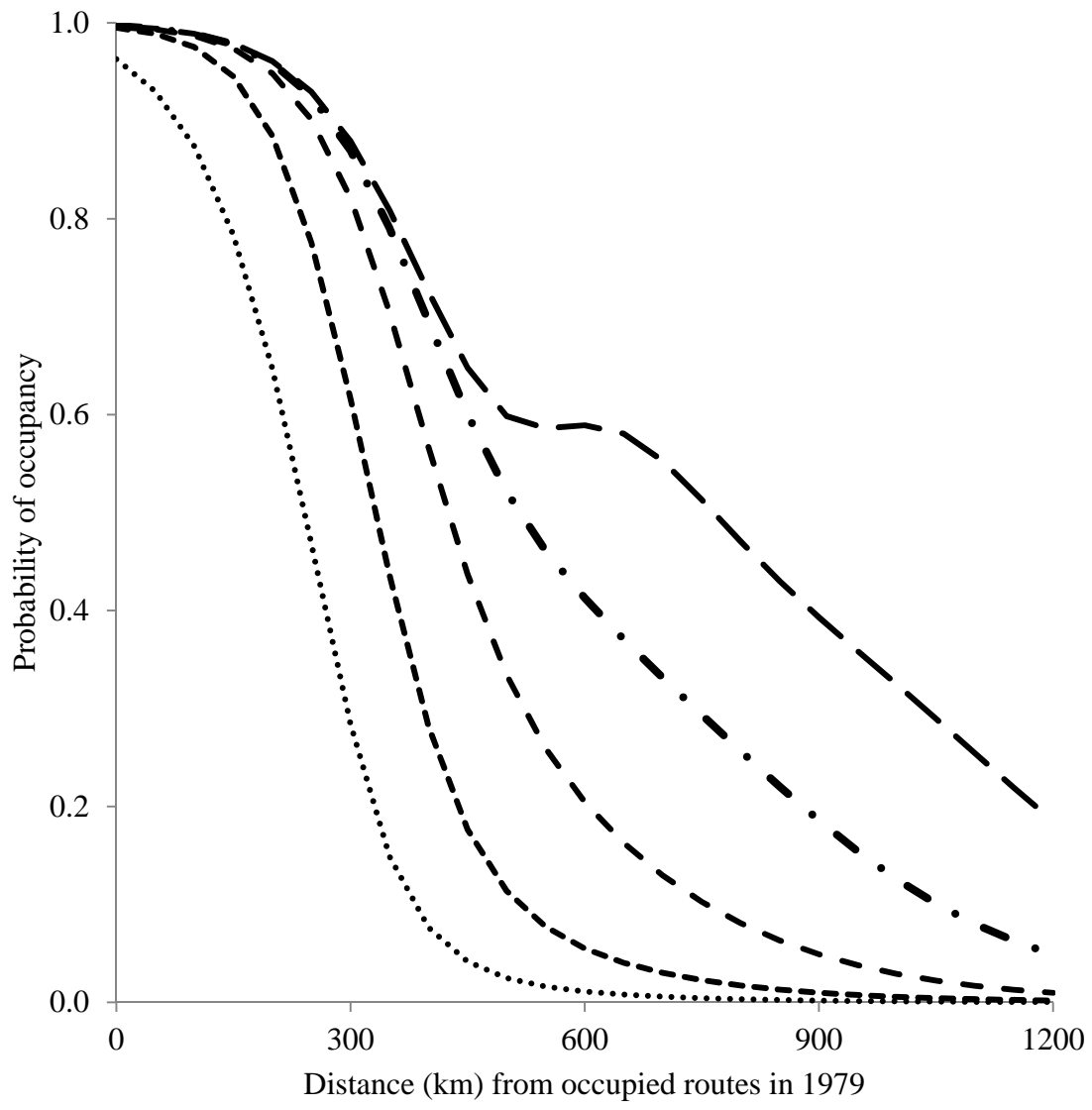


Fig9



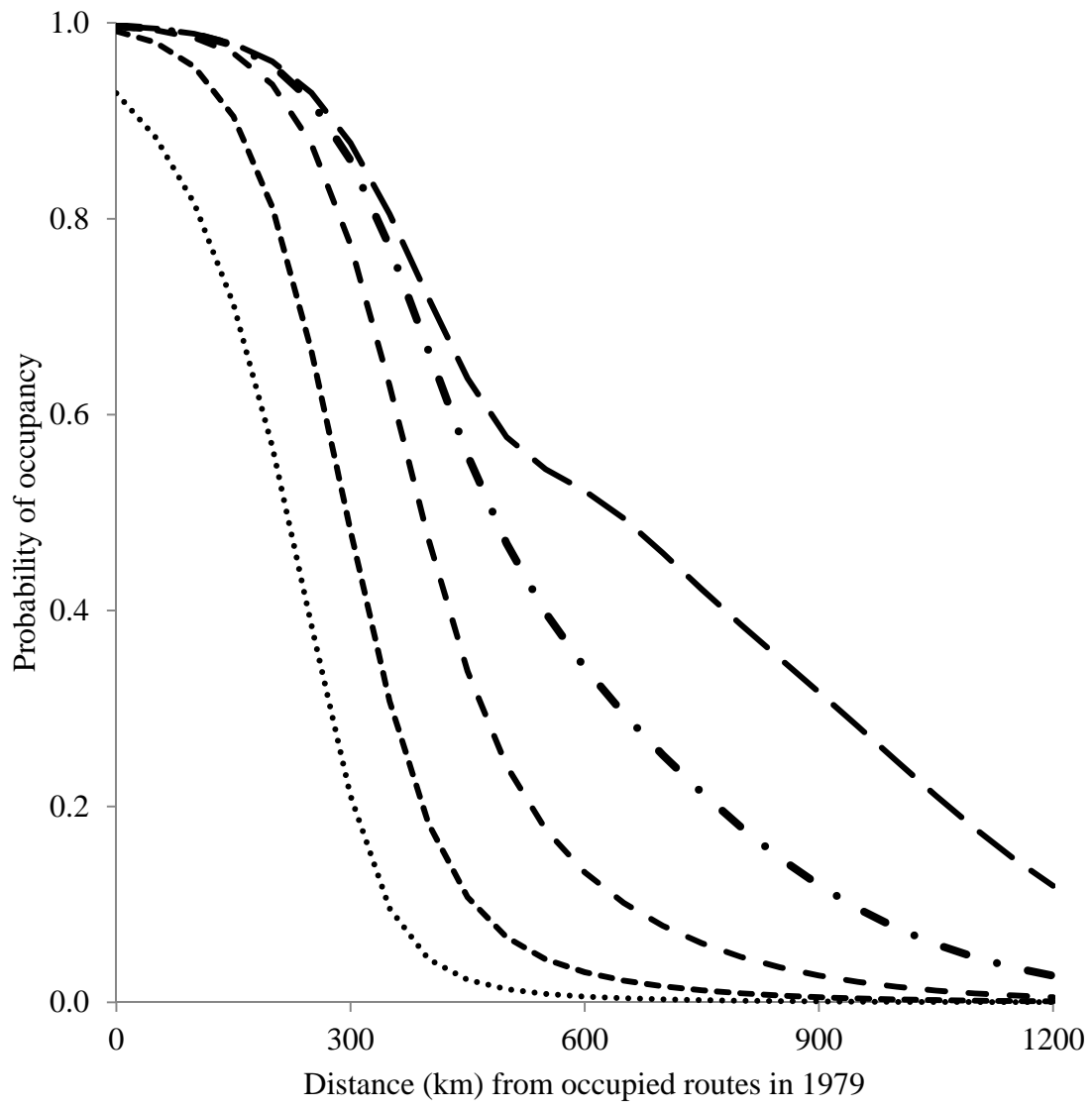


Fig10