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Research paper

Urbanisation of the wood pigeon (*Columba palumbus*) in Finland

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HIGHLIGHTS

- Wood pigeons have been breeding regularly in Finnish cities since 1991; the urbanisation process is still in progress.
- Larger cities and cities located closer to the sea were colonised first.
- Colonisation did not follow the stepping-stone model between nearest neighbouring cities.
- Changes in rural wood pigeon density did not drive the urbanisation process.
- Habitat use of wood pigeons changed during the urbanisation process.

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ABSTRACT

The urbanisation process includes three phases: arrival, adjustment and spread. While these are much studied for biological invasions, stage-specific factors promoting successful urbanisation are still poorly understood. In this paper, we study urbanisation of the wood pigeon, *Columba palumbus*, in Finland. We document the colonisation of the 20 largest Finnish cities; studying how size of the city, geographic location, population density in rural areas surrounding a city, and distance to other previously colonised cities influenced the timing of arrival. We also investigate population development and changes in habitat use during the adjustment and spread stages of the urbanisation process in the city of Turku. We obtained data on wood pigeon observations in inner-city areas from the database of BirdLife Finland, public questionnaires and systematic searches. We found that larger cities and cities located closer to the sea were colonised earlier. Colonisation seemed to be unrelated to both density of rural wood pigeon population and distance to the nearest colonised city. The settlement and spread phases of the urbanisation process followed an exponential curve. No preference for coniferous forest, the habitat type used in rural areas, or deciduous forest was observed. Nests were mainly located in deciduous patches, which are common in cities. We conclude that colonisation of cities by wood pigeons was influenced by geographic location. The hypothesis that avian urbanisation follows the stepping-stone model between neighbouring cities was not supported. Additionally, our results confirm the hypothesis that, during urbanisation, habitat use of species changes from that in rural areas.

1. Introduction

The world is becoming increasingly dominated by urban-type land use (UN, 2012). Urban sprawl has complex direct and indirect effects on the native flora and fauna. Nevertheless, the ecological effects of urbanisation have not been studied intensively until recently, and many aspects of the urbanisation process are still poorly understood (Evans, Hatchwell, Parnell, & Gaston, 2010). Apart from the possibility that individuals survive in refugia within cities and subsequently adapt and spread into non-natural parts of the urban landscape, the urbanisation process typically includes three phases: arrival, adjustment and spread of individuals in the urban area (Evans et al., 2010; Kolar & Lodge, 2001; Williamson, 1996). While these three stages are much studied for biological invasions (Clobert, Baguette, Benton, Bullock, & Ducatez, 2012), urbanisation has rarely been recorded from arrival to spread. It is, however, important to have knowledge on each stage of the process, since the urbanisation process can succeed or fail depending on various stage-specific factors.

The probability of initial arrival to an urban area depends mainly on two factors: the proportion of urban areas within the species'

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geographic range, and the time that has been available for urbanisation, i.e. the time period these urban areas have been existing (Evans et al., 2010). In birds, initial colonisations are often performed by very small groups, in extreme cases by a single breeding pair (Vuorisalo et al., 2003). Assuming a high extinction rate for such small populations, most colonisation attempts probably fail.

After arriving in the urban habitat, species have to cope with a markedly different environment compared to the original rural one (Evans et al., 2010). Differences are most visible in habitat availability and quality, with highly fragmented habitat patches and usually low habitat diversity in city centres (Marzluff & Ewing, 2001). Urban and rural environments also differ in many other ways, including physical, chemical and ecological traits (Baker, Molony, Stone, Cuthill, & Harris, 2008; Collier, 2006; Evans, Newson, & Gaston, 2009b; Fuller, Warren, Armsworth, Barbosa, & Gaston, 2008; Grimm et al., 2008; Vuorisalo et al., 2003). Urbanisation will thus require some adjustment to the novel environment (Evans et al., 2010). While dispersal processes preceding arrival have previously been relatively well studied (Clobert et al., 2012), factors promoting successful establishment ("adjustment") are less clearly understood.

The final stage of urbanisation is the spread of populations within a city after individuals have successfully adjusted to urban environments (Evans et al., 2010). The spread of urbanisation in a larger area, i.e. colonisation of separate cities, may happen as spread from one colonised urban area to another urban area. Evans et al. (2009a, 2010) called this the leap-frog model; a quite similar model, the so-called tradition-transfer model, was proposed by Vuorisalo (2010). Colonisation of new cities in these models depends on the dispersal distance of the species. If dispersal distances are low, spread from one city to another might follow a stepping-stone model between neighbouring cities (Evans et al., 2010). Alternatively, different cities may become colonised independently, e.g. due to a general increase in the population density in a larger area promoting the colonisation of cities within this area (Cannon, Chamberlain, Toms, Hatchwell, & Gaston, 2005; Evans et al., 2009a, 2010; Lambin, Aars, & Piertney, 2001). Investigations of the mechanisms driving colonisation of separate urban areas are often hindered by a lack of information on the timing of urban colonisation events. A notable exception is the urbanisation of the European blackbird, *Turdus merula*, which, based on the species' genetic structure, followed an independent urbanisation model (Evans et al., 2009a).

In addition to the above mentioned processes, several factors may affect spatial patterns in the timing of avian urbanisation. For example, coastal areas may act as migration corridors and provide more favourable environments for colonisers than inland areas (Witt, Mitschke, & Luniak, 2005). The size of the urban area may also affect colonisation probability, as larger cities may be more likely to be found by randomly dispersing individuals than smaller cities (Evans et al., 2010). There are only few analyses concerning the speed and direction of the spread of urbanisation. For example, blackbirds colonised cities in the west and south of their range first (Evans et al., 2010), and wood pigeon urbanisation in Europe started later in the east (Bea et al., 2011; Evans et al., 2010).

In this paper, we study urbanisation of the wood pigeon, *Columba palumbus*, in Finland. First, we analyse the colonisation of the 20 largest Finnish cities by the wood pigeon. We predict that (1) geographic location and size of the city influenced colonisation; (2) rural wood pigeon density around the cities affected colonisation positively due to population growth pressure. Alternatively, if colonisation followed the stepping-stone or leap-frog model between neighbouring cities, then (3) colonisation was dependent on the distance to the nearest colonised city. Second, we investigate the arrival, settlement and spread of the wood pigeon in the city of Turku in South-Western Finland. We predict that (4) after arrival to the city the population growth during the settlement phase follows a logistic curve, with a period of low population size before the onset of rapid population growth; and (5) habitat use differs during urbanisation process from that in rural areas, since effective colonisation of an urban area may require adjustment to new habitat structures.

2. Methods

2.1. Study species and its urban history in Europe

The wood pigeon is a Palearctic species, breeding in almost all European countries (Saari, 1997). It started to breed in some cities of Western and Central Europe in the early 19th century (Glutz von Blotzheim & Bauer, 1980). In Northern Europe, urbanisation started later: first urban nestings were recorded in Danish city parks in the early 20th century (Génsbøl, 1985; Jägerskiöld & Kolthoff, 1926), and in Sweden, urban wood pigeons started becoming common in the 1950's (Curry-Lindahl, 1946; Fredriksson & Tjernberg, 1996). In Finland, breeding in urban habitats was considered very rare until the 21st century (Väisänen, Lammi, & Koskimies, 1998). The species has traditionally been a strictly rural species that prefers forest margins or forest patches in agricultural areas (Tomiałojć, 1976; Vuorisalo, 1996), although wood pigeons have occasionally bred in the vicinity of rural manor houses and parks (Hortling, 1929). Since the 1970's, incubating wood pigeons have been occasionally observed in several Finnish cities. However, these were sporadic on–off events with gaps of several years between observations before regular breeding in the 1990's and the 2000's. In Finland, wood pigeons are migratory and do not winter except for single individuals in certain cities in recent years (Lehikoinen et al., 2003; Solonen, Lehikoinen, & Lammi, 2010)

2.2. Data on wood pigeons in Finnish cities

We used two types of data to determine when wood pigeons arrived to Finnish cities. First, we collected all observations of urban wood pigeons in the 20 largest cities in Finland (Table 1) from the database of BirdLife Finland (www.tiira.fi). This database is a web-based system for public recording of bird sightings in Finland. The database was launched in 2006, but may also include older observations. We used only wood pigeon observations reported as "local" (in contrast to "migratory") and observed in inner-city built environments. Several observations at the same place during the same year were counted as one observation. From the database we do not know whether reported birds were breeding in the urban area, but sightings during the breeding period in cities where wood pigeons have not been observed before should be a good indicator for an ongoing colonisation process. Second, for gaining better information on the time before 2006, we sent four questionnaires to be published in nationwide nature or ornithological journals: one per year in 1995, 1996, 1997 and 2004. Readers were asked to report all previous and recent nesting attempts of wood pigeons in urban areas.

The activity level of reporting wood pigeon observations likely depends on how many birdwatchers live in the city, which may depend on geographic location and size of the city. Therefore, we contacted known bird enthusiasts living in the cities being studied and asked how well in their opinion the reported observations of wood pigeons in the cities reflected the true breeding status. Information from these inquiries corresponded with the data we had for wood pigeon breeding history in these cities. Thus, we feel that our data should not be too biased between cities.