Birds and Butterflies in Swedish Urban and Peri-urban Habitats: a Landscape Perspective

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Abstract

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Urbanisation is considered to be one of the largest threats to biodiversity although little is known about the effect of habitat fragmentation on native flora and fauna in urban areas in general, and in Sweden specifically. In this thesis, data have been collected using remote sensing analyses of 100 cities, bird surveys in 34 cities, and experiments have been used to answer specific questions regarding dispersal and reproduction in different urban habitats. The dual processes of infill development and expansion of cities threaten remaining unprotected urban woodlands. Results showed that between 1 and 40% (average of 20%) of the proportion of the city area were comprised of urban woodland. Urban and peri-urban (surrounding) woodlands covered an area larger than the total area of protected forests in Sweden and had higher amounts of dead wood than typical non-protected forests. In contrast to previous studies, this thesis showed that many bird species breeding in urban woodlands were strongly affected by the surrounding city or landscape composition. On a smaller spatial scale (200 m), adjacent habitats affected population density and nestling quality of great tits *Parus major* breeding within urban woodlands. Movement corridors were only used by butterfly habitat specialists, and grassland corridors of intermediate quality seemed to be most efficient to promote dispersal among habitat fragments. In this thesis, I show that Sweden have relatively high proportion urban woodlands; urbanisation does not necessarily lead to a homogenisation of the bird fauna; urban habitats need to be well described in detail to allow comparisons among studies; bird faunas of local urban woodlands differ among regions and are strongly affected by composition of habitats both at city and landscape levels; movement corridors may be an efficient conservation tool if specifically managed to fit the autecologies of the species of conservation concern.

Key words; conservation, corridor, ecotone, habitat quality, landscape ecology, management, reproductive performance, urban forest, urban gradient, urban matrix, transect

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Fåglar och fjärilar i svenska städer ur ett landskapsperspektiv

Den ökande urbaniseringen av världens befolkning leder i de flesta fall till att natur i och nära städer försvinner. Få studier har undersökt hur denna fragmentering påverkar den vilda floran och faunan i svenska städer. I denna avhandling har digitala kartor för 100 svenska städer analyserats och i 34 städer har även fåglar inventerats i totalt 474 tätortsskogar. Med hjälp av experiment i Uppsala har spridningsförmågan hos fjärilar i olika typer av gräskorridorer och reproduktion hos talgoxar *Parus major* i olika skogsfragment undersökts. I Sverige både förtätas och expanderar städer genom att kvarvarande skogar exploateras. Dessa skogsfragment har oftast ett svagt legalt skydd. Avhandlingen visade att andelen skog i svenska städer varierade från 1 till 40% med ett medelvärde på 20%. Tätortsskogar och tätortsnära skogar (mindre än 5 km från stadens rand) visade sig täcka ett större område än den totala andelen skyddad skog i Sverige. Dessutom hyste skogarna i staden och i närliggande landskap en större mängd död ved än övrig, icke skyddad skog i Sverige. Resultaten understryker den stora betydelsen av omgivande skogar (både inom staden och i närliggande landskap) för att förklara tätheter av fåglar som häckar i lokala tätortsskogar. I en mindre rumslig skala (200 m) varierade talgoxens populationstäthet och kvaliteten hos fågelungar i tätortsskogar beroende på vilken typ av habitat som omgav skogarna. Endast fjärilsarter som var habitatspecialister flög utmed gräskorridorer och främst använde de korridorer som varken hade låg eller hög kvalitet för arterna i fråga. Sammanfattningsvis visar jag i denna avhandling att (a) svenska städer har en relativt stor andel tätortsskogar, (b) ökad urbanisering inte nödvändigtvis behöver leda till en utarmning av fågelfaunan, (c) vegetationen i undersökta miljöer i staden måste vara noggrant beskrivna för att tillåta jämförelser mellan olika studier av hur urbanisering påverkar fåglar, (d) fågelfaunan i lokala habitat skiljer sig mellan regioner och är i stor utsträckning påverkad av habitaten i direkt angränsande miljöer och även utanför staden, (e) korridorer skulle kunna vara en viktig sätt att gynna spridning mellan habitatfragment och på sätt minska negativa effekter av fragmentering, men då krävs att korridorernas skötsel är direkt anpassad till de arter som ska gynnas.

Cover: Map of Uppsala, ©Uppsala kommun 2007; Feeding great tit, photo Börge Petterson; Butterfly *Polyommatus semiargus,* photo Bo Söderström; Residential garden, photo Marcus Hedblom.

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Hedblom, M. & Söderström, B. Woodlands across Swedish urban gradients: status, structure and management implications.
Submitted manuscript.

II. Hedblom, M. & Söderström, B. Importance of urban and peri-urban woodlands for the avifauna in urban forest fragments: an analysis of 34 Swedish cities.
Manuscript.

III. Hedblom, M. & Söderström, B. Density and reproductive performance of Great Tits (*Parus major*) at different types of urban woodland ecotones.
Manuscript.

IV. Söderström. B. & Hedblom, M. Comparing movement of four butterfly species in experimental grassland strips.
Journal of Insect Conservation. In press.

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Introduction

Urbanisation and agriculture are two of the most important threats to biodiversity worldwide (Ricketts & Imhoff, 2003). However, urbanisation is likely to top agriculture as the dominating agent of habitat fragmentation because of an increasingly urbanised human population (Marzluff & Ewing, 2001). By 2030 the global urban population is projected to be 5 billion and, today, half of the world's population lives in urban areas (United Nation, 2005). Ecology in urban areas has for a long time been a neglected research area but is now highly topical, manifested in an increasing number of publications and conferences with focus on urban flora and fauna (e.g. Blair, 1996; Marzluff *et al.*, 2001; McKinney, 2002; Society for Conservation Biology 18th annual meeting, 2004; Chace & Walsh, 2006; Mörtberg *et al.*, 2007). However, it is still a relatively neglected research area compared to the amount of research conducted in forest and agricultural ecosystems (Fig. 1).

In general, humans live in highly productive ecosystems and species rich areas (Ricketts & Imhoff, 2003); therefore, many cities are located in areas important for biodiversity conservation. Worldwide trend is that people move from rural areas and smaller cities to larger cities, but urbanisation processes differ around the world. In North America, Australia and China, the cities increase faster in area than in urban population growth (Newman, 2005; Yu & Cho Nam, 2007), which is termed urban sprawl. Urban land use and population trends have been little studied in Europe (Antrop, 2004), perhaps due to that European cities had their most rapid growth in the 1950s and 1960s. In southern Europe, cities are very compact and densely populated compared to eastern and northern Europe. Today, more than 70% of the European population live in urban areas (Konijnendijk, 2004). Urban sprawl is not so pronounced in Europe as in other parts of the world, although it occurs (Kasanko *et al.*, 2006).

The effect of habitat fragmentation on native flora and fauna has been extensively studied in forest and agriculture ecosystems (e.g. Wilcove *et al.*, 1986; Soulé *et al.*, 1992; Kruess & Tscharntke, 1994; Fahrig & Merriam 1994; Robinson *et al.*, 1995; Söderström *et al.*, 2001; Lindenmayer & Franklin 2002; Brennan & Kuvlesky, 2005; Veech, 2006) but little is known about the effect of habitat fragmentation in urban areas (Miller *et al.*, 2001; but see e.g. Clergeau *et al.*, 2006). Snep *et al.* (2005) concluded that surroundings of the city (peri-urban nature) may act as a source of individuals for the inner-city. However, other studies performed in urban areas suggested that features of the local habitat, not the landscape surrounding the city had the greatest effects (Clergeau *et al.*, 2001; Jokimäki *et al.*, 2003). Thus, it is not clear how general effects on biodiversity in remnant urban fragments from local habitat and the surrounding landscape are. Partly this is because most previous studies were based on data from only one or a few cities or because they do not compare fragments with natural habitats. However, one of the general patterns in urban landscape ecology is that urbanisation leads to more homogenous bird faunas among cities (Blair, 2001; McKinney, 2006).

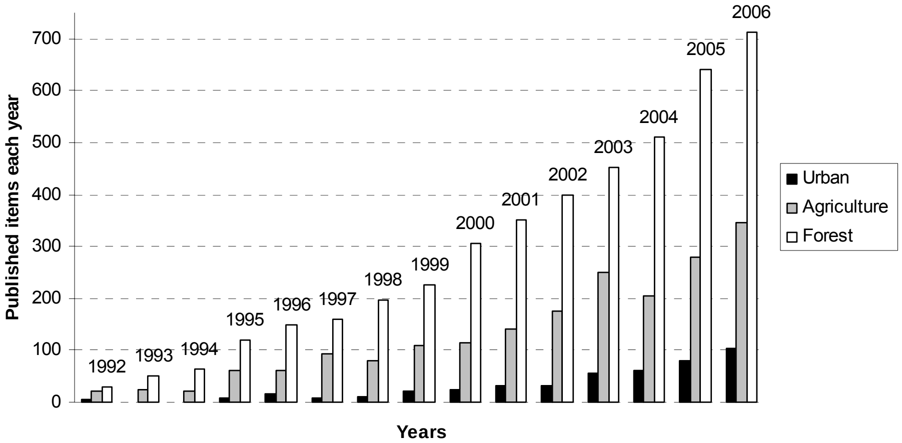

Fig. 1. Number of published articles on biodiversity in urban, agricultural and forest areas. Data from the ISI Web of Knowledge database.

In Sweden 84% of the human population live in urban areas and immigration to the largest cities is pronounced (Statistics Sweden, 2003). For example, Stockholm has an annual increase of 8,000 people (City Planning Committee, 1999). The dual processes of infill development and expansion in the 10 largest cities have caused a 5% decrease of green areas in cities, and a 3% decrease of green areas in the surrounding landscape, between 1980 and 1990 (Statistics Sweden, 1993). Some studies have been made on how fauna and flora are affected by urbanisation in Swedish cities (but see Florgård, 2000; Mörtberg, 2001; Löfvenhaft *et al.*, 2004; Sandström *et al.*, 2006a; Colding, *et al.*, 2006). Colding *et al.*, (2003) suggested that urbanisation has led to severe ecosystem loss affecting both animal and plants in Swedish cities.

No comprehensive study exists on the quantity and quality of urban woodland in Sweden. In order to study the effects of fragmentation on birds breeding in urban woodlands, the proportions of woodland within and in the surroundings of 100 cities with more than 10 000 inhabitants was estimated (*Paper I*). These variables were correlated to land use variables, human population size, and demographic population trends. Furthermore, forest vegetation structure and human activities were measured in 474 urban woodlands in 34 cities to study possible variation along an urban to rural gradient. In *Paper II*, investigations were made comparing whether the proportion of urban and peri-urban woodland affected forest birds breeding in urban woodlands. Analyses were performed on both the abundances of single species and on ecological guilds. Whether bird communities were more homogeneous in urban compared to peri-urban woodlands was also tested.

Population density may not always be a reliable cue to habitat quality (van Horne, 1983). Therefore, breeding performance of great tits *Parus major* breeding in nest boxes in and near urban woodlands were studied. In general, urban great tits have lower reproductive performance and display higher levels of stress than those breeding in non-urban areas (Hõrak, 1993; Hõrak *et al.*, 2000; Solonen, 2001; Isaksson *et al.*, 2005). However, few studies have compared adjacent habitats within cities (Tilghman, 1987; Clergeau *et al.*, 2001; Hashimoto *et al.*, 2005, Jokimäki *et al.*, 2005). Type of surrounding urban habitat (urban matrix) has been suggested to considerably influence how bird species are affected by forest fragmentation (Watson *et al.*, 2005). Friesen *et al.* (1995) showed that influences from the surrounding habitat became more pronounced through, for example, altered predation levels and changed microclimate in remaining forest fragments. The aims of *Paper III* were to investigate if surrounding habitat (residential areas, high-rise building areas and grassland) affected population density, reproductive performance and nestling condition of great tits breeding within urban woodlands.

Theoretical studies suggest that the connectivity between the city and peri-urban habitat patches could enhance the contribution of peri-urban fauna to inner-city populations (Snep *et al.*, 2006). Corridors are often proposed as a valuable conservation tool to increase connectivity and link habitat patches in fragmented landscapes (Fahrig & Merriam, 1994). However, there is no conclusive evidence from empirical studies that corridors generally increase dispersal of individuals between patches. Today, many grassland butterfly species are restricted to linear habitats such as field margins and road verges due to intensified land use in Europe (Van Swaay & Warren, 2003). In Sweden Road verges are regularly mowed to increase visibility and improve traffic safety (Sjölund *et al.*, 1999). Little research attention has been given to their potential function as corridors between fragmented habitats (but see Dover, 1997). Snep *et al.* (2006) emphasised the need to validate the importance of peri-urban areas and road verges for increasing butterfly abundance within inner-cities in real landscapes. In *Paper IV*, the aim was to investigate the behaviours of butterflies that are habitat generalists (common blue *Polyommatus icarus* and ringlet *Aphantophus hyperantus*) and habitat specialists (mazarine blue *Polyommatus semiargus* and pearly heath *Coenonympha arcania*) in experimental grassland strips that approximated road verges with different management regimes.

Methods

Description of urban woodlands (Paper I, II and III)

Studies on urban green areas have largely focused on parks and residential areas, and only few studies have been conducted in urban woodlands (but see Konijnendijk, 1999; Florgård, 2000; Rydberg & Falk, 2000; Lehvävirta & Rita, 2004; Mörtberg, 2004; Ode & Fry, 2006). It has proven difficult to compare the status, composition and structure of urban woodlands among countries since the definition of urban woodland is diverse and evolving (Lehvävirta & Rita, 2002). Florgård (2007) reviewed the numerous expressions that have been used to describe urban woodlands: remnant natural vegetation in cities; urban forest remnants, persisting natural vegetation in urban areas, woods surrounded by housing, urban natural areas, urban remnant bushland, urban bush, natural vegetation and development, forests in urban environment, and indigenous vegetation within urban areas. These urban woodlands are generally defined as structurally equivalent to a natural forest stand and the field layer is not managed as in a park (Lehvävirta & Rita, 2002). However, intensive usage of urban woodlands, manifested by e.g. walking and bicycle paths, horse paths, benches and playgrounds, is likely to increase wear and influence vegetation structure (Fig. 2).

No common definition exists of how far out from the city limit a forest fragment could be and still be referred to as peri-urban (Gundersen *et al.*, 2005). In this thesis the definition by Statistics Sweden (2001) is used: a built-up area with continuous settlement having < 200 m between houses (Fig.4; see also Ode & Fry, 2006). Forest fragments within the city limits are defined as urban woodlands and those ≤ 5 km from the city limit are defined as peri-urban woodlands.

Urban woodlands close to the city centres originate mainly from old production forests in late successional stages. These woodlands were often old at the time of urbanisation and the trees have since aged another 50 to 100 years (Rydberg & Falck, 2000). Urban woodlands are considered important for multiple objectives such as recreation, aesthetics, timber production and biodiversity (Ode & Fry, 2006) although they have weak legal protection (Tallhage Lönn, 1999). The greatest threat to urban woodlands is fragmentation, however they are also greatly affected by management. Previous management recommendations to increase the deciduous component of forests and retain old forest stands have only partly been emphasised by Swedish municipalities (Rydberg & Falck, 2000). About 60% of the urban woodlands in Sweden are municipally owned (Carlborg, 1991), while remaining woodlands are privately owned but freely accessible due to the Swedish right of common access (in Swedish: allemansrätten). More than half of the visits to Swedish forests are conducted in urban areas (Rydberg & Falk, 2000).

Fig. 2. Swedish urban woodlands with different habitat structures and management regimes (a) mixed deciduous and coniferous woodland with a walking path and a field layer dominated by bare soil (b) mixed deciduous and coniferous woodland with old pine trees *Pinus sylvestris* and unmanaged field layer dominated by blueberry *Vaccinium myrtillus* (c) deciduous woodland with unmanaged field layer dominated by grass (d) mixed deciduous and coniferous habitat with laying and standing (snags) dead wood and an unmanaged field layer dominated by lingonberry *V. vitis-idaea* and blueberry.

Study organisms

Birds and butterflies (i) have wide geographical distribution, (ii) are sensitive to environmental change and (iii) are cost effective to sample (Noss, 1990). Thus, both taxa fulfil the criteria that are essential when monitoring biodiversity at multiple scales (Noss, 1990). Both taxa have also been used in previous studies as umbrella species, that is occurrence of a species whose conservation confers protection to a large number of naturally co-occurring species (Fleishman *et al*., 2000; Roberge, 2006). Birds and butterflies have been shown to be good indicators of changes in diversity that occur when landscapes are exploited by human settlements. They respond to the urban environment at different scales, but both taxa have the highest diversity in the same habitats along the urban gradient (Blair, 1999). Birds use relatively large habitats for breeding and are therefore suitable to use when studying habitat changes on a landscape scale. Butterflies on the other hand are less mobile and respond more to occurrence of specific plant species and habitat changes on a local scale. Butterflies were selected to study movement in grassland corridors at a relatively small scale (*Paper IV*). Each butterfly species was classified as a habitat generalist or a habitat specialist based on their natural history characteristics. All four selected species occur in meadows with a mosaic of short and tall grass, but generally prefer to forage in higher grass vegetation with many flowers (Söderström *et al*., 2001). The flight periods of all four species in southern Sweden overlap during one month, from the third week of June to the third week of July.

Study design and study area

Paper I and II

In *Paper I*, almost all Swedish cities (n = 100; 55–65° N, 13–21° E) with more than 10 000 inhabitants were included in the remote sensing analyses. Vegetation structure and management were studied in a subset of 474 woodlands distributed over 34 cities in *Paper I* (Fig. 3 a,b). The subset of 34 cities and 474 woodlands from *Paper I* was used for the bird surveys in *Paper II*, (Fig. 3a). Cities were selected using digitalised maps (scale 1:250 000; National Land Survey of Sweden, 2001a). Cities with more than 10 000 inhabitants were used (i) since more than 50% of the Swedish population live in such urban areas (Statistics Sweden, 2001), (ii) this size limit has been used in previous studies (Statistics Sweden, 2000a; Fransila & Paulsson, 2004), and (iii) there is a demographic trend of people moving from smaller (<10 000) to larger cities (Statistics Sweden, 2000b). All cities were classified into three categories; commuter, large increase and stable cities based on change in human population size and commuting patterns used in analyse in *Paper I*.

In *Paper I*, additional analyses were made on 83 cities in the nemoral and hemiboreal vegetation zones (south of 55–61°). Cities south of the boreal border were chosen to avoid differences in climate, vegetation zones and bird faunas in northern Sweden (Ahti *et al*., 1968; Svensson *et al*., 1999). The study area covers 105 000 km^2 and includes 84% of the Swedish population of 9.1 million (Statistics Sweden, 2006).

To be able to distinguish possible regional differences in urban woodland structure and bird community composition, Sweden was divided into a southern, western and eastern region, (Fig. 3b). When comparing species richness between regions in *Paper II*, the Sørensen similarity index was used. Sørensen index is counted as Ss = 2a / (2a + b + c); a = number of species in sample A and sample B (joint occurrences), b = number of species in sample B but not in A and c = number of species in sample A but not in sample B (Krebs, 1999).

In each region, cities were selected in a balanced design regarding the proportion of urban woodland (1– 40%), and dominating type of surrounding landscape (arable land and forest) using digitalised maps (1:50 000; National Land Survey of Sweden, 2001b). Half of the cities in each region were located in farmland-dominated landscapes and the other half in forest-dominated landscapes. City centre, city edge and peri-urban areas were differentiated in each city (Fig. 3c). The city centre was defined as the inner 75% of a city's area and the city edge as the remaining 25%. In each triplet (i.e. city centre – city edge – peri-urban), woodland fragments were similar in size (> 1 to ≤ 3 ha, > 3 ha to ≤ 8 ha or > 8 ha) and had similar tree layer composition (i.e. deciduous or mixed coniferous-deciduous). A total of 10 cities in the southern region, 12 cities in the western region and 12 cities in the eastern region fulfilled the requirements of the balanced design. Around each city a buffer of 5 km was created using digitalised maps (1:50 000; National Land Survey of Sweden, 2001b). Peri-urban woodlands were located from 200 m up to 5 km from the city border, a distance which has been used in previous studies comparing urbanisation effects on green areas around cities (Statistics Sweden, 2000a).

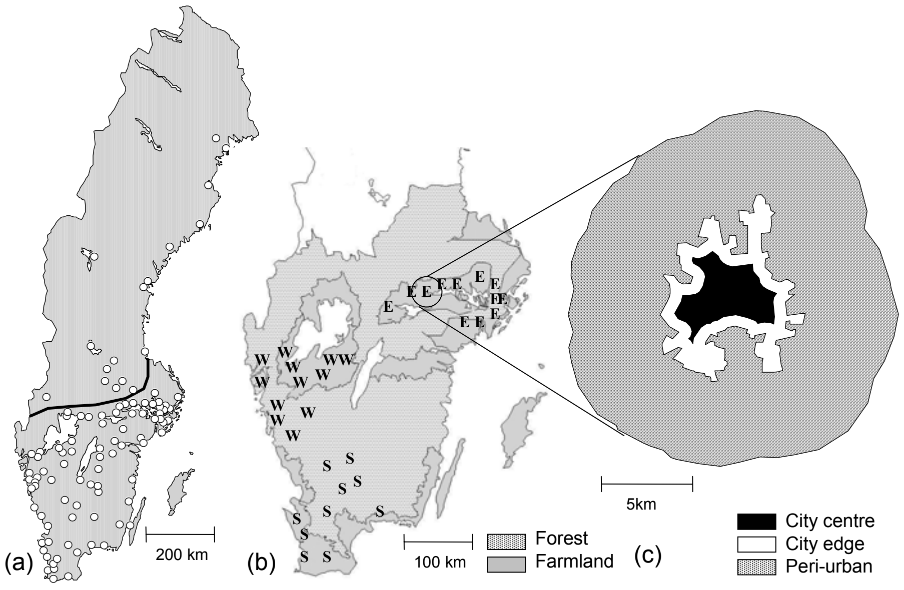

Fig. 3. (a) Map of Sweden showing the 100 cities (○) used in the GIS analysis in *Paper I*. The line across Sweden shows the boreal border (b) Southern Sweden showing the 34 cities that were used for vegetation mapping in *Paper I* and bird surveys in *Paper II* (S = southern region, W = western region, E = eastern region). (c) City of Örebro is magnified to show the three different distances (city centre, city edge and peri-urban) along the urban gradient.

Paper III and IV

Field work in *Paper III* and *IV* were conducted in the Swedish city of Uppsala (59º 49′N, 17º38′E) with 128 000 inhabitants (Fig. 4). In *Paper III*, great tit breeding along transects was monitored in four woodlands (40, 45, 58 and 152 ha, respectively) and adjacent habitats (residential areas, high-rise buildings and grassland/golf course). In *Paper IV* a 50 ha experimental area was selected 5 km south of the centre of Uppsala (Fig 4). Within this larger area, a core site of 10 ha grassland habitat was located where several experimental grassland strips were created. Previous monitoring in the area has revealed high diversity of butterflies (Söderström, unpublished data). A small-scale mosaic of different land uses allows for such high butterfly diversity: seminatural grasslands, set-asides, *Salix* plantations, mixed deciduous-coniferous woodlands, crop fields and suburban gardens found within one kilometre of the site.

Vegetation mapping

All 474 woodlands were mapped with the same methods during the field season 2004 (*Paper I*). NILS (National Inventory of Landscapes in Sweden: Esseen et al., 2006) was used as a model for the surveys. One area was sampled in the centre of each woodland. The field layer in percentage and number of saplings, smaller trees, larger trees and dead wood were calculated in circular plots with 3.5 m and 10 m radius (placed within each other). Basal area of larger trees and dead wood were calculated from the exact diameter at breast height. Data on the amount of dead wood (laying, standing and high stumps) used as a comparison to the urban and peri-urban woodlands were extracted from 5827 forest stands representing all forest categories in the nemoral and hemiboreal vegetation zones (Swedish National Forest Inventory, 2006). In *Paper III*, the vegetation mapping was performed in similar circular plots with 3.5 and 10 m radius, although these were centred around nest boxes in which a nest had been initiated. In each of the surveyed urban woodlands in Paper I, presence of different management regimes (shrub clearing and grazing), infrastructure (walking and bicycling paths, horse path, playground) and geophysical factors (hills, streams, boulders, open water) were recorded within a 50 m circle.

Bird surveys

In one year, 474 woodland fragments in southern Sweden were surveyed for birds three times; once in each period between 5 and 20 April, 5 and 20 May, and 5 and 20 June, respectively. To compensate for the later arrival of long distance migrants in the eastern region (on a higher latitude) the census period was delayed with five days. In the centre of each forest fragment, point counts were performed during a 10 minute period where all species seen or heard within a radius of 50 m were recorded (Bibby *et al.*, 1992). Bird surveys were conducted from sunrise and three to five hours onwards depending on the travelling distance between woodland fragments. The order of point counts were changed between survey periods so that the April survey started in forest fragments located in the peri-urban area, the May survey in the city centre and the June survey in the city edge. No surveys were conducted if there was heavy rain or winds and all woodland fragments of a city were surveyed during one morning (i.e. between 6 and 18 woodlands).

Fig. 4. The city of Uppsala with 128 000 inhabitants. The white line indicates the city limit based on Statistics Sweden (2001), circles indicate woodlands studied in *Paper III* and square indicates study site of *Paper IV*.

Nest box experiment design

A total of 300 nest boxes were placed along transects from the major types of adjacent habitats (residential, high-rise building, grassland/golf course habitat) into urban woodlands (Fig 5). All transects reached 150 m into the woodland and 50 m into the surrounding habitat. Five transects were located in each of the three habitat types. Each transect was divided into four (I-IV) 50 m long sections along a 100 m wide transect (Fig. 5). Five nest boxes were randomly distributed within each section (total 20 per transect). Nest box densities were enough to ensure that the nest box density was satured with at least 4 per ha for blue tit and 6 per ha for great tit. Nest boxes were made of wood and put up at a mean height of 225 cm in primarily deciduous trees. Predation risk on eggs and nestlings was minimized by using a plastic ring around the entrance hole and a piece of wood inside the nest box directly below the entrance hole.

Each nest box was visited one to three times per week from the beginning of April to the end of July in 2004 and 2005 to determine date for clutch initiation and hatching, and to measure clutch size (number of eggs), brood size (number of eggs that hatched) and the number of fledged nestlings. When nestlings were 15 days old nestlings were individually weighed and the tarsus was measured. Hatching spread (HS) was calculated according to Slagsvold & Amundsen (1992) as: 2.4 × natural logarithm (weight of heaviest nestling / weight of lightest nestling). Nestling condition (NC) was calculated as the residual from a regression of body mass on tarsus length (Ardia, 2005). Average NC of each clutch was used in statistical analyses. Non-experimental nest boxes were counted and monitored for possible breeding attempts.

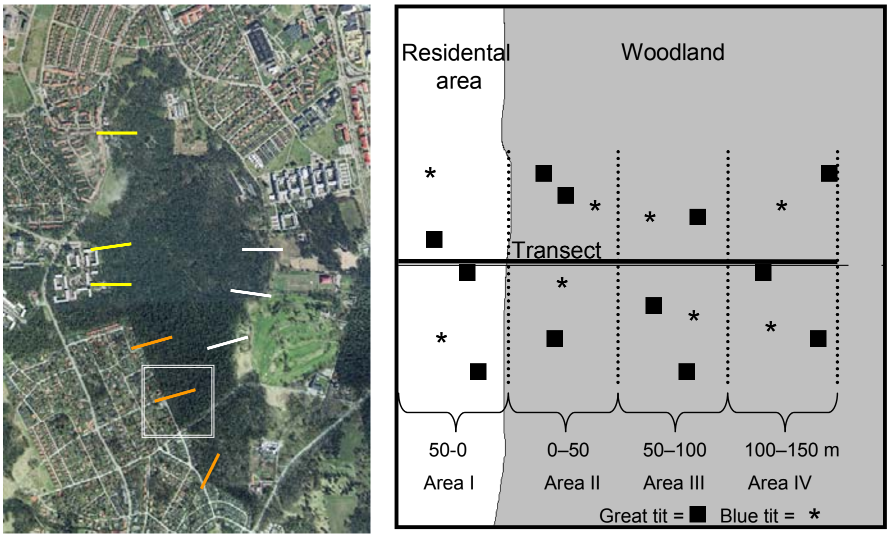

Fig.5. Aerial photograph showing an urban woodland (152 ha) with 9 out of the 15 transects. Adjacent habitats were high-rise buildings (yellow), residential areas (orange), and grasslands/golf courses (white). White square in picture is magnified to the right showing a 200 meter transect and the location of nest boxes. In each section three nest boxes had an entrance hole with 32 mm diameter (for great tit) and two with 28 mm diameter (for blue tit) (Dhondt & Adriaensen, 1999; Solonen, 2001).

Butterfly experimental design

The created experimental grassland strips simulating road verges were 30 m long and 2 m wide (Fig. 6). The four butterfly species seem to have low daily dispersal rates (Eliasson *et al.*, 2005). For example, Binzenhöfer *et al.* (2005) found in a mark-recapture experiment that pearly heaths move less than 100 m. A length of 30 m was therefore considered sufficient to investigate movement in grassland strips. The width of the experimental strips was typical of road verges in Uppsala and many other cities in Sweden.

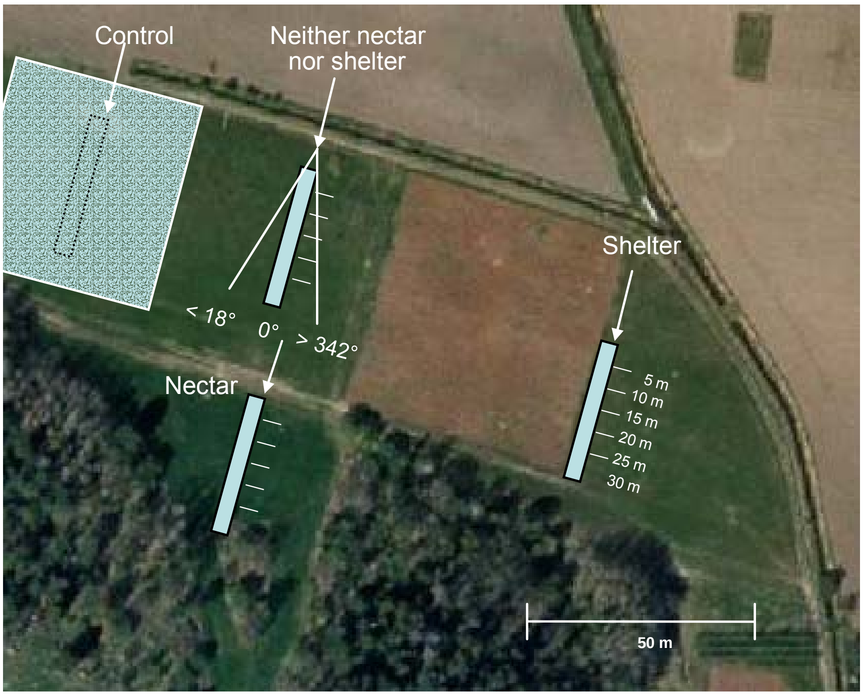

Fig. 6. Picture of the experimental arena. Three types of 2 m wide and 30 m long grassland strips were used: (1) "nectar", abundant nectar resources; (2) "shelter", few nectar resources and the Salix plantation acting as wind shelter on the left, (3) "neither nectar nor shelter", few nectar resources and no shelter from the wind. The "control" consisted of a 1-ha large set-aside, while the surrounding "matrix" consisted of 2 – 4 cm high grass and no nectar resources. Arrows indicate the point of butterfly release. In the "neither nectar nor shelter" grassland strip, criteria used to determine grassland strip movement are shown.

Fig. 7. A permanent felt pen was used to put a number on the underside of the backwing. The Picture shows a mazarine blue *Polyommatus semiargus.*

Three different strips with higher grass were created to account for the most important factors that affect butterfly movement (Munguira & Thomas, 1992; Dover, 1997; Dover & Fry, 2001; Clausen *et al.*, 2001). In all the grassland strips and the control, plant cover of different species was visually estimated in 1 m^2 squares every 5 m, while grass height was measured every 1 m using a sward stick (Stewart *et al.*, 2001).

All four butterfly species were common to fairly common in south-east Sweden (Eliasson *et al*., 2005) and present in the study area prior to the experiment. Butterflies were caught during the mornings in six grassland areas within a radius of 20 km from the experimental arena. Each butterfly was marked before release to allow individual recognition at a later stage (Fig. 7). One butterfly at a time was released in one strip and followed for two minutes before moving on to the next. To avoid intra or interspecific interactions, butterflies that were inside or close to grassland strip was removed. Butterflies were released at 0.5 m height facing the direction of the grassland strip (Fig. 6). When each butterfly was released ambient temperature, wind speed and wind direction was measured. The distance moved along the corridor and the perpendicular distance to the grassland strip were the two estimates used to calculate the flight direction of the butterfly.

Results and discussion

Status, habitat structure and management of Swedish urban woodlands

Urban woodlands are rapidly being fragmented in large parts of Europe. Our results showed that the proportion of the city area comprised of urban woodland varied between 1 and 40% with an average of 20% in Sweden (*Paper I*). This makes urban woodlands relatively common in Sweden compared to, for example, Madrid (5%; EEA, 1995), Brussels (12%; EEA, 2002), Great Britain (14%; DTLR, 2002) and the 22 largest Dutch cities (7%; Konijnendijk, 2003). The rapidly increasing expansion of larger cities was until recently only considered a trend in the U.S. (referred to as urban sprawl, see Introduction) but is now established in Europe (Kasanko *et al*., 2006; EEA, 2005). Results showed that the largest threat of fragmentation was in commuter cities close to Sweden's three largest cities (Stockholm, Gothenburg and Malmö). Cities with a greater proportion of woodland in the peri-urban landscape also had more woodland within the city limits. Therefore, our results verified that urban woodlands are formed from remnant forest vegetation (cf. Tyrväinen, 1997). Furthermore, the proportion of urban woodlands was negatively associated with indicators of exploitation (roads, residential areas and office blocks).

Urban woodlands were often old at the time of urbanisation and the trees have since aged another 50 to 100 years (Rydberg & Falck, 2000). The vegetation structure of urban woodlands in the city centre may therefore be different from peri-urban woodlands. Urban woodlands in the nemoral and hemiboreal vegetation zones consisted of 51% deciduous trees and 45% coniferous trees (4% dead wood). The dominant tree species were Scots pine (35% of basal area; m^2 ha^{-1}), oak (15%), birch (15%), Norway spruce (10%), aspen (5%), beech (5%), ash (2%), elm (2%), lime (2%), maple (2%) and other species such as rowan (3%). A shrub layer occurred in 83% of all surveyed woodlands and 57% contained small trees (4–15cm dbh). The field layer was dominated by grass (found in 67% of all the woodlands) followed by herbs (52%), bare soil (31%) and blueberry or lingonberry (26%).

Our results showed that woodland in the city edge and in the peri-urban area (< 5 km from the city limit) covered almost 1 million ha in Sweden. These urban woodlands had more dead wood than an average Swedish forest (Fig. 8). Although urban woodlands had a high proportion of dead wood, city centre contained less than half the amount of dead wood compared to woodlands in the city edge and peri-urban area (Fig. 8). Saplings and smaller trees, typical of earlier successional stages, were more common in peri-urban woodlands than in woodlands in the city centre and city edge (Fig. 8), while the number of larger trees did not differ across the urban gradient (Fig. 8). Physical structures related to recreational activities such as children's playgrounds, walking and bicycling paths, and roads were also more prevalent in central urban woodlands, which directly or indirectly (through higher use of the woodland) lead to fewer saplings and smaller trees.

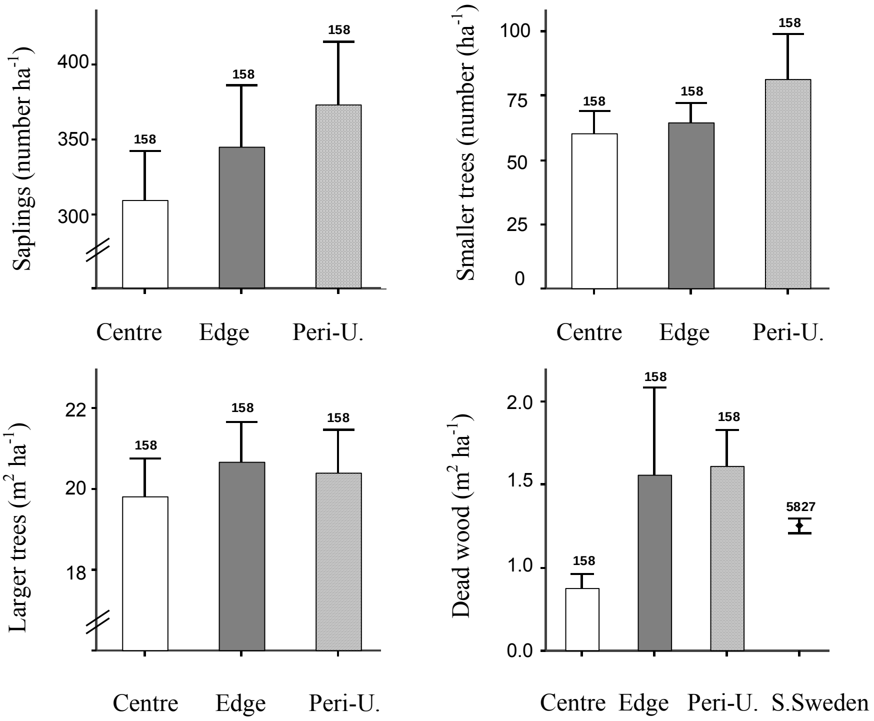

Fig. 8. Densities of trees from different vegetational stages across an urban gradient. Data from the Swedish National Forest Inventory (2006) on dead wood are shown for reference but are not included in the analyses. Sample size (above error bars) refers to the number of woodlands and error bars show mean ± 1 SE.

Trees in urban and peri-urban woodlands may be re-established at a high cost (Florgård, 2000) however, it may be impossible to re-establish field layer vegetation in frequently trampled areas in urban woodlands (Hammit & Cole, 1998). Since only a few urban woodlands in Sweden have legal protection, there is a need to develop regulations and legislation concerning urban woodlands in a broader perspective. Furthermore, decision-makers, planners, managers, nursery schools, schools, NGO's and the general public need to be aware of the costs to re-establish urban woodlands, and to instead focus on how to proper manage vegetation structure in existing urban woodlands. Municipalities, the largest owners of Swedish urban woodlands, could increase the amount of dead woodland and improve other structural elements in urban woodlands since they are not under any production command. However, Sandström *et al.* (2006b) showed that Swedish urban planners (municipal employees) had little knowledge about how to implement e.g. biodiversity polices in urban landscapes.

Importance of urban and peri-urban woodlands for birds in urban forest fragments

The results suggested that bird species breeding in urban woodlands were strongly affected by the surrounding city or landscape composition.

The significant interaction terms suggest that birds breeding in local urban woodlands may depend on the composition of habitats both at the city and landscape scales. For example, great spotted woodpecker, nuthatch and robin had significant positive associations with proportion of urban woodland only when there was less forest in the surrounding landscape. Nuthatch had generally higher population densities in urban than peri-urban woodlands, but peri-urban woodlands still seemed to affect local nuthatch abundance (Fig. 9). Interestingly, great spotted woodpecker had relatively higher abundance in cities with low proportion of peri-urban woodland (Fig. 9.). Although local abundances of many bird species within urban woodlands were associated with the proportion of peri-urban woodland, the relationships varied among species. It is therefore difficult to draw general conclusions whether local urban woodlands, surrounding urban woodlands or peri-urban woodlands are the most important (see also Lee *et al.*, 2002). However, our results indicate that the importance of urban woodlands increase when there is less forest in the peri-urban landscape.

There was no difference in total species richness between urban and peri-urban areas. Previous studies comparing urban and rural bird abundances often suggest that bird species richness decreases from peri-urban areas to city centers and that the bird fauna in cities is dominated by a few exotic species (Blair, 1996; Chace & Walsh, 2006). In contrast to previous studies, our findings suggest that the bird composition was more heterogeneous in urban than peri-urban areas. One reason for the discrepancy may be that earlier studies did not compare similar habitat types among cities (Clergeau *et al.*, 2006) or that anthropogenic habitats were included across the gradient (Blair, 1996).

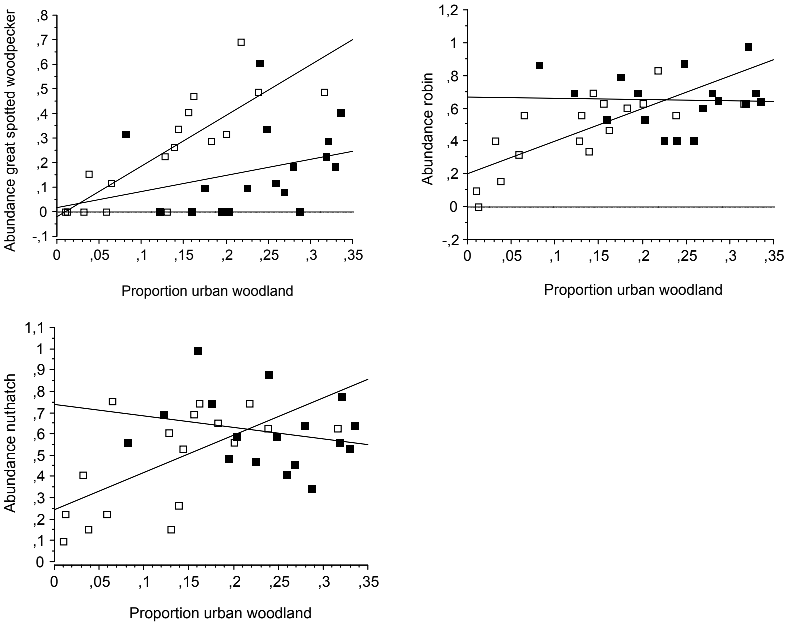

Fig. 9. Graphical illustrations of the significant interaction terms in Table 4. On the y-axis is the average species abundance per city (based on 4 to 12 urban woodlands per city) and on the x-axis the proportion of woodland within different cities. Filled squares show cities with above median proportion of peri-urban woodland (0.41) and empty squares show below median.

Twice as many bird species were significantly more abundant in urban than in peri-urban forest fragments. A total of 34 bird species occurred in more than 10% of all woodland fragments and of these twelve (35%) occurred significantly more often in urban woodlands, whereas 6 species (18%) were more common in peri-urban woodlands (Table 2). The corvids e.g. is a group that is highly successful in many urban habitats (Shochat *et al.*, 2006), and we found that magpie, jackdaw and hooded crow were more common in urban than peri-urban woodlands. There is no single reason why some birds become more urbanized than others. Johnston (2001) suggested that birds that can adjust to constantly changing environments are most likely to be abundant in urban areas.

Local abundances of one third of all bird species were significantly associated with the proportion of urban or peri-urban woodland. In accordance with Snep *et al.* (2006), these results suggest that both local and landscape factors influence the distribution of birds breeding in urban habitats.

Table 2. *Bird occurrence (%) in forest fragments located in urban (city centre and city edge) and peri-urban woodlands. Bold numbers show the highest percentage between areas for species with significant differences in occurrence or abundance(*). Bird surveys were carried out in a total of 474 forest fragments of which 316 were in urban and 158 in peri-urban areas. Only bird species occurring in > 10% of forest fragments (N > 47) were analysed; for a full species list of birds see Appendix B. Bird species are shown in systematic order and the first column shows decreasing order of frequency.*

#	Bird species	Urban	Peri-urban	G^2 /t*	P
10	Woodpigeon*	**58**	48	3.17	0.002
19	Great spotted woodpecker	23	29	2.22	0.14
26	Tree pipit	6	**38**	71.42	<0.001
24	Pied wagtail	19	20	0.17	0.68
28	Dunnock	11	**22**	9.78	0.002
30	Wren	11	17	2.63	0.10
7	Robin*	68	71	-0.46	0.65
5	Blackbird	77	73	1.52	0.13
17	Songthrush	26	**35**	4.52	0.033
32	Redwing	12	13	0.24	0.62
8	Fieldfare*	**77**	40	8.51	<0.001
34	Lesser whitethroat	**12**	6	4.43	0.035
21	Garden warbler	21	25	1.36	0.24
12	Blackcap	39	46	2.09	0.15
25	Wood warbler	19	14	2.18	0.14
4	Willow warbler*	80	87	-1.66	0.098
16	Goldcrest	23	**45**	21.65	<0.001
11	Pied flycatcher	**48**	30	13.85	<0.001
29	Marsh tit	14	16	0.30	0.58
2	Great tit*	**92**	90	2.49	0.013
3	Blue tit*	**90**	76	4.21	<0.001
9	Nuthatch	**58**	47	5.21	0.022
27	Treecreeper	11	**23**	10.80	<0.001
14	Starling*	34	35	-0.89	0.39
33	Jay	10	13	1.09	0.30
15	Magpie	**40**	17	29.91	<0.001
18	Jackdaw*	**32**	14	3.70	<0.001
13	Hooded crow	**44**	27	13.92	<0.001
31	Tree sparrow	**15**	8	4.12	0.042
1	Chaffinch*	96	99	-1.36	0.18
20	Hawfinch	**27**	13	12.01	<0.001
6	Greenfinch*	74	68	1.95	0.051
22	Siskin	20	25	1.76	0.18
23	Yellowhammer	7	**44**	87.48	<0.001

* t-tests on ln-transformed abundances for the 10 most common species.

Many Swedish cities have less woodland than the suggested theoretical threshold of 20–30 % remaining habitat on a landscape level below which effects of habitat fragmentation is higher than that from habitat loss alone (Andrén, 1994). This may be one reason that bird species with restricted habitat use or limited dispersal are absent or sparse in our data set. Further studies of how adjacent landscape composition affects local birds abundance may aid to mitigate the effects of habitat loss and fragmentation on the urban avifauna.

Are great tits breeding within urban woodlands affected by surrounding habitats?

Several previous studies have shown that urban habitats often have higher densities of tits, but that reproductive performance is lower than in rural areas (see Introduction). Reproductive performance and density may also vary, on a much smaller scale, between adjacent urban habitats (Friesen *et al.*, 1995). Our results showed significant differences in population density and hatching date for great tits within 200 m long transects running from adjacent habitats into urban woodlands. In contrast to previous large-scale studies (e.g. Cowie & Hinsley, 1987), we could not document any differences in quantitative estimates, such as clutch size or number of fledglings, on the small spatial scale where this study was conducted. Instead, estimates of hatching spread and nestling condition varied among surrounding habitats. Furthermore, only saplings and smaller trees, and not larger trees, were associated with hatch date and nestling condition for great tits, demonstrating the importance of vegetation structure in the lower strata.

Great tits reached their highest breeding density in residential transects. When only including pairs breeding inside the woodlands, density in woodlands bordering to residential habitats tended to be higher than those adjacent to grassland habitats. Clutches hatched earlier in the surrounding habitat than in urban woodland (Fig. 10). Furthermore, clutches hatched two to three days earlier in residential and high-rise building transects (average 19 and 20 May, respectively) than in grassland transects (average 22 May).

Estimates of young condition quality (hatching spread and nestling condition) were related to distance along the transect. Weight differences among nestlings were greater in surrounding habitats than in the woodland (Fig. 10). Nestling condition was lower in the surrounding habitat than in the forest, particularly in residential areas (i.e. significant interaction term, see Fig. 10). Positive values of nestling condition were mostly found in urban woodlands adjacent to residential and high-rise building transects. In addition, nestling condition was higher when more coniferous saplings were near the nest box. It is possible that the better condition of nestlings when there were more saplings near the nest reflected that parents could more easily approach the nest box unnoticed; thus avoiding predators that use visual stimuli (Eggers *et al.*, 2005).

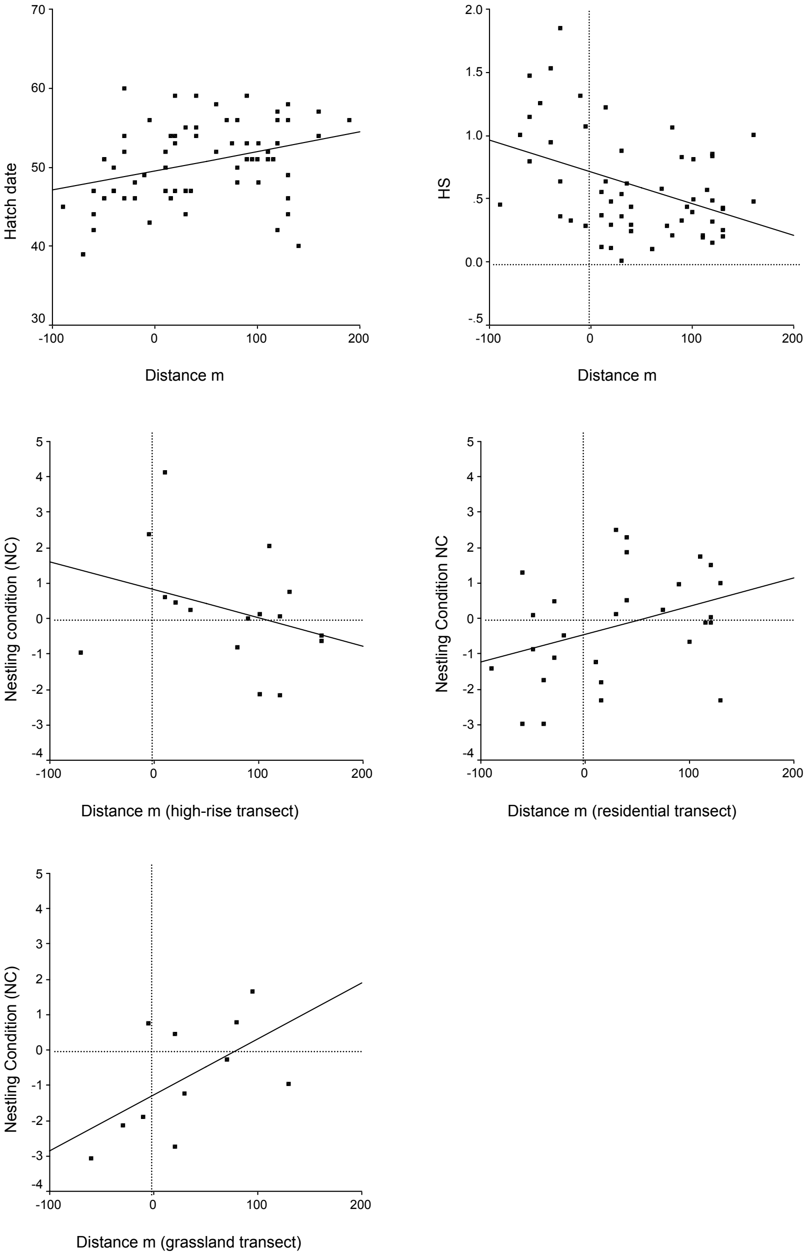

Fig. 10. Differences for great tit in hatch date (top left) and hatching spread, HS (top right). Hatch date was counted from 1st of April. Differences in nestling condition for great tits along transects with different surrounding habitats. High-rise transect (middle left), residential transect (middle right) and grassland (bottom left) (-100 – 0 is adjacent habitat and 0 – 200 m is woodland).

We observed high numbers of cats in the residential and high-rise building habitats during the experiment. Moreover, the number of deciduous saplings and coniferous small trees influenced hatch dates so that earlier breeding occurred in areas with less vegetation.

Highest density of breeding pairs, earlier hatch dates and lower nestling condition in the residential habitat compared to the other two habitats suggest that there is a mismatch between preference, as shown by density and hatch date, and quality of nestlings. Moreover, hatching spread was higher in all three of the surrounding habitats compared to adjacent forest. There are at least five not mutually exclusive explanations for these results: food, competition (inter- or intra-specific competition for food and nesting holes), predation on nestlings and adults, microclimate and anthropogenic disturbances (Cowie & Hinsley, 1987; Hõrak, 1993; Dhondt & Adriaensen, 1999; Solonen, 2001; Isaksson *et al.*, 2005; Jokimäki *et al.*, 2005).

Adjacent habitats may act as buffer zones to urban woodlands and are therefore important for habitat quality even within woodlands (Marzluff & Ewing, 2001; Watson *et al.*, 2005). The results suggest that it is important to consider the differential external influences of surrounding habitat types on remaining urban woodland fragments. Residential areas seemed to have larger effects on breeding density and reproductive performance than grasslands/golf courses with lower intensity of human land use and the high-rise habitat with higher intensity of human land use.

Dispersal of butterflies in grassland corridors resembling road verges

Habitat specialists may benefit most from corridors since they are most likely to be isolated by fragmentation (Mech & Hallett 2001; Hudgens & Haddad 2003). The results of *Paper IV* indicate that both habitat specialists, but none of the habitat generalists, used grassland strips as movement conduits more than expected by chance. The results suggested that the two habitat specialists did not favour the same type of grassland strips: the blue (mazarine blue) followed the ‘‘shelter’’ grassland strip whereas the brown (pearly heath)moved along the ‘‘nectar’’ grassland strip. This is surprising given what is known about the species’ autecologies. If butterfly movement rates would have been linked to grassland strip quality, specialist blues were expected to follow the ‘‘nectar’’ grassland strip with a high percentage cover of clovers that are essential both as nectar and larval host plants (Eliasson et al., 2005). Specialist browns, in contrast, were expected to move in the ‘‘shelter’’ grassland strip, which had an ecotone between the Salix plantation and open land similar to the species’ habitat requirements (e.g. meadows with higher grass close to shrubs; Eliasson et al., 2005). Instead, it was in these grassland strips butterflies were least inclined to move. It seems as if conditions in the grassland strip reflecting the habitat requirements of different species may slow down movement. The ‘‘neither nectar nor shelter’’ grassland strip was not used by any butterfly species. Therefore, the experiment suggests that grassland strips of intermediate quality may promote higher dispersal rates than both low-quality and high quality grassland strips (Table 3).

Table 3. *Number of butterflies that moved in the grassland strips (did not move in grassland strips). Grassland strip movement is defined as travelled > 5 m, and < 18° or > 342° angle from the direction of the grassland strip. Numbers in bold show significant different numbers moving in one of the grassland strips compared to the control (G^2-test, $P < 0.05$; all other tests were non-significant).*

Species	Nectar	Shelter	Neither nectar nor shelter	Control	Total
Generalist blue	4 (16)	3 (17)	2 (20)	2 (18)	11 (71)
Specialist blue	4 (25)	**11 (16)**	5 (24)	1 (25)	21 (90)
Generalist brown	7 (24)	8 (22)	7 (21)	5 (22)	27 (89)
Specialist brown	**12 (19)**	4 (23)	5 (25)	4 (24)	25 (91)
Total	27 (84)	26 (78)	19 (90)	12 (89)	84 (341)

Table 4. *Environmental conditions that significantly affected butterfly speed, time in flight and travelled distance. Estimate and significance values of backward stepwise linear regressions are given.*

Species	Dependent variable	Model R^2 (%)	Temperature	Wind speed	Cloud cover
Generalist blue	Speed	7.3*	+0.04*		
	Distance	5.4*	+0.03*		
Specialist blue	Speed	7.6**	+0.06**		
	Time in flight	9.2**	–0.04**		
Generalist brown	Time in flight	3.0(*)		–0.30(*)	
Specialist brown	Speed	4.7*			–0.61*
	Time in flight	7.9*		–0.26(*)	+0.69**

** $p < 0.01$, * $p < 0.05$, (*) $p < 0.10$

The two butterfly families were different affected by environmental conditions. Higher ambient temperature increased the flight speed of blues (Table 4). When the temperature increased, generalist blues also flew further while specialist blues flew for a shorter period of time. In contrast, browns did not associate with temperature but they seemed to be more sensitive to wind. Both species spent less time in flight as wind speeds were higher (Table 4). Specialist browns flew even on more cloudy days but then with reduced flight speed and for longer periods of time.

If road verges are to be used as a conservation tool to increase dispersal between habitat fragments, they need to be managed to fit the autecologies of the concerned species. In severely fragmented farmland landscapes where no larger fragments of seminatural grasslands are preserved, it may be better to manage road verges to optimally benefit butterfly reproduction. This study have shown a novel way to study butterfly behaviour while controlling for confounding factors. Future attempts to study behaviour of dispersing butterflies of grassland butterflies may use large fields of set-asides within the EU agri-environment scheme to allow broad-scale, replicated experiments.

Conclusions

Throughout this thesis I have had a landscape perspective on factors that affect the distribution, dispersal and reproduction of urban fauna. Observational data have been collected using extensive remote sensing analyses and bird surveys, while experiment have been set up to answer specific questions regarding dispersal and reproduction in different habitats. Three major results of this thesis partly contradict results of earlier studies performed in urban areas: urbanisation does not necessarily lead to a homogenisation of the bird fauna; urban habitats need to be described in detail to allow comparisons among studies and thus/subsequently general conclusions; bird faunas of local urban woodlands differ among regions and are strongly affected by composition of habitats both at city and landscape levels.

There is a general pattern that urbanisation leads to a more homogeneous fauna among cities (Blair, 2001; McKinney, 2006). However, the results of this thesis suggest that bird composition are as heterogeneous in urban as in peri-urban woodlands. This means that human development is not predestined to lead to a more homogenized bird fauna. Possible explanations for the differences among studies could be that (i) a relatively high proportion of urban woodland in Swedish cities remains, allowing self-sustaining urban populations, (ii) urban woodland and peri-urban woodland are often connected, which may allow forest-dwelling birds to immigrate into urban areas, (iii) a relatively heterogeneous vegetation structure of Swedish urban woodlands, (iv) earlier studies did not compare similar habitat types among cities or that anthropogenic habitats (e.g. golf course and residential areas) were included along the gradient. Moreover, not only generalist and omnivorous bird species occurred in urban woodlands but also species with a more restricted habitat use (*Paper II*).

Most studies of the effect of urbanisation on birds, hitherto, have inventoried plots across urban to rural gradients. However, if the local habitat structure is not described in detail, it is difficult to draw general conclusions whether differences in bird abundance were due to the distance along the urban to rural gradient, adjacent landscape composition or local habitat quality (*Paper I* and *II*). There may also be large regional differences (*Paper II*), which may confound the conclusions of studies carried out in only one or a few cites. An extensive review of bird abundances in cities in different European countries only described where along the urban gradient a bird species occurred, i.e local habitat was not included (Clergeau *et al*., 2006). This may confound results as I in this thesis found large differences in density of great tits in different habitats at a small spatial scale (within 200 m long transects, *Paper III*).

Previous studies in urban environments have suggested that local habitat quality and not the adjacent landscape have the greatest effects on bird communities within cities (Clergeau *et al*., 2001; Jokimäki *et al*., 2003). However, this thesis shows that many bird species breeding in urban woodlands were strongly affected by the surrounding city or landscape composition (*Paper II* and *III*). Since most urban woodlands are highly fragmented, even more so than woodlands in the surrounding landscape, edge effects are likely to be important. On a smaller scale, adjacent habitats may affect population density, breeding performance and nestling condition of birds breeding in woodlands (*Paper III*). In future studies, it is important to quantify possible edge effects in urban areas and try to identify mechanisms causing, for example, different patterns of distribution. Many bird species may also use several habitats in the city matrix both during breeding and non-breeding seasons (e.g. nesting in urban woodlands but foraging at the forest edge or in surrounding city habitats). In larger urban woodlands edge effects are probably not that important, instead local management may have a stronger effect on bird densities. Breeding densities may not always be a reliable indicator of habitat quality (van Horne, 1983). Urban habitats often have higher densities of tits, but lower reproductive performance, than rural habitats. This thesis also showed such a mismatch between habitat preference (as shown by density and hatch date) and quality of nestlings, but on a much smaller spatial scale (*Paper III*). Therefore, it is important to not only count bird numbers across gradients but also try to estimate reproductive performance (and probably also survival) in urban ecological studies. Such an approach may also identify the most important mechanisms that affect birds in urban areas.

Management and conservation

Urban woodlands are important for recreation purposes as demonstrated by the fact that more than half of the visits to a Swedish forest are conducted in urban woodlands (Rydberg & Falk, 2000). Moreover, urban woodlands may be the only contact with nature most city people experience. They are therefore important to increase awareness for biodiversity conservation issues of the general public, also in other environments than in cities (McKinney, 2006, Dunn *et al*., 2006). This thesis has clearly shown that urban woodlands contain high biological values that by themselves motivate that they should be of conservation concern.

Urban and peri-urban woodlands cover an area as large as the total amount of protected forests in Sweden, and they have a larger proportion of dead wood and deciduous trees than production forests. Few urban woodlands are protected, which means that large areas with potential high values for biodiversity are at risk (Niemelä, 1999). Thus, new legislation of urban woodlands may be needed if urban biodiversity is to be kept at present status or grow as suggested by the government bill 2004/05:150. Commuter cities surrounding the two largest cities in Sweden had a high proportion of urban woodland remaining. However, these cities are likely to experience a continued increase in human population size, which will probably lead to a decrease in forest area. It is also important to acknowledge the importance of where a city is located (i.e. regional and landscape context) to adjust conservation and management of biodiversity accordingly (*Paper II*). For example, cities located in a farmland-dominated landscape may have altogether a different bird fauna than those located in forest-dominated landscapes. Within cities, different types of adjacent habitats differentially affect breeding density and reproductive performance of tits breeding in local urban woodlands (*Paper III*). Thus, potential effects of infill development need to include adjacent habitats as well.

If movement corridors are to be used as a conservation tool to increase abundance of species within cities (from peri-urban populations), it is important that suitable habitats for reproduction are found within urban areas. The corridors would otherwise act as ecological traps. Moreover, management of the movement corridor needs to be adapted to the species of conservation concern to successfully enhance movement among habitat fragments (*Paper IV*). Ecological corridors are often discussed among city planners in Swedish cities and our study showed that more focus should be put on corridor quality, and not only rely on leaving a linear structure such as a forest strip or an unmanaged road verge.

Urban woodlands with dead wood, old deciduous trees and unmanaged understorey vegetation benefit several bird species that have a more restricted habitat use, and likely also other organisms (*Paper III*). However, there is a conflict of interest between biodiversity conservation on one hand and recreation on the other (*Paper I*). Shrub clearing and recreational activities were more common closer to the city centre, clearly demonstrated by, for example, the many walking paths and children play grounds (*Paper I*). Parts of urban woodlands could be actively managed to fulfil aesthetical and safety requirements while other parts could be managed to increase the prevalence of dead wood, saplings and large trees. By leading paths and roads around the latter areas and informing the public of the reasons for an unmanaged shrub layer, presence of dead wood etc., both human-associated activities and ecological interests could be integrated into the same woodland.

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