

The establishment of an urban bird population

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Summary

1. Despite the accelerating global spread of urbanized habitats and its associated implications for wildlife and humans, surprisingly little is known about the biology of urban ecosystems.
2. Using data from a 60-year study period, this paper provides a detailed description of how the northern goshawk *Accipiter gentilis* L. – generally considered a shy forest species – colonized the city of Hamburg, Germany. Six non-mutually exclusive hypotheses are investigated regarding the environmental factors that may have triggered this invasion.
3. The spatio-temporal analysis of 2556 goshawk chance observations (extracted from a total data set of 1 174 493 bird observations; 1946–2003) showed that hawks regularly visited the city centre decades before the first successful breeding attempts were recorded. Many observations were made in parts of the city where territories were established in later years, demonstrating that these early visitors had encountered, but not used, potential nest sites.
4. Pioneer settlement coincided with: (i) an increase in (legal) hunting pressure on goshawks in nearby rural areas; (ii) an increase in avian prey abundance in the city; and (iii) a succession of severe winters in the Greater Hamburg area. On the other hand, there was no evidence to suggest that the early stages of the invasion were due to: (i) decreasing food availability in rural areas; (ii) major habitat changes in the city; or (iii) rural intraguild dynamics forcing hawks into urban refugia. While breeding numbers of a potential rural source population were at a long-term low when the city was colonized, prior to first settlement there was a sharp increase of goshawk chance observations in the city and its rural periphery.
5. The urban population expanded rapidly, and pair numbers began to stabilize after about 10 years. Ringing data (219 ringed nestlings from 70 urban broods; 1996–2000) demonstrated that most urban recruits had fledged in the city, but also confirmed considerable gene flow between urban and rural habitats. Analysis of chance observations (as raw data or as detrended time series) suggested a tight coupling of population dynamics inside and outside the city.
6. City-colonizations such as the one described here provide a valuable opportunity to study some fundamental aspects of population ecology on a scale at which detailed monitoring is logistically feasible. Furthermore, a good understanding of urban ecology has become essential for efficient wildlife conservation in modern, human-altered environments.

Key-words: behavioural flexibility, dispersal, ecological trap, invasion success, population bottleneck, range expansion, source-and-sink dynamics, territory occupancy

Introduction

In the city of Hamburg, Germany, blackbirds *Turdus merula* and red squirrels *Sciurus vulgaris* forage on meadows in local public parks; red foxes *Vulpes vulpes* roam the streets late at night; and roe deer *Capreolus capreolus* visit suburban backyards early in the morning to feed on garden plants. Northern goshawks *Accipiter gentilis* L. (hereafter ‘goshawk’) also live in the city and, during their daily search for prey, patrol parks,

residential areas and shopping streets, manoeuvring fast and low between houses and parked cars. Just a few decades ago, these animal species were shy forest inhabitants, avoiding humans where possible. Somehow they have found ways to cope with the challenges presented by highly urbanized habitats, and they now form an integral part of the fauna of many cities across Europe. Here I describe how and why goshawks colonized the city of Hamburg, providing a detailed case study of an avian city-invasion from beginning to end.

Despite the accelerating global spread of urban habitats, and its associated implications for wildlife and humans

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(Vitousek *et al.* 1997; Palmer *et al.* 2004), surprisingly little is known about the biology of urban ecosystems. Research has traditionally focused on pristine, 'undisturbed' habitats (McDonnell 1997), and even fundamental ecological processes in urbanized environments remain poorly understood. A good example is the colonization of cities by wildlife. Both the ultimate reasons and the proximate mechanisms of such invasions have rarely been studied – most quantitative population studies on urban wildlife to date were conducted when the study species had already established itself in an area, after pioneer settlement and expansion had taken place (for raptors, see Bird, Varland & Negro 1996; Andersen & Plumpton 2000; Love & Bird 2000; but cf. Oliphant & Haug 1985; Sodhi *et al.* 1992). Furthermore, in most ornithological studies, the dynamics of non-breeders remain unknown, probably because they are more difficult to study with conventional field techniques than are breeding pairs (Rutz & Bijlsma 2006).

For two main reasons, interest in urban ecology has increased sharply during the past decades (McKinney 2002; Alberti *et al.* 2003). First, researchers have started to appreciate that studying urban ecosystems can substantially advance our understanding of fundamental processes in population ecology (McDonnell & Pickett 1990). Colonization events in cities, for example, are of interest because they provide a valuable opportunity to study key aspects of invasion dynamics (see Shigesada & Kawasaki 1997) at a comparatively small scale, where detailed monitoring is logistically feasible. Second, in a rapidly urbanizing world, efficient wildlife conservation depends increasingly on a good understanding of the processes by which animal populations colonize and persist in human landscapes (McKinney 2002). In some cases, animals seem to be attracted to urbanized areas by abundant, unexploited resources such as food or nest sites, but they subsequently suffer increased mortality rates due to collisions with anthropogenic obstacles (e.g. Sweeney, Redig & Tordoff 1997) or novel diseases (e.g. Boal 1997). Hence under certain circumstances, cities may constitute 'ecological traps' for wildlife (Dias 1996; but note that conclusive empirical evidence is currently lacking: Robertson & Hutto 2006). On the other hand, some animal species have been shown to thrive in the midst of human enterprise (Erz & Klausnitzer 1998; Kelcey & Rheinwald 2005). Thus urban populations can exhibit a demographic surplus, acting as a source of individuals within a regional network of local populations (Dias 1996).

As the terminology in certain areas of urban ecology is still inconsistent and ambiguous, I offer a brief summary of relevant definitions. Following earlier work (Tomiałojć 1982; Luniak 2005), I distinguish between two major phases in the successful establishment of an urban animal population. In a first stage, which is the focus of the present paper, individuals from non-urban areas invade the urban habitat, and the urban population passes through three more-or-less distinct phases – pioneer settlement, expansion and saturation (cf. Shigesada & Kawasaki 1997). The first phase is commonly referred to as 'colonization', 'invasion' or 'establishment'. Like many other authors, I use these terms interchangeably,

but I recommend avoiding a fourth one, 'urbanization', which should remain reserved strictly to describe habitat composition or habitat change (McDonnell & Pickett 1990). To emphasize reference to urban environments, I suggest using 'city-' as a prefix for 'colonization' and 'invasion'. In the second stage, urban-living individuals develop specific adaptations to the novel urban habitat – either as the result of (long-term) genetic changes or through the expression of phenotypic plasticity (Partecke, Van't Hof & Gwinner 2004). Thirty years ago this second stage was termed 'synurbization' (Andrzejewski *et al.* 1978), and as urban ecologists have started using the term, it seems worth keeping (note, however, that some later studies use the term 'synurbanization' interchangeably, which should be avoided). As the field of urban ecology matures, and more research is carried out on wildlife city-invasions, a further tidying of terminology may be desirable.

Typically, goshawks are sensitive to human activity and prefer large stretches of undisturbed, mature woodland for nesting and hunting (Kenward 2006). During the past decades, however, goshawks have started colonizing urban environments throughout their European breeding range (for review see Rutz *et al.* 2006a). Nowadays, the species lives in a variety of metropolitan habitats, ranging from suburban districts to highly urbanized city centres. Several large cities already have established populations at capacity level, whereas others have just been colonized by first pioneer settlers (Rutz *et al.* 2006a). The expansion of goshawk populations into hitherto uncolonized urban habitats is paralleled by similar trends in other hawks (*Accipiter nisus*: McGrady 1991; Risch, Dwenger & Wirth 1996; *Accipiter cooperii*: Rosenfield *et al.* 1996; Mannan *et al.* 2007; Stout *et al.* 2007) and birds of prey in general (for reviews see Bird *et al.* 1996; Andersen & Plumpton 2000; Love & Bird 2000).

Using a 60-year data set, I describe how goshawks colonized the city of Hamburg – from first rare visits of foraging hawks in the late 1940s to the establishment of a breeding population in the 1980s, which in recent years apparently stabilized at capacity level. I also explore several hypotheses regarding the extrinsic factors that may have ultimately triggered this city-colonization. I have described behavioural adaptations of urban-breeding goshawks elsewhere (Rutz 2003a, 2006; Rutz *et al.* 2006a).

Materials and methods

STUDY AREA

This study was conducted in the Greater Hamburg area (53°34' N, 9°59' E; total study plot size 2122 km²), northern Germany, including the city of Hamburg (35% of total area) and its suburban/rural periphery, consisting of parts of the federal states of Schleswig-Holstein (12%) and Niedersachsen (53%). The city of Hamburg is a typical, highly fragmented urban environment with patches of green space (4.0% parks; 1.1% cemeteries; hospital grounds, etc.) interspersed in a matrix of built-up habitat, with some larger forested areas at the periphery (3.8% deciduous; 2.2% coniferous) (for more details and maps, see Mitschke & Baumung 2001).

CHANCE OBSERVATIONS (1946–2003)

I made use of a database of bird observations compiled and managed by Hamburg's local ornithological working group (Arbeitskreis an der Staatlichen Vogelschutzwarte Hamburg; Geißler 2003). Since 1946, members of the group – mainly amateur birdwatchers – have recorded bird observations within the 2122-km² area described above. Database entries give bird species, date and Gauß-Krüger coordinates (resolution 1 km²), often with additional information on sex, age and activity of the bird(s). My own goshawk observations (see below) were not included in the database because they were mainly the result of systematic field research and would therefore have biased results. In 2003, the database contained 1 174 493 observations for a total of 373 bird species (H.-H. Geißler, personal communication).

As a first step, I extracted all goshawk observations from the database compiled during 1946–2003 ($n = 5910$ unique sightings with $n = 6878$ hawks). However, these raw data were not suitable for the purpose of the present paper as they were likely to be confounded in several ways. First, the goshawk is a charismatic, elusive species that is admired by birdwatchers, so the discovery of an active breeding territory can lead to opportunistic 'goshawk watching' near nests, inflating the number of observations. This effect was probably most pronounced during the early years of the study, when the species was still comparatively scarce in the area. Second, overall observation effort of the working group varied between years (mean \pm SE, range for: number of observers per year, 83 ± 4 , 7–131; number of observer-days in the field per year, 2893 ± 255 , 19–5818; number of bird observations per year, $20\,250 \pm 2343$, 30–55 402).

To obtain a relatively unbiased measure of goshawk abundance in the area that permitted robust assessment of temporal trends, I discarded all breeding-period observations (March–July inclusive) and those that were likely to have been made near nests at other times of the year (displaying or calling birds, observations of pairs, etc.). This produced a subsample of 2556 observations, on which all subsequent analyses are based. To control for variation in fieldwork effort, I expressed annual goshawk observation counts in two different ways: (i) 'percentage of the annual total number of bird observations (all species pooled) made in an area' (annual counts of bird observations were available for individual 1-km² cells, so different denominators could be used for urban and rural parts of the study area); and (ii) 'observations per observer-day in the field' (annual totals of observer days refer to the entire 2122 km² study plot, and a breakdown into different parts of the study area was impossible).

Despite these stringent data-selection criteria, a long-term increase in observer effort (Geißler 2003) – as the group attracted new members and fieldwork gained momentum – might still have caused a general increase in observations during the study period. These changes, however, cannot explain the marked short-term increase in goshawk observations (Fig. 1a) and the results obtained with detrended time series data (Fig. 2; see below). Importantly, comparisons between urban and rural areas are robust, as one of my measures of goshawk presence (percentage of goshawks) takes into account possible habitat-specific variation in observer effort.

POPULATION MONITORING (1996–2000)

During 1996–2000, I investigated the local urban goshawk population, using standard ornithological field techniques (Bijlsma 1997). My study plot (307 km²) covered the city centre and some parts of the suburban periphery of Hamburg, north of the River Elbe. Systematic colour-ringing of urban nestlings (1996–2000; exhaustive

ringing of all urban broods in the study area in 1997–99; 219 ringed nestlings in 70 broods; pooled sex ratio: 60% males) enabled the investigation of dispersal and recruitment patterns. I used two independent data sets for analyses: (i) data obtained through my own attempts to identify individual breeders, especially 1-year-old recruits, at urban nests (using colour-ring readings, moulted feathers with stamped code numbers and recaptures of marked hawks; data collected mainly during systematic searches during 1997–2000 with a few additions from 2001–03); and (ii) recoveries of ringed hawks, which were later reported by members of the general public (ring-recovery data up to and including 2005 were provided by the Vogelwarte Helgoland).

I reconstructed the foundation and expansion of the urban goshawk breeding population by combining my own monitoring data with unpublished information provided by three local raptor experts who worked in the same area (H. Wirth, M. Risch and A. Dwenger, unpublished data); from 1982 onwards these colleagues had conducted a systematic long-term study on urban-breeding sparrowhawks (Risch *et al.* 1996), which resemble goshawks in behaviour and habitat requirements (Newton 1986). I cross-checked my final data set on settlement patterns with breeding-period chance observations from the electronic database (see above), but could not find any inconsistencies.

ENVIRONMENTAL VARIABLES

I made an attempt to identify the environmental factor(s) that triggered the invasion of goshawks in Hamburg. A recent literature review concluded that goshawk breeding numbers in Europe are limited mainly by food supplies and nest-site availability, with access to both resources being ultimately controlled by the local level of (illegal) killing by humans (Rutz *et al.* 2006a). I therefore examined whether the invasion coincided with marked changes in these extrinsic factors, and a few others, exploring six hypotheses that are not mutually exclusive.

H1 *The invasion of urban Hamburg was due to population pressure from nearby rural goshawk populations at capacity level.* I used a long-term data set from a potential rural source population in 'Schleswig' (Schleswig-Holstein), some 60 km north of the city of Hamburg (Looft 2000).

H2 *The legalization of the targeted removal/killing of goshawks in rural areas encouraged hawks to visit the city, where persecution was not permitted.* From 1980–93 at least 742 hawks were legally trapped in Schleswig-Holstein, and most of them probably killed (Busche & Looft 2003).

H3 *Increased intraguild pressure forced rural goshawks into urban refugia* (cf. Sergio, Marchesi & Pedrini 2003). Eagle owls *Bubo bubo* are the main intraguild predator of goshawks in Germany and are also known to displace hawks from breeding territories by occupying their stick nests (Rutz *et al.* 2006a). Eagle owls were reintroduced into rural areas of Schleswig-Holstein by releasing large numbers of captive-bred birds. Data were taken from Hamann (2004).

H4 *Rural hawks responded to increasing prey abundance in the city (H4a) and/or decreasing prey abundance in rural areas (H4b).* A recent review revealed that goshawk diet in western and central Europe is dominated by only a few prey groups (see Table 3 in Rutz *et al.* 2006a). Taken together, pigeons (and doves), corvids and thrushes comprise, on average, 64% (range 37–90%) of goshawk breeding-season diet ($n = 18$ studies). I attempted to map possible changes in food availability by focusing on five prey species: feral pigeon *Columba livia*, blackbird, magpie *Pica pica*, jay *Garrulus*

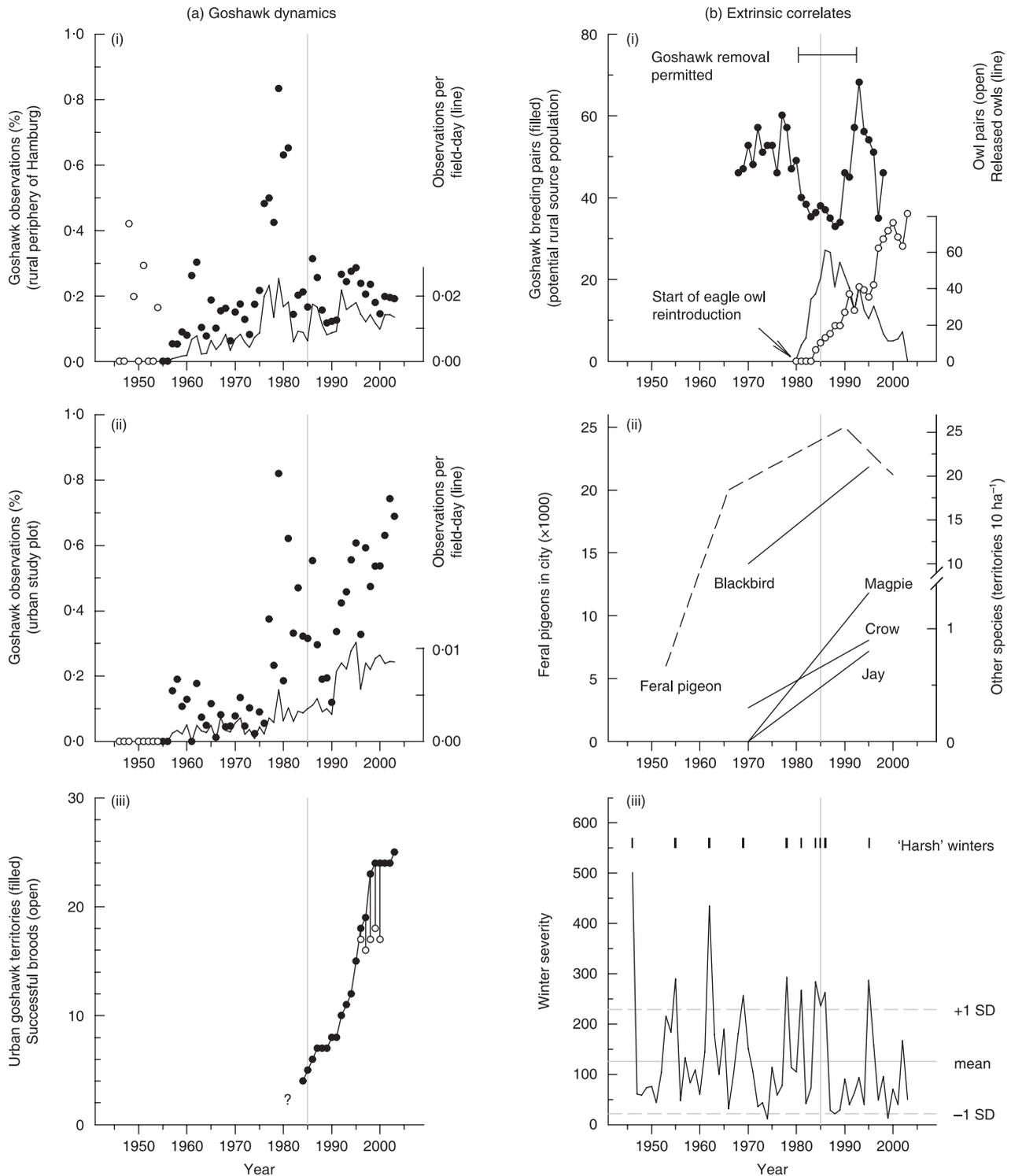


Fig. 1. Colonization of the city of Hamburg by northern goshawks: goshawk population dynamics (a) and extrinsic correlates (b). (a) Panels (i) and (ii) show, respectively, the temporal variation in goshawk observation levels in the rural periphery of Hamburg and in the urban study plot (307 km²). Goshawk presence is expressed either as percentage of all bird observations made (in the urban or rural areas, respectively; filled circles) or as observations per observer-day in the field (for the whole area; lines). Open symbols mark years with <600 observer-days in the field. In 1985 (grey vertical line), the first goshawk breeding territory was established in highly urbanized habitat (iii); the urban breeding population expanded rapidly (cumulative number of territories; filled circles) and apparently stabilized in the late 1990s (broods; open). (b) Panels show: (i) the breeding density of a rural goshawk population in Schleswig (c. 60 km north of Hamburg; Looft 2000; filled circles) together with the time period when killing or live removal of goshawks was legal (horizontal bar), as well as the build-up of an eagle owl population (open) in the federal state of Schleswig-Holstein due to the release of captive-bred birds (line); (ii) the levels of five principal prey species of goshawks (data from Mitschke *et al.* 2000; Mitschke & Baumung 2001 and sources therein); and (iii) winter severity in the city of Hamburg (black marks identify particularly harsh winters with values \geq mean + 1 SD). For further details, see text.

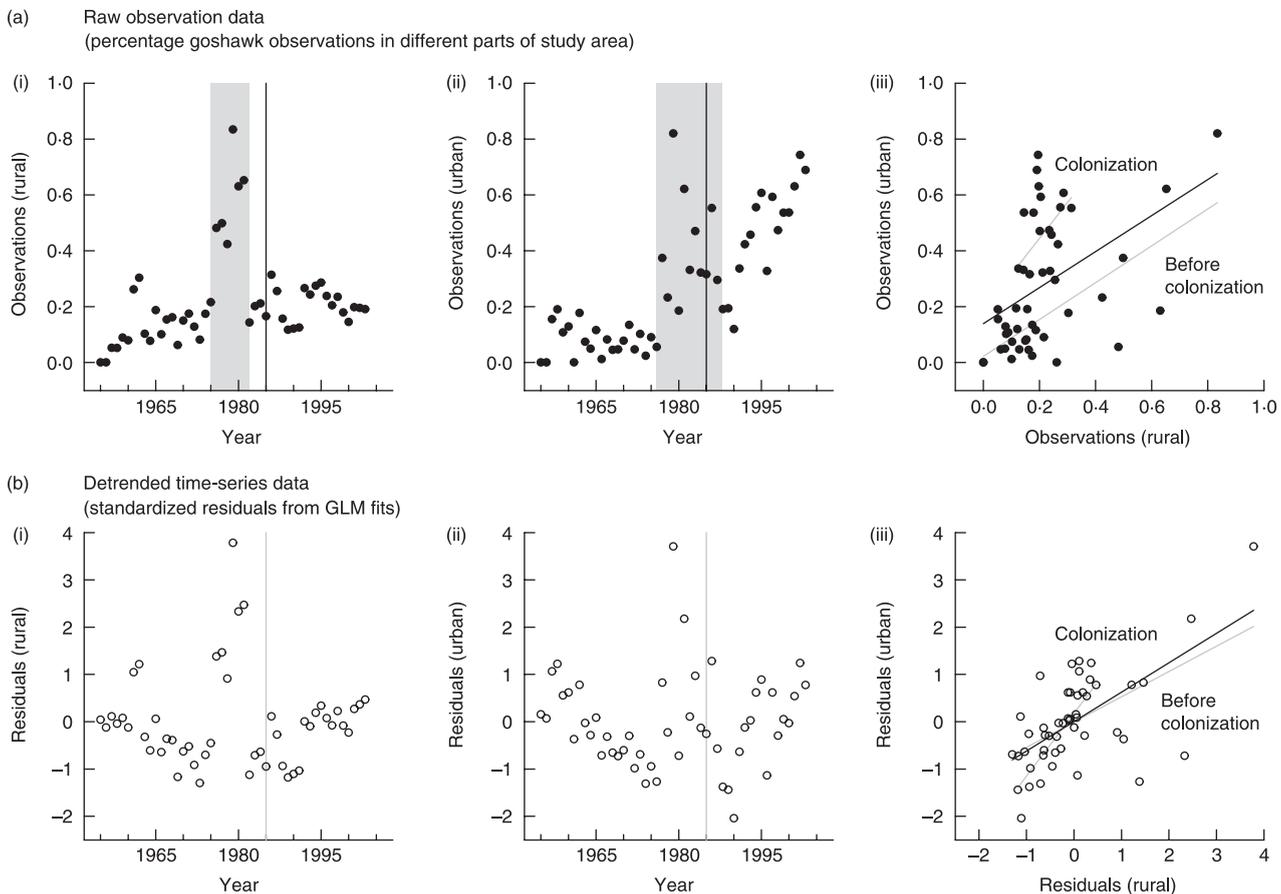


Fig. 2. Invasion dynamics of northern goshawks in the city of Hamburg. (a) Temporal trends of goshawk observations (expressed as percentage of all bird observations made in the respective plots) are shown for the rural periphery of Hamburg (i) and the urban study plot (ii), together with a correlation between the two data sets (iii). (b) Raw time series from panels in (a) were detrended by fitting general linear models (GLM) with linear (and quadratic) terms; data shown are standardized residuals with zero mean and unit variance. Grey areas in (a) highlight time periods with exceptionally high observation levels. Vertical lines in (a) and (b) mark the year 1985, when the first goshawk breeding territory was established in highly urbanized habitat. For illustration, fits of GLMs are shown in panels [a(iii)] and [b(iii)], with black lines for the whole data set and separate grey lines for fits to the data before and after first breeding in 1985.

glandarius and carrion crow *Corvus corone* (the first three species have become the staple prey of urban goshawks in Hamburg; unpublished data). In urban Hamburg, four censuses had been conducted to assess feral pigeon populations (1953, 1966, 1990, 2000; Mitschke & Baumung 2001 and references therein), and densities of the other four species had been estimated in a set of small replicate plots in the 1960s and 1970s, with repeat censuses in the same plots in the 1990s (Mitschke, Garthe & Mulsow 2000). Qualitative data on rural prey availability were extracted from Berndt, Koop & Struwe-Juhl (2002).

H5 *Goshawk nest-site availability in the urban area had increased due to afforestation and/or forest maturation* (Risch *et al.* 1996). According to my investigations, there is no published quantitative information on changes in forest cover and stand structure in the city of Hamburg, but descriptions by Walden (2002) enabled a qualitative assessment of this hypothesis.

H6 *The settlement of pioneer pairs was related to severe winter-weather conditions in the Hamburg area.* Standard meteorological data (mean daily temperature in January, °C; mean daily rainfall in January, mm) were obtained from the database of the Deutscher Wetterdienst. Additionally, I investigated a proxy measure of 'winter severity' (sum of the values of all negative mean daily

temperatures, °C, between 1 November and 31 March of each year), using an unpublished time series communicated by H.-J. Heinemann (for methods, see Heinemann 2005).

DATA HANDLING AND STATISTICS

Throughout, I refer to my 307-km² monitoring plot as the 'urban area/plot' or 'city' ($n = 777$ unique chance observations) and to the remainder of the 2122-km² area as the 'rural area/plot' or 'rural periphery' ($n = 1779$). I use the term 'rural' in a rather loose sense (cf. Marzluff, Bowman & Donnelly 2001a) to enhance the readability of the text by emphasizing habitat differences between the two study plots. It is important to note, however, that the rural area comprises suburban habitats and even some urban areas, especially south of the River Elbe. In a wider context, I occasionally refer to 'non-urban' habitats (*sensu* Rutz 2006). I explore goshawk population dynamics in my urban and rural areas by conducting both temporal and spatial analyses.

Most relevant relationships could be examined by inspecting scatter plots of the raw data, but I also analysed associations with Pearson correlation coefficients and general linear models (GLM) (Grafen & Hails 2002), implemented in MINITAB ver. 14.1. In some

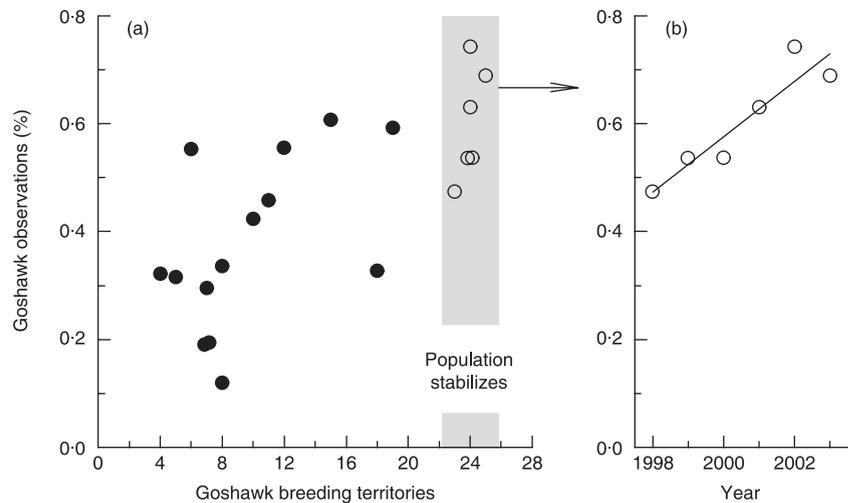


Fig. 3. Population expansion and floater dynamics of urban northern goshawks in the city of Hamburg. (a) Goshawk observations made in the urban study area plotted as a function of the cumulative number of breeding territories in the same area. The grey area marks the time period when the population appeared to stabilize (1998–2003) [cf. Fig. 1a(iii)]. (b) The increase in observation levels during 1998–2003 suggests the build-up of a floater pool. For further details, see text.

cases, time series were detrended by fitting GLMs with linear (and quadratic) terms, and residuals were standardized to zero mean and unit variance (Ranta, Lundberg & Kaitala 2006). All tests were two-tailed with a critical level of significance of 0.05, and means are reported with standard errors.

To obtain a robust and intuitive illustration of spatial spread (see Fig. 4), I marked all 1-km² cells with at least one goshawk observation in a certain time period, rather than displaying an absolute or relative measure of observation numbers. At least during later years, when many birdwatchers were involved in the programme (1975–2003), observer coverage for the urban plot was fairly complete because most members of the working group lived and worked in the city.

Results

COLONIZATION DYNAMICS

Chance observations

Goshawk dynamics were characterized by several distinct stages (Figs 1 and 2). In rural areas surrounding the city of Hamburg, observations increased in 1955–60, remaining at a fairly constant level thereafter, with the exception of a marked peak in 1976–81 [Fig. 1a(i) and 2a(i)]. In the urban area, goshawk observations fluctuated at a low level in the first two decades (1955–76) (GLM: $F_{1,20} = 0.26$, $P = 0.616$), exhibited a major peak in 1977–87 and increased sharply thereafter (1988–2003) [Fig. 1a(ii) and 2a(ii); $F_{1,14} = 39.56$, $P < 0.0001$]. For 1955–75, observation levels were significantly higher in rural areas ($0.12 \pm 0.02\%$ hawks) than in urban areas ($0.08 \pm 0.01\%$) (paired t -test: $n = 21$ years, $t_{20} = 2.31$, $P = 0.031$).

Peaks in rural and urban observation levels partly overlapped and directly preceded pioneer settlement in urban Hamburg in 1985 (see below); detrending time-series data revealed large standardized residuals during both peak phases [Fig. 2b(i,ii)]. Similar temporal patterns were found when goshawk presence was expressed as goshawk observations per observer-day in the field [lines in Fig. 1a(i,ii)].

Goshawk observations in the urban and rural habitats were significantly correlated [Fig. 2a(iii); Pearson correlation: $n = 49$ years, $r = 0.461$, $P = 0.001$]; the relationship remained significant when analysed separately for the time periods before ($n = 30$, $r = 0.713$, $P < 0.0001$) and after ($n = 19$, $r = 0.427$, $P = 0.068$) the establishment of the first urban breeding pair in 1985. Likewise, detrended time series for urban and rural observations were significantly correlated [Fig. 2b(iii); overall: $n = 49$, $r = 0.620$, $P < 0.0001$; before: $n = 30$, $r = 0.603$, $P < 0.0001$; after: $n = 19$, $r = 0.781$, $P < 0.0001$], and there was some evidence for a time lag between rural and urban dynamics (statistics based on detrended data; rural_{*t*} vs. urban_{*t+1*}: $n = 48$, $r = 0.342$, $P = 0.017$; rural_{*t*} vs. urban_{*t+2*}: $n = 47$, $r = 0.481$, $P = 0.001$). Urban observations increased with increasing urban territory numbers (Fig. 3a; GLM: $F_{1,18} = 19.40$, $P < 0.0001$). After 1998, when the population had stabilized (grey area in Fig. 3a), observation levels kept increasing over time (Fig. 3b; $F_{1,4} = 24.40$, $P = 0.008$).

The spatial distribution of observations (1-km² cells with at least one goshawk observation; Fig. 4) shows that hawks were absent from large parts of the city centre before 1985, with observations clustered in the northern periphery. In 1985–94, the number of cells visited in the western parts of the city centre increased markedly, but occurrence in the east remained sparse. During the final stages of the colonization (1995–2003), goshawks eventually also spread into this part of the city. In recent years, goshawks have been observed regularly by working-group members in all parts of the city of Hamburg.

In five of six 5-year time blocks with sufficient data, the sex ratio (percentage males) of hawks observed in the city exceeded that of rural birds (Fig. 5a). Before pioneer settlement in 1985, most sexed hawks in the rural periphery were females, which contrasted with an apparent male bias for the city area. In later years, the sex ratio was close to unity for both habitats. Only a few database entries contained information on the age of hawks, especially for the early years of the study (Fig. 5b). After 1985, the proportion of adult hawks among aged individuals was about 35% for both urban and rural habitats.

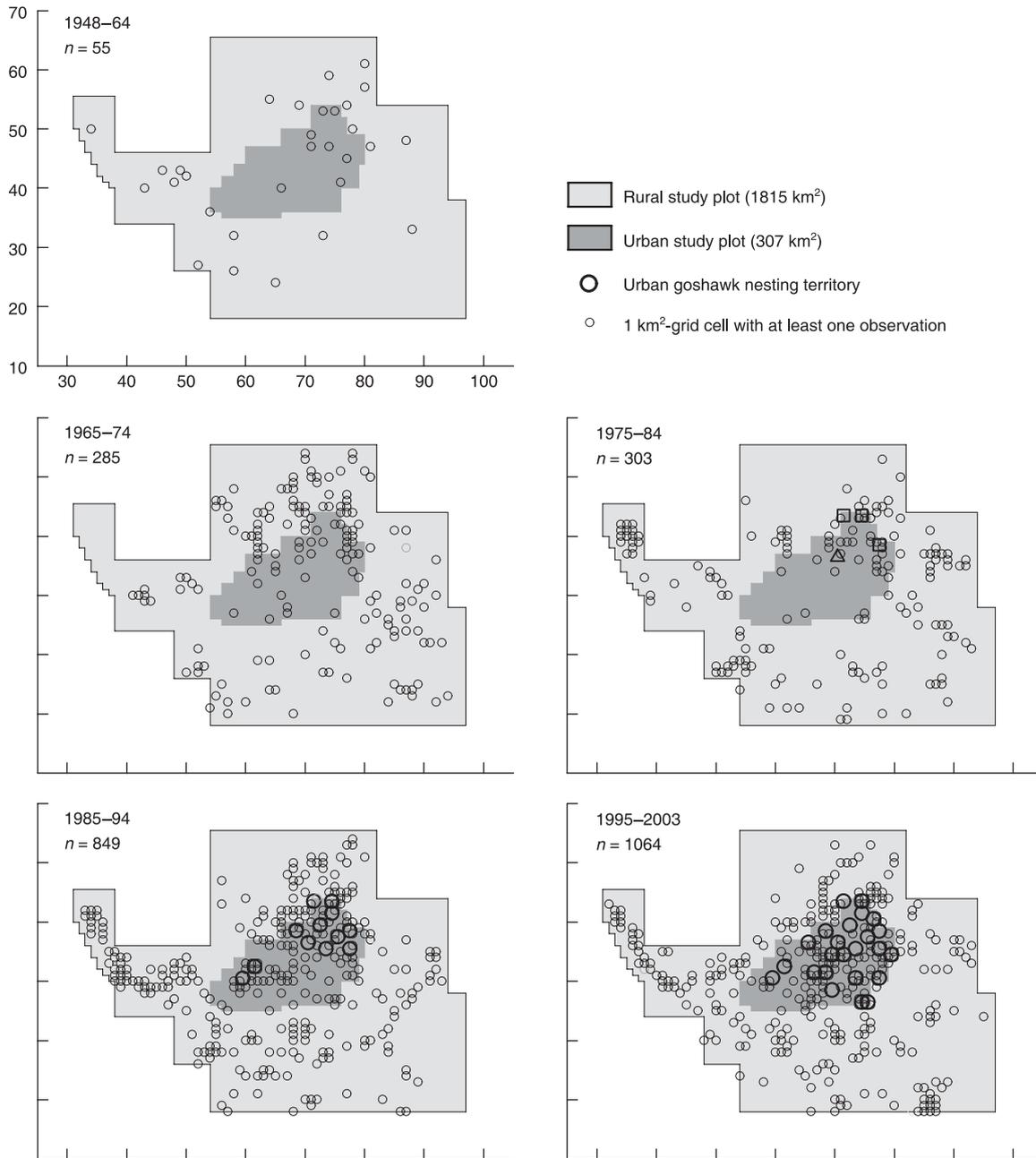


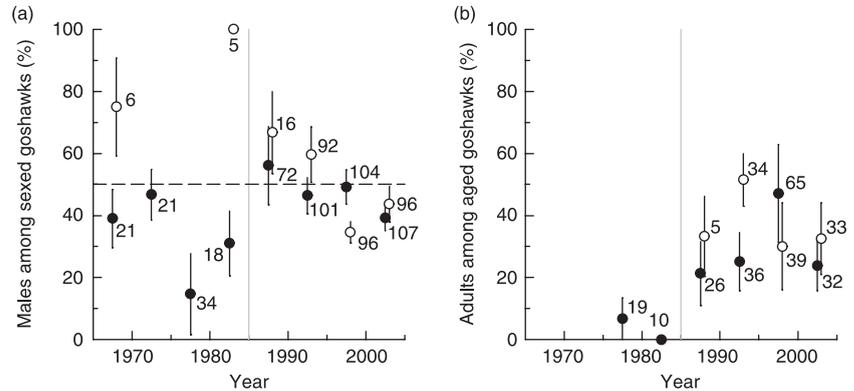
Fig. 4. Spatial dynamics of the invasion of the city of Hamburg by northern goshawks, which ultimately led to the establishment of a breeding population (first recorded brood in highly urbanized habitat in 1985). Axis labels refer to Gauß–Krüger coordinates (tick-mark resolution is 10 km²). Note that observer effort increased over time (see Materials and methods and Discussion), so absolute numbers of observations (n) must be interpreted cautiously. Large open circles mark urban nesting territories that were used at least once by goshawks during the entire study period. In the plot for 1975–84, squares mark three nesting territories for which the exact year of first breeding could not be established; the triangle marks a territory that was probably established in the early 1990s, but was first discovered in 1996. For further details, see text.

Population monitoring data

Before 1985, there were at least three known territories within the urban study plot, all of which were located at the northern urban–rural interface (squares in the plot for 1975–84 in Fig. 4). These early nest sites had stand characteristics similar to those of typical goshawk territories in non-urban habitats. The first goshawk breeding pair in the city centre was recorded in 1985 [Fig. 1a(iii)]. From 1986 onwards, new

breeding territories were established in various urban habitats, including public parks, cemeteries, hospital grounds and backyards. The urban population showed greatest expansion during 1990–99. Shortly afterwards, breeding density stabilized at about six breeding pairs per 100 km² [1996–2000; open symbols in Fig. 1a(iii)], and only one new territory was discovered (in 2003) during semiquantitative snapshot surveys in 2001–04. Typically, hawks were present at potential nest sites for several years (Fig. 4) before first

Fig. 5. Sex (a) and age (b) of northern goshawks observed in the rural periphery of the city of Hamburg (filled circles) and in the 307-km² urban study plot (open). For both panels, annual values were grouped into 5-year blocks to calculate mean and SE; estimates are shown only for periods in which five or more hawks were sexed or aged (sample sizes are shown next to symbols). The broken horizontal line in (a) marks sex-ratio equality; the vertical grey lines in both panels mark the year when the first goshawk breeding territory was established in highly urbanized habitat. For further details, see text.



breeding attempts were made (not necessarily by the same individuals); for example, in an inner-city public park (Stadtspark), hawks were displaying in March 1990 and again in 1992, but it was not until 1995 that a pair bred.

During 1997–2000, at least 31 hawks (29 aged) were recruited into the urban breeding population ($n = 18$ females: 1-year, 50%, 2-years, 17%, ≥ 3 -years, 33%; $n = 11$ males: 1-year, 18%, 2-years, 36%, ≥ 3 -years, 45%; failed broods included), including the founders of six new breeding territories. Not all new breeders could be checked for colour-rings, but nine recruits (29%) in 1997–2000 were identified as individuals that had fledged in the city; in two cases, both partners at newly established urban territories were colour-ringed (during 2002–03 another three colour-ringed hawks were trapped on urban territories). All 1-year-old recruits in 1998–2000 (that had fledged during the period of exhaustive ringing in the urban study area, 1997–99) could be identified conclusively (six females, two males). Of these, two females were definitely not marked (one bird observed, one bird trapped) and were probably immigrants from non-urban areas. Rural habitats were not searched systematically for ringed recruits, but in 2001–02 three urban-fledged hawks were trapped as breeders at rural nest sites, with two of these birds (fledged from two different urban nests) being pair-partners.

Ring recoveries by the general public further illustrated the movement of urban hawks between urban and non-urban habitats. From 219 nestlings that had been ringed in urban nests, 9% (five females, 15 males; repeated recoveries of the same birds excluded) were later recovered dead or alive during or after their dispersal, 55% of which (two females, nine males) were found in non-urban areas.

ENVIRONMENTAL CORRELATES

In 1980, killing of goshawks was legalized in Schleswig-Holstein [Fig. 1b(i)], including rural areas adjacent to the urban study plot. This change in legislation resulted in a marked increase in persecution levels, which was reflected in a drop in goshawk breeding numbers in a large study population in Schleswig [Fig. 1b(i); note that the population recovered to previous levels after the goshawk had regained full protection; Looft 2000]. Pioneer settlement in urban

Hamburg occurred just five years after hunting laws had been changed, and coincided with the time period when the potential rural source population in Schleswig had reached its lowest level [Fig. 1b(i)].

Eagle owls were first released in the federal state of Schleswig-Holstein in the early 1980s, but it took about 10 years until a sizeable breeding population was established [Fig. 1b(i); note that pair numbers presented by Hamann 2004 are probably vastly underestimated; cf. Klose & Koop 2007]; eagle owls therefore cannot have contributed to the goshawk's sudden niche expansion.

The feral pigeon population in urban Hamburg increased markedly from 1953 to 1966 and remained at a high level thereafter [Fig. 1b(ii)]. Median densities of the other four potential prey species were significantly higher in the 1990s than in the 1960/70s [Fig. 1b(ii); blackbird: $n = 15$ plots, $P < 0.01$; magpie: $n = 11$, $P < 0.05$; jay: $n = 10$, $P < 0.01$; carrion crow: $n = 11$, $P < 0.05$; for details see Mitschke *et al.* 2000]. In Schleswig-Holstein, including rural areas close to the city of Hamburg, these species showed mixed trends: blackbird and jay remained stable, the carrion crow probably increased, and the magpie decreased in rural areas but increased in urban habitats. Feral pigeons do not typically breed in non-urban areas, but woodpigeons *Columba palumbus* increased markedly in Schleswig-Holstein during the past 100 years (Berndt *et al.* 2002). Overall, data from non-urban areas were insufficient for statistical analyses, but there was no evidence to suggest that the goshawk's prey base had crashed.

Notwithstanding substantial logging activities during World War II, many urban parks, cemeteries and other patches of green space in urban Hamburg contained forest stands (Walden 2002) that were suitable for goshawk nesting – in terms of tree age and spacing (for review see Rutz *et al.* 2006a) – long before they were colonized by hawks (J. Dien, personal communication). This included sites where some early inner-city territories were established, such as the Nienendorfer Gehege (first goshawk brood in 1985), the Volksdorfer Wald (1992), the Altonaer Volkspark (1993), the Stadtspark (1995) and the Ohlsdorfer Friedhof (1996). While habitat change is therefore unlikely to explain pioneer settlement in the 1980s, postwar afforestation and subsequent maturation

of (mainly conifer) stands certainly provided additional urban nest sites for hawks in the 1990s. In some cases, goshawks are known to have established territories by displacing resident sparrowhawks (Risch *et al.* 1996).

Temperature and mean daily rainfall in January were relatively poor direct predictors of annual goshawk observation levels, both inside the city ($n = 49$ years, GLMs, controlled for the effect of 'year': temperature: $F_{1,46} = 2.21$, $P = 0.144$; rainfall, $F_{1,46} = 1.27$, $P = 0.265$) and outside the city (temperature, $F_{1,46} = 2.71$, $P = 0.107$; rainfall: $F_{1,46} = 0.85$, $P = 0.360$). On the other hand, relationships with a measure of winter severity approached significance (urban: $F_{1,46} = 3.50$, $P = 0.068$; rural: $F_{1,46} = 2.95$, $P = 0.092$). The marked increase in urban observations [Fig. 1a(ii)] – which was associated with first settlement in 1985 [Fig. 1a(iii)] – coincided with a succession of five particularly cold winters in the 1980s [Fig. 1b(iii)].

Discussion

COLONIZATION DYNAMICS

Non-breeders

In the city of Hamburg, goshawks visited urban habitats decades before the first breeding territories were established. Interestingly, goshawks were observed regularly in parks where breeders settled in later years (Fig. 4), demonstrating that early visitors had encountered, but not used, potential nest sites. This begs the question as to why breeding had not taken place much earlier. It is unlikely that early (pre-1985) goshawk territories were overlooked, because during these years much of my urban study plot was searched systematically for breeding sparrowhawks (see above). Pioneer settlement was probably triggered by special environmental conditions, as discussed in detail below.

Goshawk dynamics in rural and urban areas appeared to be coupled: observation levels in the city were positively correlated to those in Hamburg's rural periphery, both before and during colonization (Fig. 2). The slope for the colonization period seemed steeper, hinting at the possibility that the movement of goshawks between habitats was affected by the expansion dynamics of the urban population. The use of detrended, standardized time series demonstrated that the correlations were not artefacts of a temporal increase in observation effort. While I attempted to control for spatial variation in observer effort by using different denominators for computing the percentages of goshawk observations in urban and rural habitats, respectively, my data set does not permit an investigation of how much patterns were influenced by possible spatial synchronization of observer effort within years.

In many raptor populations at capacity level, some sexually mature individuals are denied breeding because all suitable nest sites are occupied; these 'floaters' typically remain in the area and wait until a breeding vacancy becomes available (for raptors, see Hunt 1998; Kenward, Marcström & Karlbom 1999; Kenward *et al.* 2000; Rutz & Bijlsma 2006). In the goshawk, quantitative radio-tagging of juvenile cohorts

revealed that each year about 30% of males and 60% of females do not breed in a stable population (Kenward *et al.* 1999; for review see Rutz *et al.* 2006a). My study in Hamburg covered the time period when the breeding population started stabilizing. The continuing increase in goshawk observation levels after the population had stabilized (Fig. 3b) suggests that a floater pool started building up.

The database of chance observations contained comparatively few entries with information on sex and age of hawks. Sexing goshawks can be difficult under field conditions, but assuming that sexing errors were equally likely for urban and rural areas, and across years, three main results were obtained (Fig. 5a): (i) the sex ratio in the city consistently exceeded that in rural areas throughout the study period; (ii) the rural sex ratio was strongly female-biased before the city was colonized but was more balanced in later years; and (iii) there was a strong male bias in the city in early years (but this is based on small sample sizes). The demographic anomaly in rural areas (female bias) may reflect sex-differential mortality due to extrinsic factors (see below), while the male bias in the city could indicate sex differences in dispersal strategies, with a higher propensity in males to explore novel habitats (Kenward 2006).

The plumage of yearling goshawks (before their first moult) is very different from that of older birds (Kenward 2006), so ageing mistakes are unlikely to affect my comparisons between these two age classes. Sample sizes are small, but it is interesting that between 1975 and 1985 fewer than 10% of all sexed rural hawks were adult, which contrasts with later years, where the proportion of adults was much higher at 20–50% for both habitat types (Fig. 5b). The time period with a disproportionately high proportion of young hawks in rural areas preceded first breeding attempts in the city, and coincided with a suite of environmental changes (see below).

For much of the results discussed above, I lack relevant data for comparison. I am not aware of any other published quantitative study on birds or mammals that investigated the non-breeder dynamics before and/or during the establishment of an urban breeding population. Such information may be available, but is currently unpublished, for peregrine falcons *Falco peregrinus*, which started invading urban environments in recent decades (Cade & Burnham 2003). Across large parts of Europe and North America, peregrines were reintroduced after the 'DDT crash', and most conservation schemes employed systematic colour-ringing and postrelease monitoring. Therefore it might be possible to establish, for some urban populations, the origin of the first non-breeding city visitors and how first pairs formed from an early non-breeder pool. A similar analysis might be possible for urban-breeding gulls (Raven & Coulson 1997). Such studies would make extremely valuable contributions to our understanding of wildlife city-invasion dynamics.

Breeding population

The establishment of the goshawk breeding population in the city of Hamburg consisted of three distinct phases: (i) pioneer

settlement in the 1980s; (ii) rapid expansion in the 1990s; and (iii) saturation in recent years [Fig. 1a(iii)]. Similar logistic growth has been described for an urban goshawk population in the city of Cologne (Würfels 1999), and is likely for another population in Berlin (Altenkamp 2002). The colonization dynamics of urban goshawk populations resemble those of recovering or recently founded rural goshawk populations (for review see Rutz *et al.* 2006a), and fit the general pattern of biological invasions (Shigesada & Kawasaki 1997). Similar trajectories have been reported for expanding urban populations of other raptors (e.g. merlin, *Falco columbarius*; Oliphant & Haug 1985) and non-raptorial bird species (e.g. herring gull, *Larus argentatus*; Monaghan 1980). Goshawks and most other raptor species (Bird *et al.* 1996; Andersen & Plumpton 2000; Love & Bird 2000) actively colonize urban environments; this contrasts with some other animal species, which have been found to persist as relict populations in pockets of wildland habitat as the urban habitat spreads (Erz & Klausnitzer 1998; Greenwood & Chamberlain 2003).

In Hamburg, a large proportion of male and female breeding recruits were only 1 or 2 years old, a pattern characteristic of young or expanding goshawk populations; in undisturbed, established populations, new breeders are typically 3 years or older (for review see Rutz *et al.* 2006a). The observation that a floater pool started building up in later years (Fig. 3b) leads to the testable prediction that recruitment age should increase as hawks begin queuing for territory vacancies. Consistent with results from other studies, capacity-level breeding density in the city of Hamburg clearly exceeded densities attained by nearby non-urban populations (Rutz *et al.* 2006a).

At least for the saturation phase (1997–2005), my ringing data demonstrated gene flow between city and adjacent non-urban areas. About half of all ringed, urban-fledged goshawks that were recovered later on were reported from non-urban areas (unpublished data; a more detailed analysis of this material will be presented elsewhere). Furthermore, non-urban individuals were found to immigrate into the city and recruit successfully into the urban breeding population. Radio-tracking of urban-fledged hawks on their natal dispersal revealed that birds move freely between habitat types: one tagged male in Hamburg frequented a roost site in an urban park, but made regular foraging trips into the city's suburban/rural periphery (see Figure 1b in Rutz 2003a). Taken together, this is sufficient evidence to reject the hypothesis that urban populations are genetically isolated and that the expansion process is driven entirely by urban-fledged individuals. Genetic analyses are necessary to investigate whether Hamburg's urban goshawk population experienced a 'bottleneck' when it was founded (Rutz *et al.* 2004).

The number of successful breeding attempts [open symbols in Fig. 1a(iii)] stabilized at a time when new territories were still being established in the urban study plot [that is, the cumulative number of territories increased; filled symbols in Fig. 1a(iii)]. Nest attempts in these newly founded territories were often successful, confirming that the sites were suitable for breeding. This observation suggests that goshawk breeding numbers in urban Hamburg were not generally limited by the

availability of nest sites. It is possible that different factors – food and nest sites – limit goshawk numbers in different parts of the same city (Rutz *et al.* 2006a).

ENVIRONMENTAL CORRELATES

An important question is whether goshawks were 'pulled' into the urban habitat by good living conditions, or were 'pushed' out of non-urban areas by unfavourable conditions. My data suggest a combination of both processes – pioneer settlement in urban Hamburg coincided with: (i) an increase in (legal) hunting pressure on goshawks in adjacent rural areas (H2); (ii) an increase in prey abundance in the city (H4a); and (iii) severe winter-weather conditions in the Greater Hamburg area (H6). On the basis of the available evidence, I can reject the hypotheses that the invasion was the result of intraguild dynamics (H3) or collapsing rural food supplies (H4b), and it seems unlikely that it was due to pressure from rural breeding populations at capacity level (H1) or to urban habitat change (H5).

My results for goshawks in Hamburg contrast with the findings of a recent review paper on goshawks (Rutz *et al.* 2006a), which observed that the colonization of cities across Europe coincided with the large-scale decrease in levels of persecution by humans. In the present paper, I had to assume that the population in Schleswig [Fig. 1b(i)] served as the source for the urban population in Hamburg, but hawks might have come from other nearby areas, where persecution was not permitted but for which I lacked data. Presently, I cannot determine whether it was the long-term, large-scale reduction of persecution levels or the short-term, localized increase in persecution levels that contributed to the invasion observed in Hamburg. However, a marked drop in rural population levels [Fig. 1b(i)] was associated with a sharp increase in chance observations in urban Hamburg [Fig. 1a(ii) and 2a(ii)], hinting at the possibility that hawks redistributed themselves in response to local variation in persecution levels.

Urban goshawks apparently capitalize on the comparatively high abundance of some prey species. In 2003, goshawk breeding pairs in urban Hamburg preyed primarily on feral pigeons (43.8%), magpies (10.6%) and blackbirds (9.3%) ($n = 593$ prey items for 13 pairs; cf. Rutz 2003b), while pairs in nearby rural areas of Schleswig-Holstein focused on wood-pigeons (19.1%), blackbirds (18.5%) and feral (homing) pigeons (13.5%) ($n = 303$ prey items for seven pairs) (unpublished data). Feral pigeons and other profitable goshawk prey species have increased substantially in urban Hamburg over the decades, which may have attracted hawks. Several independent studies reported that the use of pigeons by individual goshawk pairs is associated with substantial fitness benefits (for review see Rutz, Whittingham & Newton 2006b).

Weather conditions do not generally seem to affect goshawk breeding numbers in temperate Europe (Rutz *et al.* 2006a). In my study, however, unusually severe winter weather could have decreased foraging efficiency and/or increased energy requirements of rural hawks (especially

males; Sunde 2002; cf. Fig. 5a) to the point where birds had to explore food-rich, but potentially dangerous, habitats to avoid starvation. Hungry hawks may have been forced to feed under conditions that are unfamiliar or generally perceived as dangerous, such as those encountered in urban areas, where human activity and noise levels are high and anthropogenic obstacles abound. Weather has been shown to drive habitat choice in birds through its effects on the 'starvation–predation risk trade-off' (Hilton, Ruxton & Cresswell 1999; Yasué, Quinn & Cresswell 2003).

In any case, it is important to note that the factors causing first settlement might be very different from those promoting rapid expansion, which in turn might differ from those that regulate the established population once it has reached capacity level. For example, habitat change (afforestation and forest maturation) in the city of Hamburg cannot explain the founder event in the mid-1980s, but it has certainly facilitated population expansion (Risch *et al.* 1996).

Investigating the generality of the above conclusions requires a detailed comparison of colonized and uncolonized cities (e.g. regarding forest cover and prey abundance). I attempted such an analysis (see Table 5 in Rutz *et al.* 2006a), but found no unifying pattern, except for the fact that all known colonizations in Europe had taken place after large-scale killing by humans had ceased (see above). It seems puzzling, however, that many cities that appear suitable for goshawks have not yet been colonized. My study suggests that pioneer settlement may depend on the complex (and potentially rare) interaction of several different factors. Once first breeders have settled, however, urban populations expand rapidly (see above); this could be due to the displaying activity of pioneer pairs, which attracts other non-urban individuals to the city, exposing them to potential nest sites and abundant food resources. It may be possible to trigger city-invasions experimentally by releasing hawks that are used to human activity, such as falconry birds, into as-yet uncolonized cities (Rutz 2006). The spatial and temporal pattern of city-colonization in Europe, my ring-recovery data, and our general knowledge of goshawk biology indicate that goshawks repeatedly invaded cities rather than spreading from city to city (Tomiałojć 1985).

Although the literature on urban-breeding birds is growing rapidly, only a handful of projects to date have documented colonization events from beginning to end (merlin, Sodhi *et al.* 1992; gulls, Monaghan 1980; Raven & Coulson 1997), and I am not aware of any studies that explicitly tested several competing hypotheses regarding the environmental circumstances that might have triggered or promoted an invasion. Recent summaries of urban bird ecology (Marzluff *et al.* 2001b; Greenwood & Chamberlain 2003; Kelcey & Rheinwald 2005) suggest that, not surprisingly, different factors vary in their importance across species, but abundant food supplies and release from predation risk and/or interspecific competition in the urban habitat emerge as key correlates of successful city-colonization events. To advance in our understanding of urban ecology, we need many more detailed case studies of wildlife city-invasions.

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