Studies in Avian Biology No. 31:158–197

POPULATION LIMITATION IN THE NORTHERN GOSHAWK IN EUROPE: A REVIEW WITH CASE STUDIES

Christian Rutz, Rob G. Bijlsma, Mick Marquiss, and Robert E. Kenward

Abstract. This paper investigates factors limiting breeding densities in populations of Northern Goshawk (*Accipiter gentilis gentilis*) in western, central, and southern Europe. We review the current status of the species and describe major population trends during the last century. Large-scale trends in numbers coincided with marked changes in the external environment (early 20th century—extensive human persecution; 1950s—maturation of forests providing new nesting habitat; 1960s—organochlorine pesticide use in agriculture). We present four lines of evidence suggesting that goshawk breeding numbers in Europe are indeed limited by extrinsic factors, rather than fluctuating at random: (1) temporal stability of breeding numbers, (2) existence of non-breeders in stable populations, (3) growth dynamics of newly-founded and recovering populations, and (4) regular spacing of territories in continuously suitable nesting habitat. We evaluate the published literature to assess the relative importance of seven potentially limiting factors. Consistent with other raptor species, we identify nest-site availability and food supply as the two principal factors limiting breeding numbers in the goshawk. Importantly, their relative influence appears to be affected by the degree of illegal killing. Currently in Europe, killing by humans rarely has direct effects on breeding population levels. However, even moderate levels of killing may limit goshawks indirectly, by preventing their full use of habitats in close proximity to human activity. In the absence of illegal killing, goshawks in western Europe are highly adaptable to intense human activities. They readily occupy a wide range of nesting habitats, including small woodlots in highly fragmented rural landscapes and even urban parks in metropolitan areas. In such settings, goshawks show extraordinary degrees of tolerance of human activities, and enjoy comparatively high productivity, indicating that these habitats offer good living conditions. Hence, the nest-site preferences reported for European populations may not always or entirely represent natural ecological needs, but partly reflect choices imposed on the species by human activities. Populations subject to little illegal killing in areas where nesting sites are freely available seem to be limited mainly by food supply. In some areas, goshawks appear to suffer from nest-site competition with the dominant Eurasian Eagle-Owl (*Bubo bubo*). Weather conditions may account for some of the year-to-year variation in breeding density, probably acting through an effect on spring food supplies, but they do not generally limit goshawks in temperate Europe. Circumstantial evidence suggests that pesticide use negatively affected goshawk populations in the 1960s. However, present-day levels of organochlorines and other environmental pollutants generally seem to be too low to have significant population-level consequences. The role of parasites and diseases in limiting goshawks is unknown, but likely to be negligible according to work on other species. We put our findings into context by contrasting goshawk ecology between Europe and North America. Goshawks in North America (*Accipiter gentilis atricapillus* and *A. g. laingi*): (1) live at lower densities than in Europe, (2) make less use of artificial habitats (small woodlots, towns, and parks) for foraging and breeding, (3) use mammalian foods more often, and (4) produce fewer young per pair. Differences in goshawk ecology between continents are probably due to some underlying extrinsic factor, such as prey availability, rather than a discrete subspecific difference attributable to particular morphology or intrinsic behavior. Field methods and the format for reporting results should be further standardized to obtain comparable data. We encourage researchers to pool existing data sets for reanalysis, as such large-scale approaches with appropriate independent replication at the population-level are needed to produce statistically robust insights into goshawk population biology. Gaps in our knowledge on the species include: (1) biology of non-breeders, (2) the effect of food shortage on population dynamics, and (3) habitat use during breeding season and winter. We propose several lines of future research; for virtually all areas of goshawk biology, there is a particular need for carefully-designed experiments.

Key Words: *Accipiter gentilis*, avian population limitation, competition, density dependence, Eurasian Eagle-Owl, habitat use, intra-guild competition, meta analysis, Northern Goshawk, pesticides and environmental pollutants, urban ecology, wildlife management and conservation.

LIMITANTES EN LAS POBLACIONES DE GAVILÁN AZOR EN EUROPA: UNA REVISIÓN CON CASOS DE STUDIO

Resumen. El presente artículo investiga factores que limitan las densidades reproductivas del Gavilán Azor (*Accipiter gentilis gentilis*) en el occidente, centro y sur de Europa. Revisamos el estatus actual de la especie y describimos las principales tendencias de la población durante el último siglo. Tendencias de larga escala en números coincidieron con cambios marcados en el medio ambiente externo (principios del siglo

20—persecución extensiva por humanos; en la década de los cincuenta—maduración de bosques, proveyendo hábitat nuevo para anidación; en la década de los sesenta—uso del pesticida organoclorin en la agricultura). Presentamos cuatro líneas de evidencia que sugieren que los números reproductores del gavilán en Europa están de hecho limitados por factores extrínsecos, en vez de fluctuaciones al azar: (1) estabilidad temporal de números reproductores, (2) existencia de no-reproductores en poblaciones estables, (3) dinámica de crecimiento de poblaciones recién encontradas y en poblaciones en recuperación, y (4) espaciamiento regular de territorios en hábitat susceptible para anidación. Evaluamos la literatura publicada para estimar la importancia relativa de siete factores potencialmente limitantes. Consistente con otras especies de raptor, identificamos que la disponibilidad de sitio de anidación y el suministro de alimento son los dos factores principales los cuales limitan el número reproductivo en el gavilán. Significativamente, su influencia relativa parece ser afectada por el grado de caza ilegal. Actualmente en Europa, la cacería por humanos raramente tiene efectos directos en los niveles de las poblaciones reproductoras. Sin embargo, niveles moderados de cacería quizás limiten a los gavilanes indirectamente, al impedir la plena utilización del hábitat en proximidad a la actividad humana. Con la ausencia de caza ilegal, los gavilanes son altamente adaptables a actividades humanas intensas en Europa occidental. Ellos fácilmente ocupan un amplio rango de hábitats de anidación, incluyendo pequeños sitios forestales en paisajes rurales altamente fragmentados, e incluso en parques urbanos en áreas metropolitanas. En dichos escenarios, los gavilanes muestran un extraordinario grado de tolerancia a las actividades humanas, y gozan comparativamente de una productividad alta, indicando que estos hábitats ofrecen condiciones buenas para vivir. Por lo tanto, las preferencias de sitios de nido reportadas para poblaciones Europeas quizás no siempre o completamente representen necesidades ecológicas naturales, pero en parte reflejan opciones impuestas en la especie por actividades humanas. Las poblaciones sujetas a por lo menos un poco de caza ilegal en áreas en donde los sitios de anidación están libremente disponibles, parecen estar limitadas principalmente por la disponibilidad de alimento. En algunas áreas, los gavilanes parece que sufren por competencia del sitio de nido con el dominante Búho-Águila de Euroasia (*Bubo bubo*). Las condiciones climáticas quizás influyan para algunas de las variaciones de año tras año en la densidad de reproducción, probablemente actuando a través de un efecto en el abastecimiento de alimento en primavera, pero estos generalmente no limitan a los gavilanes en la Europa templada. Evidencia circunstancial sugiere que el uso de pesticidas afectó negativamente a las poblaciones de gavilán en la década de los sesenta. Sin embargo, los niveles actuales de organoclorines y otros contaminantes para el medio ambiente generalmente parecen ser muy bajos como para tener consecuencias significativas a nivel de población. El papel de los parásitos y enfermedades en la limitación de gavilanes se desconoce, pero parece ser insignificante de acuerdo al trabajo realizado con otras especies. Pusimos nuestros hallazgos en contexto, contrastando la ecología del gavilán entre Europa y Norte América. Los gavilanes en Norte América (subespecie: *Accipiter gentilis atricapillus* y *A. g. laingi*): (1) viven en menores densidades que en Europa, (2) hacen menor uso de hábitats artificiales (pequeños lotes arbolados, pueblos y parques) para forrajeo y reproducción, (3) utilizan más a menudo a mamíferos como alimento, y (4) producen menos juveniles por pareja . Las diferencias en la ecología de los gavilanes entre continentes quizás se deban a algunos factores fundamentales extrínsecos, tales como la disponibilidad de la presa; en vez de una diferencia discreta subespecífica la cual puede ser atribuida a morfología particular o a comportamiento intrínseco. Tanto métodos de campo, como el formato para reportar resultados deberían ser más estandarizados para obtener datos comparables. Alentamos a los investigadores para mancomunar el conjunto de datos existentes para reanalizar, por ejemplo, aproximaciones de larga escala con replicación independiente apropiada al nivel de población las cuales son necesarias para producir penetraciones estadísticas robustas en la biología de las poblaciones de gavilán. Los huecos en nuestro conocimiento sobre la especie incluyen: (1) biología de no reproductores, (2) efectos en la escasez de alimento en las dinámicas poblacionales, y (3) utilización del hábitat durante la época reproductiva y el invierno. Proponemos varias líneas de investigación para el futuro, virtualmente para todas las áreas de la biología del gavilán existe una necesidad particular para experimentos diseñados cuidadosamente.

In this review, we attempt to identify major factors limiting breeding numbers of Northern Goshawks (*Accipiter gentilis gentilis*, hereafter goshawk) in western, central, and southern Europe. Populations in northern Europe differ in their biology, associated with cyclic prey populations (Tornberg et al., *this volume*), so we only occasionally refer to Scandinavian studies to highlight important points or to present additional support for some lines of argument.

The ecological processes underlying population limitation in birds have been reviewed by Newton (1998). Following his terminology, we distinguish between extrinsic (environmental) and intrinsic (demographic) factors influencing breeding numbers. Extrinsic factors are features of the external environment, including food and nest sites, competitors, humans, natural predators, and parasites, and are generally defined as ultimate causes of population limitation. Their effect is mediated by intrinsic factors—the rates of births, deaths, immigration, and emigration. Changes in these demographic features affect population density at the proximate level. External factors that act in a density-dependent manner are said to regulate breeding numbers.

Apart from its heuristic value, an understanding of the causes of population limitation is crucial for conserving and/or managing animal populations (Newton 1991, 1998). Our main focus is the ultimate level of density limitation, but we also review demographic responses (productivity and mortality), where this elucidates the relative importance of a particular factor, or when nothing more is available in the published literature. Earlier reviews identified food supplies and nest sites as the main ultimate factors limiting breeding numbers of raptors (Newton 1979a, 1991, 2003a). We shall concentrate on these aspects, but in the goshawk, human-related factors such as deliberate killing and pesticide impact also deserve scrutiny.

The goshawk has been studied extensively in Europe. This is in part due to its charismatic appearance and behavior, but mainly because it is an avian top predator that is particularly time and cost effective to study (Bijlsma 1997, Rutz 2003a). The goshawk is often used as a model organism for addressing fundamental ecological questions (Kenward 1978a, b; Dietrich 1982, Ziesemer 1983, Kenward and Marcström 1988, Bijlsma 1993, Rutz 2001, Drachmann and Nielsen 2002, Krüger and Lindström 2001, Nielsen and Drachmann 2003, Rutz 2005b, Rutz et al. 2006), or as a bio-indicator for monitoring pollution levels in terrestrial ecosystems (Ellenberg and Dietrich 1981, Hahn et al. 1989, Kenntner et al. 2003, Mañosa et al. 2003). Moreover, some European goshawk populations prey on game species (Kenward et al. 1981a, Ziesemer 1983, Mañosa 1994, Nielsen 2003), domestic poultry (Ivanovsky 1998), and/or racing pigeons (*Columba livia*, Opdam et al. 1977, Bühler et al. 1987, Bijlsma 1993, Nielsen 1998, Nielsen and Drachmann 1999b, Shawyer et al. 2000), so applied studies have addressed stakeholder conflict and the issue of predator control (Kenward and Marcström 1981; Kenward 1986, 2000; Galbraith et al. 2003); as management has moved on from past persecution to eradicate predators, we use the terms culling, selective removal and illegal killing for contemporary human impacts on goshawks (REGHAB 2002).

As a consequence of this general interest, a large body of literature on European goshawk populations has accumulated, including reviews of the species' general biology (Kramer 1972, Glutz von Blotzheim et al. 1971, Cramp and Simmons 1980, Kenward and Lindsay 1981, Fischer 1995) and detailed reports on local population ecology (Holstein 1942, Opdam 1978, Looft 1981, Ziesemer 1983, Brüll 1984, Link 1986, Jørgensen 1989, Bijlsma 1993, Drachmann and Nielsen 2002).

Here, we critically review published information within the context of population limitation. We start with a reassessment of the species' status in western and central Europe and a description of the major population trends during the last century, updating Bijlsma (1991a), and Bijlsma and Sulkava (1997). We show that large-scale trends in numbers coincided with marked changes in the external environment. We then: (1) summarize evidence that population densities are indeed limited, rather than fluctuating at random, (2) explore a selection of putative limiting factors and assess their relative importance, and (3) use results from urban study areas, which differ markedly from natural or rural breeding habitats, to evaluate our account of non-urban populations. Our review enables a comparison of patterns of population limitation in the European goshawk with those suggested for the North American subspecies (*Accipiter gentilis atricapillus* and *A. g. laingi*). We close the paper by identifying gaps in our knowledge on goshawk biology and by proposing several lines of future research.

METHODOLOGICAL NOTES

LITERATURE REVIEW AND DATA HANDLING

We made every possible effort to locate relevant information on the species, which has been published from about 1950 onward (for population trends, from about 1900 onward). We mainly focused on peer-reviewed material, which we compiled by standard bibliographic searching techniques, but also considered results in academic theses, technical reports, or non-refereed journals if the presentation of the data allowed us to evaluate the validity of the authors' conclusions. We might have missed some publications from southern and especially central Europe, mainly because they appeared in non-indexed journals. The apparent bias towards German and Dutch studies might partly be the result of our own familiarity with this literature, but it also reflects the greater research intensity in these countries compared to elsewhere in Europe.

Throughout this paper, we support important arguments by giving reference to studies which produced conclusive evidence. In the case of more trivial statements, we quote one or two key references, which will guide the reader to related publications. In addition to the critical review of the literature, we will illustrate important points with detailed case studies, mainly based on our own research and including hitherto unpublished material.

For several sections of this review, we compiled data from the original literature for meta-investigations, which treat individual studies or goshawk populations as the unit of observation. Quantitative analyses of this material will be presented elsewhere (Rutz 2005b, C. Rutz et al., unpubl. data). In some cases, we asked authors to provide unpublished information or original data for (re-)analysis. Time constraints prevented us from sampling such material at a scale which would have produced an exhaustive data set, leaving much scope for future collaborative work.

To give as complete a summary of the current knowledge on the species as possible, we had to consider studies which differ markedly in their field methods as well as in their statistical analyses. In two cases, we decided to tag studies to draw the reader's attention to methodological aspects that we consider important for evaluating the presented data. Firstly, we indicate whether a study estimated brood size by observation from the ground (OFG) or by climbing nest trees, because the former method is known to underestimate nestling numbers (Bijlsma 1997, Goszczyński 1997, Altenkamp 2002). Secondly, we note when we felt that multiple statistical testing (MT), without correcting probability values appropriately, might have led to spurious conclusions (Rice 1989).

The population levels of some forest raptors can be reasonably indexed using mean nearest-neighbor distances (NND) in continuously suitable woodland habitat (Newton et al. 1977). An advantage of the NND-method is that it is comparatively robust to the arbitrary delineation of study areas; on the other hand it overestimates actual population density—particularly where suitable nesting habitat is limited relative to foraging habitat. Because few studies reported NND values, we were constrained to using overall density estimates (pairs/100 km^2) in most contexts. Estimates of goshawk breeding densities are significantly affected by the size of the study plot (Fig. 3 in Gedeon 1994). We acknowledged this problem by restricting our analyses to density values obtained for plots >50 km^2 in size (the largest variation has been found for plots <50 km^2), or even >100 km^2 in some cases, and by controlling for plot size in all statistical models.

General(ized) linear (mixed) modeling (GL[M]M) was carried out in GenStat 6.0 and Minitab 12.0, using standard procedures (Crawley 1993, Grafen and Hails 2002).

Cross-continental Comparison

When comparing goshawk biology between Europe and North America, we were aiming to highlight marked differences between continents that are unlikely to be artifacts of fieldmethod variations. A more quantitative cross-continental comparison, employing statistical models that can control for confounding factors, is in preparation (C. Rutz et al., unpubl. data).

We made an attempt to build exhaustive databases of key demographics and life-history traits for goshawks on both continents. Our European database was created, using sources and searching techniques described above. For the North American database, we used recent literature reviews (Block et al. 1994, Kennedy 1997, Squires and Reynolds 1997, USDI Fish and Wildlife Service 1998a, Kennedy 2003, Andersen et al. 2004; Squires and Kennedy, *this volume*) as a starting point, and subsequently filled in gaps by standard searching techniques. Studies were entered more than once, if they reported data for two or more distinct study plots. At the time of writing, our European and North American databases contained 225 and 99 entries, respectively.

We omitted all studies that had been completed before 1975 because goshawk populations in Europe were subject to much illegal killing and pesticides before that time. For breeding density estimates, we only used studies, where study plots were between 100–2,500 km^2 in size, did not contain 100% woodland cover, and were surveyed for at least 3 yr. In this way, we aimed to exclude studies that had actively selected optimal goshawk habitat, which inadvertently results in density overestimation. Our criterion for minimum plot size was more stringent than in other analyses in this review, because we could not easily control for percentage woodland cover in this comparison (most American studies do not give quantitative estimates of forest cover). Areas >2,500 km^2 overcome problems of biased habitat composition but are difficult to search reliably—see Smallwood (1998) for the relationship of breeding density *vs*. study area size in North American studies. We used maximum breeding density (the maximum annual number of active nests) if given in the original source, and mean breeding density otherwise.

In the case of diet composition, we only used studies that were based on direct observations at nests, collection of prey remains around nests, radio tracking, or any combination of these techniques. These methods typically provide a unique record for each prey individual. We omitted pellet-only data because this method represents hair or feathers from one prey in several pellets while unique identifiers like particular bones are often digested by hawks. Reliance on pellet analysis has been shown to produce severely biased diet descriptions (Goszczyński and Piłatowski 1986, Mañosa 1994, Padial et al. 1998, Lewis et al. 2004). Parameters of breeding performance (nest success, clutch size, brood size, and productivity) were only used for studies that had investigated at least five nests. In this exploratory analysis, we pooled studies where nest trees were climbed for nestling banding with those where observations were made from the ground.

Applying the above filtering criteria to our data bases and excluding data from duplicate publications to avoid pseudo-replication resulted in a data set containing material reported in a total of 117 sources (plus four unpublished data sets) from Europe and 57 from North America (Table 5). For Europe, we had access to almost all original sources (96%) for data extraction; whereas for North America, we had to compile values from other review articles for about 39% of all studies. We do not think that this additional source of error led to serious misinterpretations, although we discovered several inconsistencies in values given in three review articles (USDI Fish and Wildlife Service 1998a, Kennedy 2003, Andersen et al. 2004). Data for comparison between areas are presented as ranges of values, with medians if they come from four or more areas.

CURRENT STATUS AND POPULATION TRENDS

The goshawk is a widespread inhabitant of coniferous and deciduous forests in western and central Europe (Fig. 1). Regional densities generally vary between 0.5–6.2 pairs/100 km² of land (Table 1), but local densities can reach values of well over 10 pairs/100 km² (Poland—13.9 pairs/100 km², Olech 1998; Germany—15.6 pairs/100 km², Mammen 1999; The Netherlands—15.0–52.5 pairs/100 km², Bijlsma et al. 2001). The altitudinal distribution of nesting sites ranges from below sea level (Müskens 2002, Busche and Looft 2003) up to the tree line (Gamauf 1991, Oggier and Bühler 1998). The population in Britain is small, because it is only recently established from loss and deliberate release by falconers, and is still in the early stages of colonization (Petty 1996a, *Case study 3*). Large gaps in distribution, such as in northwest France, western Belgium, and the floodplain of the River Po in northern Italy, coincide with agriculture in lowlands and a lack of woodlands (Bijlsma and Sulkava 1997).

The total population in central and western Europe—Poland through France—was estimated at 29,000–44,000 breeding pairs in the early 1990s (Bijlsma and Sulkava 1997). Despite further increases in range and numbers, these figures are probably still valid. Mebs and Schmidt (unpubl. data) estimate the total breeding population of the western Palearctic to be 159,000 pairs (range = 135,000–183,000).

Goshawks were much reduced in density and distribution in the first half of the 20th century by intensive human persecution. From the start of World War II, human persecution abated in many parts of Europe due to legal protection of the species, declining numbers of gamekeepers, or changes in forestry and hunting practices. In western and central Europe, the large-scale planting of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) on heaths, moors and otherwise unproductive habitats, and the conversion of deciduous into non-native coniferous woodland reached its peak between the mid-1800s and the early 1900s. These new forests gradually matured in the first half of the 20th century, providing new habitat for goshawks on a large scale (*Case studies 1, 3*). Similarly, though starting somewhat later, extensive planting of conifers also took place in Great Britain (Petty 1996b, *Case study 3*). The combination of reduced persecution and increased acreage of coniferous forest resulted in goshawk population increases over much of Europe through the mid-1950s.

The subsequent population crash between 1956 and 1971 (Table 2) paralleled the massive application of persistent organochlorine and mercurial pesticides and seed dressings in farmland areas, presumably via impaired reproduction and adult survival (Conrad 1977, Thissen et al. 1981). Populations away from intensive farming, such as in the central Alps, remained unaffected by pesticides and showed stable numbers throughout the 1960s and 1970s (Bühler and Oggier 1987). The recovery and expansion of remaining populations in various regions started more or less synchronously in the 1970s, coinciding with successive bans in the uses of organochlorines, and numbers leveled off in the 1980s or 1990s (Tables 1, 2).

Regional variations in intensity of killing by humans, food availability and possibly nest-site competition with Eurasian Eagle-Owls (*Bubo bubo*) were responsible for sometimes curtailed expansion or localized declines. Nevertheless, by the late 20th century, abundance and distribution of goshawks in much of Europe had reached unprecedented levels compared to the past century, despite continued

FIGURE 1. Breeding distribution of the Northern Goshawk in Europe from Clark (1999), reproduced with permission of Oxford University Press.

killing. This was not only due to the increased area of coniferous woodland, but also habitat fragmentation, eutrophication (*Case study 1*), and the novel tendency exhibited by the species to exploit human-dominated environments.

EVIDENCE FOR DENSITY LIMITATION

Four inter-related lines of evidence suggest that breeding densities in European goshawk populations are limited, rather than fluctuating at random. The data for goshawks presented here are consistent with results from other raptor studies (Eurasian Sparrowhawk [*Accipiter nisus*], Newton 1989; Eurasian Kestrel [*Falco tinnunculus*], Village 1990; Golden Eagle [*Aquila chrysaetos*], Watson 1997), and with conclusions from a comparative study, reviewing patterns observed in various diurnal raptors (Newton 1979a, 1991, 2003a)

Stability of Breeding Numbers

Local breeding densities often remain fairly stable over periods of several years in the absence of significant perturbations, e.g., deliberate killing, and pesticides, or environmental changes, e.g., change in

TABLE 1. OVERVIEW OF DISTRIBUTION AND ABUNDANCE OF GOSHAWKS IN WESTERN AND CENTRAL EUROPE IN THE SECOND HALF OF THE 20TH CENTURY.

Country/period	Occupied squares	N pairs/territories	Sources
Britain (except Northern Ireland: 244,000 km², 9.4%)			
1968–1972	35	(<35)	Marquiss (1993).
1988–1991	236	200	Marquiss (1993).
mid-1990s	?	400	Petty (1996a).
Denmark (43,000 km², 10.8%)			
1950–1960	?	100	Grell (1998).
1971–1974	299	150–200	Grell (1998).
1985	?	650	Jørgensen (1998).
1993–1996	796	700	Grell (1998).
Germany (356,750 km², 31%)			
1970	?	2125	Kostrzewa and Speer (2001).
1978–1982	?	5,150–6,950	Kostrzewa and Speer (2001).
1998–1999	?	8,500	Kostrzewa and Speer (2001), *cf.* Mammen (1999).
The Netherlands (42,318 km², 7.2%)			
1950	?	400	Bijlsma (1989).
1969	?	75–100	Bijlsma (1989).
1973–1977	210	500–600	Bijlsma (1989).
1979–1983	?	1,200–1,400	Bijlsma (1989).
1986	?	1,300–1,700	Bijlsma (1989).
1988	594	1,500–1,800	Bijlsma (1993).
1989–1994	770	1,800–2,000	Bijlsma et al. (2001).
1995–1999	928	1,800	Bijlsma et al. (2001).
1998–2000	959	1,800–2,000	Müskens (2002).
Belgium (Flanders: 13,672 km², 10.8%)			
1973–1977	7	(<10)	Devillers et al. (1988).
1985–1988	?	110–160	G. Vermeersch and A. Anselin, pers. comm.
2000–2003	>100	300–400	Gabriëls (2004), J. G. Vermeersch and A. Anselin, pers. comm.
Belgium (Wallonia: 16,844 km², 31.4%)			
1973–1977	107	130–200	Devillers et al. (1988).
2001–2003	?	430–440	J.-P. Jacob, pers. comm.
Luxembourg (2,586 km², 31.7%)			
1976–1980	97	50–60	Melchior et al. (1987).
France (547,030 km², 27%)			
1970–1975	369	(400)	Yeatman (1976).
1979–1982	?	3,000–4,500	Thiollay and Terrasse (1984).
1985–1990	688	2,200–3,100	Joubert (1994).
2000	?	4,600–6,500	Dronneau and Wassmer (2004).
Switzerland (41,293 km², 30%)			
1972–1974	238	600	Oggier (1980).
1985	?	1,300	Bühler and Oggier (1987).
1993–1996	376	1,400–1,600	Oggier and Bühler (1998), Winkler (1999).
Austria (83,849 km², 39%)			
1981–1985	435	2,300	Gamauf (1991), Dvorak et al. (1993).
Czech Republic (78,641 km², 33.3%)			
1973–1977	707	?	Šťastný et al. (1987).
1985–1989	577	2,000–2,800	Šťastný et al. (1996).
1990	?	2,000–2,500	Danko et al. (1994).
Slovakia (48,845 km², 41%)			
1973–1977	282	1,700	Šťastný et al. (1987).
1985–1989	378	1,600–1,800	Danko et al. (2002).
Poland (312,683 km², 29%)			
1990	?	3,500–5,000	Heath et al. (2000).
2000	?	5,000–6,000	Tomiałojć and Stawarczyk (2003).

Notes: For each country, total area and percentage woodland cover are given in brackets. Distribution is expressed as number of 10-km squares occupied (square size 24 × 27 km in France, 8 × 10 km in Belgium in 1973–1977, 5 × 5 km in The Netherlands and Luxemburg, and 12 × 11.1 km in Czech Republic and Slovakia in 1985–1989) and abundance as the number of pairs/territories. Note that some estimates or mappings were considered inaccurate by later sources. T. Mebs and D. Schmidt (unpubl. data) estimate the total breeding population of the western Palearctic to be 159,000 pairs (range 135,000–183,000) based on recent estimates including unpublished data.

TABLE 2. TRENDS OF GOSHAWKS IN WESTERN AND CENTRAL EUROPE IN THE SECOND HALF OF THE 20TH CENTURY AT THE POPULATION (P) AND RANGE (R) LEVEL.

	1950–1970		1970–1990		1990–2000		
Country	P	R	P	R	P	R	Sources
Britain	a	a	2	2	2	2	Marquiss (1993), Petty (1996a), Petty et al. (2003b).
Denmark	-2	-	2	2	0	0	Grell (1998), Jørgensen (1998), Nielsen and Drachmann (1999a).
Germany	-2	-	2	1	0/-	0	Kostrzewa and Speer (2001), Mebs (2002).
Schleswig-Holstein	-	-	+/0	+	0/-	0	Looft (2000), Berndt et al. (2002), Busche and Looft (2003).
Niedersachsen	-2	-	+	+	0	0	Kostrzewa and Speer (2001).
Nordrhein-Westfalen	-2	-	+	+	0	0	Kostrzewa et al. (2000), Arbeitsgruppe Greifvögel NWO (2002).
Hessen	-	-	1	+1/0	0/-	0	Hausch (1997).
Baden-Württemberg	-2	-	+	+	0	0	Hölzinger (1987).
Bayern	-2	-	+	+	0/-	0	Link (1986), Bezzel et al. (1997a).
The Netherlands	-2	-2	2	2	0	2	Bijlsma et al. (2001), Müskens (2002).
East	-2	-2	2	2	0/-1	0	Bijlsma et al. (2001), Müskens (2002).
West	a	a	2	2	2	2	Bijlsma et al. (2001), Müskens (2002).
Belgium	-2	-	2	2	2	2	Devillers et al. (1988).
Flanders	-2	-	2	2	2	2	Geuens (1994), De Fraine and Verboven (1997), Gabriëls (2004).
Wallonia	-2	-	2	2	0	0	Heath et al. (2000).
Luxembourg	-	-	+	+	0	0	Heath et al. (2000).
France	-2	0	1	1	0	0	Yeatman (1976), Thiollay and Terrasse (1984), Joubert (1994), Dronneau and Wassmer (2004).
Switzerland	-2	-	2	2	1	0	Oggier and Bühler (1998), Winkler (1999).
Austria	-	-	1	1	0	0	Dvorak et al. (1993), Gamauf (1991).
Czech Republic	-	-	1	1	-	0	Kren (2000), Šťastný et al. (1996).
Slovakia	-	-	1	0	0	0	Danko et al. (2002).
Poland	-2	-	1	1	1	1	Drazny and Adamski (1996), Tomiałojć and Stawarczyk (2003).

Notes: a = absent; + = increase (1 = <50%, 2 = >50%); - = decline (1 = <50%, 2 = >50%); 0 = stable/fluctuating; +/0/- = various trends in different regions.

prey abundance, deforestation, and habitat succession (Table 2). Examples of populations, for which breeding numbers fluctuated on average by no more than 15% of the mean over at least 15 yr, are shown in Fig. 2a. On the other hand, when numbers change systematically, and are not indicative of the recovery of formerly depleted populations, trends often coincide with obvious alterations in the environment. This observation suggests causal relationships between extrinsic factors and breeding numbers, and we explore these potential links in detail later.

We are aware of the fact that the investigation of numerical population stability is problematic, because the choice of time frame over which counts are assessed and the definition of stability are arbitrary (Newton 1998). Further, populations should ideally be monitored together with quantitative estimates of various environmental key factors but no study on goshawks has yet accomplished this difficult task satisfactorily. We therefore simply note that most long-term data sets on population trends we examined fit qualitatively into the general picture described above.

More importantly, some evidence suggests that year-to-year stability in numbers, exhibited by several goshawk populations, is due to density-dependent processes. For example, the percentage of change in numbers of territorial pairs appears to correlate negatively with the number of pairs in the previous year (Fig. 2b); in other words, years of lowest densities are followed by the greatest proportional increases, whereas years of highest densities are followed by the greatest declines (Newton and Marquiss 1986, Newton 1998). This finding should be interpreted with care, however, because such a pattern could also be found in a non-regulated population that exhibits random fluctuations (Newton 1998). Statistical investigation of density dependence is still an area of hot debate (Turchin 2003), and clearly beyond the scope of our review.

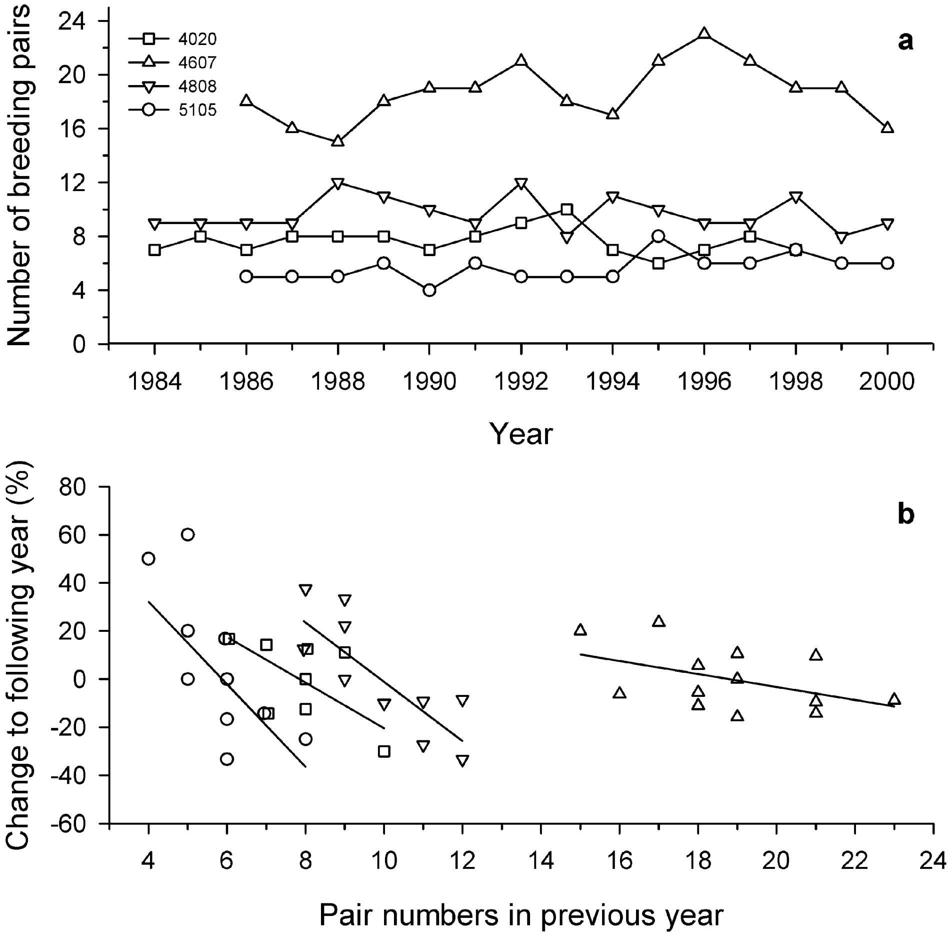

FIGURE 2. Long-term dynamics of four undisturbed goshawk populations in Nordrhein-Westfalen, Germany (numbers are Gauss-Krüger coordinates of study plots; see Arbeitsgruppe Greifvögel NWO 2002). (a) Population trends. (b) Graphic test for density dependence (percentage of change in population, *y*, in relation to population level, *x*, in previous year). Best-fit lines in (b) are shown for illustration purposes only (Newton and Marquiss 1986, Newton 1998). Note that some points in (b) overlap. Stability of breeding numbers and density-dependent population regulation can be found in many other stable populations. Unpublished trend data were collected by E. and B. Baierl, D. Becker, G. Müller, U. Siewers, and G. Speer, and communicated by E. Guthmann.

Krüger and Lindström (2001) failed to find a direct link between the per capita growth rate of their study population and the breeding pair density of the preceding season. Interestingly, population growth was significantly related to an interaction between density and autumn weather conditions, suggesting a coupling between density-dependent regulation and density-independent limitation.

Further support for the existence of density-dependent population regulation comes from the growth patterns of increasing populations, and the observation that productivity falls as breeding density increases (Looft 1981, Link 1986, Möckel and Günther 1987, Bijlsma 1993, Krüger and Stefener 1996 [OFG], Altenkamp 2002). The latter result, however, seems not very robust, as some studies have documented the converse pattern. An increase in productivity with density was reported for a population in central Poland (Olech 1998), and three populations in southern Germany (Bezzel et al. 1997a [OFG]). Olech (1998) interpreted her finding as an artifact of killing by humans, which affected the age-structure of the breeding population which in turn may have caused changes in productivity. Likewise, Bezzel et al. (1997a) hypothesized that their results were probably attributable to the effects of persistent illegal killing and habitat destruction which held breeding numbers well below carrying capacity. An increase in breeding performance with density could also occur as a response to a substantial change in food supply, as discussed later.

NON-BREEDING POPULATION

Several studies demonstrated that breeders are replaced soon—often within a few days—after their disappearance due to death or breeding dispersal (Looft 1981, Link 1986, Bijlsma 1991b). Further, some authors reported that extra birds visit active nests (Kollinger 1974, Bednarek 1975, Link 1986) or hold singleton-territories (Bezzel et al. 1997a, Penteriani et al. 2002b) during the breeding season. Both observations suggest the existence of a surplus population (Newton 1979a, 1991; Kenward et al. 1999, 2000) of non-breeders (also called floaters), which are physiologically capable of breeding, but will not do so until a breeding place becomes available.

Conclusive evidence that some individuals are excluded from breeding can only be produced by controlled removal experiments in populations with identifiable individuals (Village 1990, Newton and Marquiss 1991), or by following cohorts of radio-tagged hawks through their early life (Kenward et al. 1999, 2000). In goshawks, individuals can also be identified by comparing length, shape, coloration, and pigment patterning of molted primaries (Opdam and Müskens 1976, Ziesemer 1983, Kühnapfel and Brune 1995, Rust and Kechele 1996, Bijlsma 1997). Three investigators compared shed feathers of replacement birds to those sampled from known breeders in the study population in an attempt to estimate the extent of breeding dispersal. Ziesemer (1983) reported that only five (3.3%) of 151 new female breeders (N = 463 female years) had bred at another territory in the study area before. This is in close agreement with results by Link (1986) in his Erlangen study plot, who found that only four females (2%, N = 268 female years) and two males had bred previously in another territory. In an urban population in the city of Hamburg, not a single case of breeding dispersal was found (C. Rutz, unpubl. data; *cf.* Bezzel et al. 1997a). Because so few breeders within large study areas change territories, we can assume that most new breeders are unlikely to have previously bred elsewhere. In other words, the majority of new recruits appear to have been floaters, despite already having adult plumage.

Due to their elusive behavior, non-breeders are difficult to study, and little is known about this crucial component of goshawk populations. So far, the only quantitative estimate of the proportion of non-breeders in a goshawk population comes from a large-scale radio-tagging study on the Baltic island of Gotland (N = 318 tagged hawks; Kenward et al. 1999). It was estimated that in this stable population each year about 30% of males and 60% of females did not breed (for use of molted feathers, see Link 1986).

Theory suggests that there is a tight coupling between breeder and non-breeder dynamics (Newton 1988a, 2003b; Hunt 1998). As non-breeders do not depend on habitat with suitable nest sites, they can potentially exploit areas and prey resources denied to breeders. However, the floating sector of a population is inevitably limited by the numbers and productivity of breeders; the total number of non-breeding hawks is likely to be set at an equilibrium point, where annual additions match the annual substractions (Hunt 1998). On the other hand, non-breeding numbers could directly affect breeding numbers, as it is the floater pool that provides new breeding recruits that fill vacant territories. If the non-breeding sector has collapsed, for example, breeders that died or emigrated can no longer be replaced (*Case study 2*). Generally, non-breeders will form a small proportion of depleted or increasing populations and a large proportion of stable populations at capacity level (Newton 2003b). This intriguing model of population regulation has not yet been tested in goshawks but our current knowledge of goshawk population biology is largely consistent with these ideas.

DYNAMICS OF EXPANDING POPULATIONS

When established populations experienced a marked decline in density, breeding numbers often returned to the original level at the end of the recovery phase (Bezzel et al. 1997a, Olech 1998, Looft 2000, Krüger and Lindström 2001, Arbeitsgruppe Greifvögel NWO 2002). However, this is not invariably the case, as populations in some areas increased well beyond their original density in recent decades (*Case study 1*).

More convincing evidence of density limitation comes from the growth trajectories of newly founded populations, which generally exhibit a logistic pattern, characterized by three phases—establishment, expansion, and saturation (Shigesada and Kawasaki 1997). The observation that numbers do not grow indefinitely but level off toward the end of the colonization process indicates that the populations are limited by some external factor (Newton 1998). Examples, which we shall describe in detail, include the expansion of the Dutch goshawk population during the 1980s and 1990s (Bijlsma 1993, Lensink

1997, *Case study 1*), the spread of goshawks in several areas of Great Britain (Petty et al. 2003a; P. Toyne, unpubl. data, *Case study 3*) and the recent establishment of urban populations (Würfels 1999, Rutz 2001, Altenkamp 2002). Similar patterns of spatial and numerical expansion have been described for other populations (Geuens 1994, Albig and Schreiber 1996, De Fraine and Verboven 1997, Nielsen and Drachmann 1999a, Greifvögel NWO 2002; G. Vermeersch and A. Anselin, pers. comm.).

REGULAR SPACING OF TERRITORIES

In well-forested areas, nest sites often show a pattern of regular spacing (Fig. 3; Bednarek 1975, Waardenburg 1976, Link 1986, Bühler and Oggier 1987, Jørgensen 1989, Bijlsma 1993, Mañosa 1994, Penteriani 1997, Kostrzewa et al. 2000, Krüger and Lindström 2001). Most probably, this is the result of a spacing mechanism that maintains the minimum distance between adjacent nesting territories, despite increasing numbers of birds of breeding age, and which ultimately obliges some individuals to delay breeding until a vacancy occurs. For goshawks in Norway, Selås (1997a) could show that the removal of breeders by hunters led to an increase in goshawk breeding density in periods with increasing food supplies, but not in periods in which prey density remained unchanged. This observation strongly suggests that the territoriality of established breeders can hold breeding densities below levels that would otherwise be permitted by the available food supply. Similar experimental evidence for the operation of a spacing mechanism in goshawks does not exist for western, central or southern Europe, but its key components—territorial behavior of breeders and exclusion of potential breeders—are well-documented.

The existence of territorial behavior in the goshawk has been shown by direct observation at nest sites (Holstein 1942, Brüll 1984, Link 1986, Norgall 1988, Bijlsma 1993, Penteriani 2001) and more recently by monitoring radio-tagged individuals (Ziesemer 1983, 1999; Rutz 2001, 2005a). In The Netherlands, the probability of nest failure tended to increase with decreasing NND values, possibly as a result of increased levels of aggressive interactions (re-analysis of data from Appendix 26 in Bijlsma 1993; GLM [binomial error, logit link-function], Δ deviance = [χ^2] = 3.06, df = 1, P = 0.083; *cf.* Link 1986). Territorial behavior leads to the exclusion of some individuals from the breeding population which is best illustrated by the observation that the age of first-breeding varies with the degree of intraspecific competition in a population (Olech 1998).

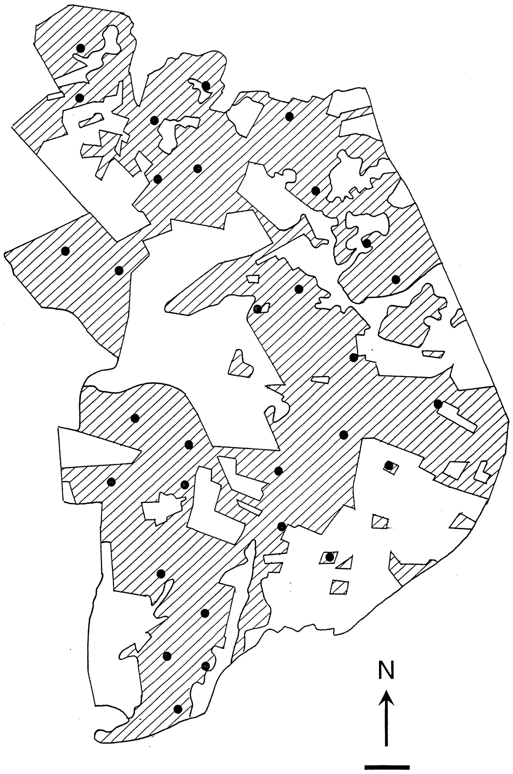

FIGURE 3. Breeding dispersion of goshawks in a Dutch study area (SW-Veluwe; R. G. Bijlsma, unpubl. data), illustrating the regular spacing of territories, characteristic of established populations at capacity level (hatched = woodland; unhatched = heaths, farmland, built-up; scale bar = 1 km). The figure depicts the situation in 1990, in which the following nest numbers of other raptor species were recorded in the same area: 54 *Accipiter nisus*, 74 *Buteo buteo*, 32 *Falco subbuteo*, 9 *Falco tinnunculus*, 19 *Pernis apivorus*.

In comparatively undisturbed goshawk populations, new breeding recruits are usually ≥2 yr of age (Bednarek 1975, Ziesemer 1983, Link 1986, Bijlsma 1993). Both male and female hawks can be sexually mature in their first year of life, but circumstantial evidence suggests that they are generally forced to delay breeding because of dominance by older individuals which occupy all the available territories (Newton 1979a, Fischer 1995, Kenward et al. 1999, Nielsen and Drachmann 2003). However, in situations where competition is relaxed, because a large proportion of breeding hawks is killed by man (Kollinger 1974, Bednarek 1975, Looft 1981, Grünhagen 1983, Link 1986; Bijlsma 1991b, 1993; Bezzel et al. 1997a, Rust and Mischler 2001), or hitherto uncolonized habitat becomes available for (re-)colonization (Waardenburg 1976, Thissen et al. 1981; Würfels 1994, 1999; Rutz et al. 2006), birds will breed in their first year of life.

In the absence of extensive illegal killing or habitat destruction, the regular spacing of nesting territories in continuously suitable woodland habitat changes little from year to year (Bednarek 1975, Bühler and Oggier 1987, Selås 1997a), because of the species' strong fidelity to prime nesting territories (Kostrzewa 1996, Krüger and Lindström 2001, Krüger 2002a). Territories are often used over long periods of time, despite the turnover of occupants (Ziesemer 1983, Ortlieb 1990, Bijlsma 2003).

FACTORS LIMITING BREEDING NUMBERS

NEST-SITE AVAILABILITY

The goshawk is a prime example of a forest-dwelling raptor species. Its close association with woodland habitat is strikingly illustrated by its breeding distribution, which mirrors the availability of forests at both global (Cramp and Simmons 1980) and European scales (Fig. 1). In this section, we focus on potential nest-site limitation in areas that provide at least some forested habitat. Specifically, we ask whether evidence suggests that a shortage of suitable nesting sites can hold goshawk breeding densities below levels that would otherwise be permitted by available food supplies.

A major difficulty in addressing this question arises from the fact that goshawks use forests not only for nesting but also for foraging (Gamauf 1988a, Kenward and Widén 1989, Ziesemer 1999); hence, goshawk numbers in areas with low woodland cover may be limited by a shortage of suitable nest sites, forest-dwelling prey, and/or structural habitat features necessary for nesting and efficient hunting. We attempt to separate these effects by employing a two-step approach. Firstly, we review current knowledge of typical goshawk nesting and hunting habitats. We then proceed to quantify the species' dependence on forest habitat, looking for both spatial and temporal correlations between forest availability and breeding densities.

During the past two decades or so, much goshawk research in western Europe has focused on describing features of nesting habitat (Penteriani 2002). Studies were conducted at different ecological scales (nest tree, nest stand, landscape level, and cross-scale approach) and varied considerably regarding the robustness of the study design (e.g., use of appropriate controls) and the sophistication of the data analyses (quantitative descriptions—Dietzen 1978, Looft 1981, Link 1986, Anonymous 1989, Dobler 1990, Bijlsma 1993, Mañosa 1993, Toyne 1997, Steiner 1998, Weber 2001; multivariate modelling—Kostrzewa 1987a, Gamauf 1988a, Penteriani and Faivre 1997, Penteriani et al. 2001; Krüger 2002a, b).

Despite marked regional differences in nest stand characteristics (Penteriani 2002), the goshawk generally shows a strong preference for nesting in large, mature forests with a low degree of disturbance by humans. Pairs typically nest some distance away from the forest edge (Looft 1981, Link 1986, Gamauf 1988a, Bijlsma 1993) within the most mature parts of the forest (Penteriani 2002). The nest stand is often characterized by a dense canopy and good flight-accessibility, and the nest is built in one of the largest trees within the stand (Penteriani 2002). Goshawks seem to avoid proximity to human settlements and areas of high human activity (Kostrzewa 1987a, Gamauf 1988a, Krüger 2002a; but see Dietzen 1978, Dietrich 1982). Some of the above characteristics were shown to be significant predictors for patterns of territory occupancy and productivity (Möckel and Günther 1987, Bijlsma 1993, Kostrzewa 1996 [MT], Krüger and Lindström 2001, Krüger 2002a), indicating that nest-site choice had fitness consequences for breeding pairs. An alternative interpretation is that the nest site contributes little to fitness, the statistical association arising mainly from the best quality birds occupying nest sites with favored characteristics.

It is tempting to conclude from these data that goshawks can be limited by the availability of suitable nest sites in areas where forests do not offer mature stands that fulfill the above criteria. However, detailed studies in The Netherlands and Germany have shown that goshawks exhibit a surprising plasticity in nest-site choice. Where few hawks are killed by humans, they occupy a wide range of forests, including woodlots of <0.5 ha, lanes of broad-leaved trees along roads in open polders (*Case study 1*), and even nest successfully in small city parks completely surrounded by buildings and with extraordinary high levels of human activity. We therefore suggest that any remaining preference for nesting in large mature forests could be an artifact of differences in killing by humans. Avoidance of humans could reflect shyness selected by decades of persecution. Deliberate killing would have been most common in fragmented habitats with a high proportion of farmland, because nests are easily detected in small woodlots (Bijlsma 1993, Olech 1998), private landowners often resented predation by raptors, particularly goshawks, and law enforcement was commonly absent or successfully frustrated.

To clarify, goshawks may not require mature woodland for successful nesting in the absence of killing by humans, but they may still prefer this habitat type, and their use of resources will often be dictated by environmental habitat availability. In areas with abundant prey supplies, goshawks may use less preferred nest sites if good ones are not available. This may be the situation in parts of western Europe.

Comparatively little is known about goshawk foraging habitats in Europe, particularly in the western, central, and southern parts. Only few radio-tracking studies have been conducted, and the majority of them investigated ranging behavior during the winter time (Kenward 1979, 1982; Dietrich 1982, Ziesemer 1983, Kluth 1984, Straaß 1984; Rutz 2001, 2003b; Meier 2002, Lechner 2003; C. Rutz et al., unpubl. data). Habitat-use and home-range data based on chance observations of unmarked individuals (Gamauf 1988a, Krüger 1996, Lõhmus 2001) or collections of molted feathers or pluckings (Brüll 1984, Link 1986, Krüger and Stefener 1996) are clearly biased and must be interpreted cautiously (Altenkamp 1997).

For foraging, goshawks generally seem to prefer richly-structured habitats, probably because the success of their principal hunting techniques—short-stay-perch hunting and contour-hugging flight (Rudebeck 1950–51, Hantge 1980, Fox 1981, Kenward 1982, Widén 1984)—depends chiefly on cover for self concealment. Usually, this cover is provided by forested habitat. Near Oxford, England, most of the 60 winter kills registered with four radio-tagged males were made in woodland (58%) or within 100 m of woodland (25%; Kenward 1982). Some evidence shows that goshawks inhabiting well-forested habitats make extensive use of forest-edge zones (Kenward 1982, 1996), but foraging in very open parts of agricultural landscapes has also been observed (Dietrich 1982, Ziesemer 1983, Meier 2002; C. Rutz et al., unpubl. data). Chance observations from Austria showed that goshawks spent more time in forests during the breeding season (65% of observations) than in winter (47%; Gamauf 1988a; *cf.* Dietrich 1982). Kenward (1996) reviews how the ecology of the main prey species affects ranging behavior in Scandinavian goshawks.

Despite doubts about the species' need of forests when food is abundant elsewhere (Kenward and Widén 1989), the literature almost unequivocally emphasizes the overriding importance of this habitat type. However, goshawks can hunt efficiently in terrain that lacks forest cover. As Olech (1997) pointed out, this can be inferred indirectly from prey lists, which often contain a considerable amount of species thriving in open habitats (Zawadzka and Zawadzki 1998). Goshawks readily use anthropogenic elements for cover during low and fast prey-searching flights and even adopt alternative hunting strategies that do not rely on concealment at all. Two such techniques closely resemble hunting behavior typically shown by Peregrine Falcons (*Falco peregrinus*), namely exposed perched hunting and high soaring and stooping (Erzepky 1977, Grünhagen 1981, Alerstam 1987, Rutz 2001). In conclusion, thanks to its remarkable behavioral plasticity, the goshawk can forage efficiently in a wide range of habitats, including forests, woodland-farmland mosaics and even metropolitan areas, provided they offer sufficient prey. Nevertheless, in the light of the insights produced by a review on goshawk-habitat interactions in Fennoscandia (Widén 1997), we stress the need for more data on goshawk ranging and hunting behaviour. Widén (1997) warns that the species might only need a small patch of suitable habitat for nesting, but that it can be seriously affected by forest fragmentation where this can potentially decrease foraging efficiency on certain kinds of prey.

We will now try to quantify the goshawk's dependence on forested habitat. At a regional scale, we found no relationship between the estimated countrywide breeding density per 100 km^2 of area, and per 100 km^2 of woodland, respectively and the country's percentage woodland cover (Fig. 4; Table 1). This is not surprising, because we were unable to control for various confounding factors and because the accuracy of density estimates varies substantially across countries. However, when we restricted the analysis to areas where several adjacent populations could be compared directly, local breeding density increased significantly with the amount of forested habitat (Fig. 4b; GLMM, P <0.001). Importantly, study plots with high forest cover held higher absolute numbers of pairs (Fig. 4b), but fewer pairs per unit of woodland area (Fig. 4d; GLMM, P <0.001; *cf.* Goszczyński 1997). This implies that spacing of nests in heavily forested areas is wider. Because of the inevitable circularity of this analysis (the *x* variable is part of the *y* variable), we tried to confirm this finding with an additional index of population density—mean NND. In a cross-study analysis, mean NND was not related to forest availability (Fig. 5; GLM, P >0.05), and the same result was obtained when we re-analyzed data from Bühler and Oggier (1987) for ten Swiss populations (GLM [normal error, identity link function, controlled for plot size], $F_{1,7} = 1.98$, P = 0.203) (Bednarek 1975, Link 1986). An obvious need exists for more data to understand

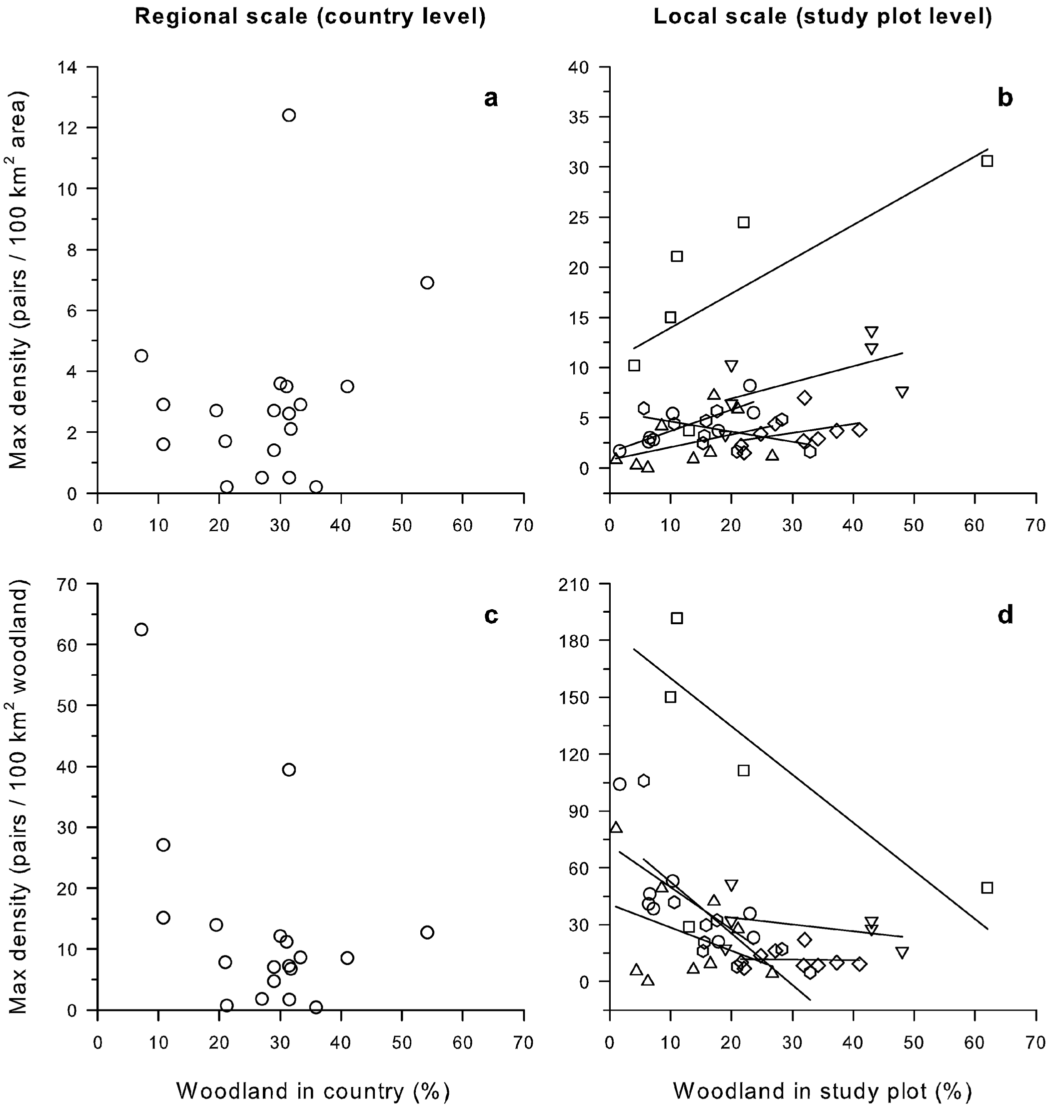

FIGURE 4. Goshawk breeding density (pairs/100 km^2 area, or pairs/100 km^2 woodland) in relation to woodland cover. (a) and (c): Regional scale; data from19 European countries (Table 1). No relationship (GLM [normal error, identity link function] on square-root-transformed data) was found between the estimated countrywide breeding density and the country's percentage woodland cover (pairs/100 km^2 area, $F_{1,17} = 0.69$, $P = 0.417$; pairs/100 km^2 woodland, $F_{1,17} = 3.32$, $P = 0.086$). Conclusions were not altered by controlling for country size (pairs/100 km^2 area, $F_{1,16} = 1.06$, $P = 0.319$; pairs/100km^2 woodland, $F_{1,16} = 3.94$, $P = 0.065$). (b) and (d): Local scale; data from studies that investigated ≥6 nearby sub-populations (total: N = 47; Switzerland, N = 9, Bühler and Oggier 1987 [diamonds]; Denmark, N = 8, Nielsen and Drachmann 1999a [circles]; The Netherlands, N = 6, Bijlsma et al. 2001 [squares]; Germany, N = 6, Link 1986 [inverse triangle], two sets, each N = 9, Weber 2001 [triangle, hexagon]; all plots <50 km^2 excluded). Here, GLMMs were built with study-identity modeled as a random effect (six levels), and plot size (covariate) and percentage forest cover (covariate) as fixed effects. This approach ensured that: the influence of plot size was eliminated, and conclusions could be generalized beyond the study areas investigated. Maximum breeding density increased significantly with forest cover (b) (Wald statistic = [χ^2] = 16.86, df = 1, $P < 0.001$), whereas maximum breeding density per unit of woodland decreased significantly with the amount of forest in the plot (d) (Wald statistic = [χ^2] = 18.01, df = 1, $P < 0.001$). Note that *y*-axes have different scales and that for illustration purposes, all figures show raw data with best fit-lines produced by linear regression.

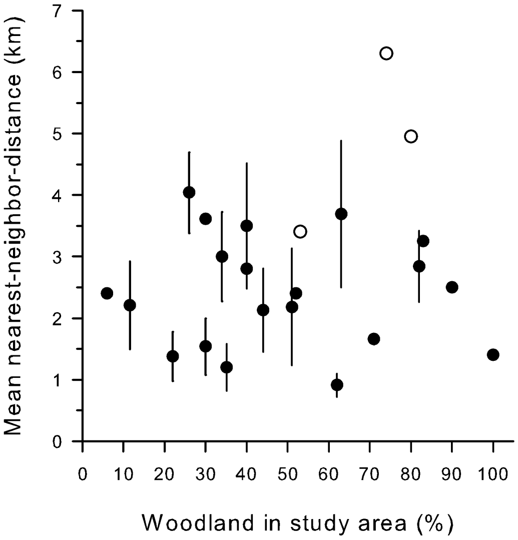

FIGURE 5. Nest spacing of goshawks (nearest-neighbor-distance, NND, mean ± SD) in relation to woodland cover of the study area; data are from western, central and southern Europe (filled), and from northern Europe (open). Sources: Pielowski (1968), Dietzen (1978), Dietrich (1982), Widén (1985b), Bühler and Oggier (1987) combined with Bühler et al. (1987), Gamauf (1988a), Anonymous (1990), Mañosa et al. (1990), Dobler (1991), Mañosa (1994), Penteriani (1997), Selås (1997a), Jędrzejewska and Jędrzejewski (1998), Olech (1998), Zawadzka and Zawadzki (1998), Kostrzewa et al. (2000), Weber (2001), Penteriani et al. (2002b), R. G. Bijlsma, unpubl. data, R. E. Kenward et al., unpubl. data. The association (GLM [normal error, identity link function]) was non-significant for western, central, and southern European data ($N = 20$, $F_{1,18} = 0.11$, $P = 0.744$), and for western, central, southern, and northern European data ($N = 23$, $F_{1,21} = 0.66$, $P = 0.425$).

goshawk nest spacing in relation to habitat composition at various spatial scales.

The experimental manipulation of nest-site abundance is impractical in this species. However, in some regions, the availability of suitable woodland habitat changed significantly in the course of time, as a result of forestry activities (Hölzinger 1987) or natural processes, and we can ask whether goshawk numbers changed correspondingly. Without doubt, large-scale logging of forests can have devastating effects on goshawk populations. The widespread destruction of woodland across Europe during the Middle Ages until the beginning of the 19th century may have caused dramatic population declines (Bijleveld 1974). Nowadays, forestry practices may still affect local populations (Bezzel et al. 1997a, Widén 1997, Ivanovsky 1998), but moderate timber harvesting appears to have no effect on population levels, as long as cover reduction does not exceed about 30% (Penteriani and Faivre 2001). Forestry operations during incubation and the early nestling stage may cause breeding failures (Toyne 1997), but are unlikely to cause reduction of breeding density, unless substantial areas are clear felled. The felling of active nest trees—intentional or accidental (Bijlsma 1993, Bezzel et al. 1997a, Kostrzewa et al. 2000)—seems to be infrequent and thus unimportant. So far, the only attempt to assess the impact of forestry operations on goshawk populations on a countrywide scale was made in The Netherlands. Bijlsma (1999a, b) estimated, based on a representative sample of 559 goshawk nests out of a total population of about 1,800 pairs, that forestry operations caused the loss of 45 goshawk broods (8%) in 1998 (see also Drachmann and Nielsen 2002).

Another cause of habitat deterioration in Europe is forest dieback, e.g., the widespread tree mortality due to acid rain (Hölzinger 1987, Flousek et al. 1993). Such wide-scale phenomena could potentially affect goshawk populations across Europe (Kostrzewa 1986, Hölzinger 1987, Gamauf 1988b), but as yet remain speculative. Afforestation can provide new nesting habitat when stands are allowed to mature and enter the stage at which they become attractive for Goshawks. We illustrate the positive effects of such habitat alterations in detail in *Case studies 1* and *3* (Risch et al. 1996, Olech 1998).

In conclusion, the nest-site preferences reported for most European areas probably only partly reflect essential ecological needs, as has been proposed repeatedly (Penteriani 2002). Rather, they almost certainly evidence behavior selected partly by past human persecution (Krüger 2002a). Impressive examples of the species' behavioral and ecological plasticity occur mainly in areas without deliberate killing.

In areas with extensive woodland cover and negligible human disturbance, territorial behavior of breeding pairs probably renders structurally suitable nesting habitat unavailable for other prospective breeders, as suggested from the regular spacing of nests discussed above (Newton et al. 1977, 1986). Further, hunting conditions in large forest stands without farmland nearby might be less profitable than hunting in open woodland-mosaics with greater abundance of suitable prey (Kenward 1982, Krüger 2002a, but see Widén 1997).

An interesting feature of many stable undisturbed goshawk populations is that, despite the presence of non-breeders, some suitable nest sites remain vacant (Ziesemer 1983, Bühler et al. 1987, Kostrzewa 1996, Nielsen and Drachmann 1999a, Krüger and

Lindström 2001). Nest territories apparently vary in quality, as some are used every year, others intermittently, or only occasionally (Krüger and Lindström 2001). This suggests that breeding numbers may be limited by factors other than nest-site availability, e.g., the supply of potential prey.

Case study 1. The Netherlands—the effect of habitat alteration

The changes in numbers, distribution and behavior of goshawks living in a rapidly altering landscape can be illustrated by studies in The Netherlands. This small country in western Europe, situated in the floodplains of the rivers Rhine, Meuse, and Waal, reached an average human density of 462 inhabitants/km² in the early 2000s, at least two–three times as many as in any other western European country except Belgium. During the 20th century, the human population trebled, the number of houses increased sevenfold and the number of cars exploded from zero to >7,000,000. In less than a century, a mainly rural society transformed itself into a high-tech society where farming is industrialized and natural habitats are all but lost (<4% of surface by 1996); each square meter nowadays feels the stamp of human impact (Bijlsma et al. 2001). Nevertheless, goshawk densities are higher than anywhere else in Europe, showing a 40-fold increase in the past century (Fig. 6).

In the early 20th century, three important developments triggered the initial population growth. Firstly, widespread planting of coniferous forests in the late 19th and early 20th century on sandy heaths and moors in the eastern and southern Netherlands enlarged the potential breeding area substantially. By the late 20th century, almost 10% of the Dutch land surface was covered with woodland, including regions where woodland had been previously scarce or even absent. These forests became attractive breeding sites 10–15 yr or 40–50 yr after planting, depending on soil type and tree species. Secondly, goshawks received legal protection in 1936. Until then, goshawks were relentlessly persecuted (Bijleveld 1974, Bijlsma 1993). Although some legal killing continues to the present, its impact rarely suppresses density, and, if so, only locally and temporarily. Conversely, systematic persecution in the past has been shown to reduce nesting success, increase the turnover of breeding birds and reduce their mean lifespan (Bijlsma 1993). Thirdly, the availability and density of major prey species (pigeons, thrushes, and corvids; Table 3) increased markedly from the 1940s through the 1980s (Thissen et al. 1981, Bijlsma et al. 2001) due to significant changes in land use and farming practice, and the maturation of woodland habitat.

The combination of these three factors resulted in an expanding goshawk population, from an estimated 50 pairs at the start of the 20th century to 1,800–2,000 pairs in 1998–2000 (Fig. 6; Bijlsma 1989, 1993; Müskens 2002). This growth was briefly interrupted in the late 1950s and 1960s (Fig. 6b), when massive application of persistent organochlorine pesticides in farmland led to excessive adult mortality and impaired breeding success (Thissen et al. 1981, Bijlsma 1993). Since the early 1970s, after DDT, aldrin, dieldrin, and mercury in seed dressings had been successively banned, goshawks recovered quickly. The first stage of recovery took place exclusively in the coniferous woodlands of the eastern Netherlands, which, though largely depleted of goshawks during the 1960s, still held sparse populations.

After reaching saturation levels in the core breeding range in the 1980s (mainly coniferous forests in the eastern and central Netherlands), goshawks started to colonize hitherto unoccupied habitats between the large forests, and spread into marshes and newly created deciduous forests of the central and western Netherlands, outside the main range of coniferous woodland (Fig. 6a). This westward trend into the agricultural, industrial and densely populated lowlands of The Netherlands continues. Now goshawks nest in previously unoccupied habitats: small woodlots (<0.5 ha) and tree lanes in open farmland, duck decoys, thickets, suburbs, city parks and recreational sites; in 2001, even a failed breeding attempt on an electricity pylon was discovered. Consequently, breeding goshawks occupied >1,000 5-km squares by the year 2000, covering some 60% of the total land surface, compared to only 214 in 1973–1977 (471% increase). Whereas the goshawk is still spreading, breeding density started to decline in parts of the eastern Netherlands since about the early 1990s, following precipitous declines in major prey species (*Case study 2*).

FOOD SUPPLIES

It is intuitively obvious that goshawk breeding density must be related to the availability of food resources. In areas where profitable prey is scarce, hawks face an energetic bottleneck and may cease breeding altogether. A powerful test of whether food limits density would be to increase its supply over a large area experimentally and monitor the subsequent numerical response of the local goshawk population (Boutin 1990, Newton 1998). When breeding numbers increase, we may conclude that

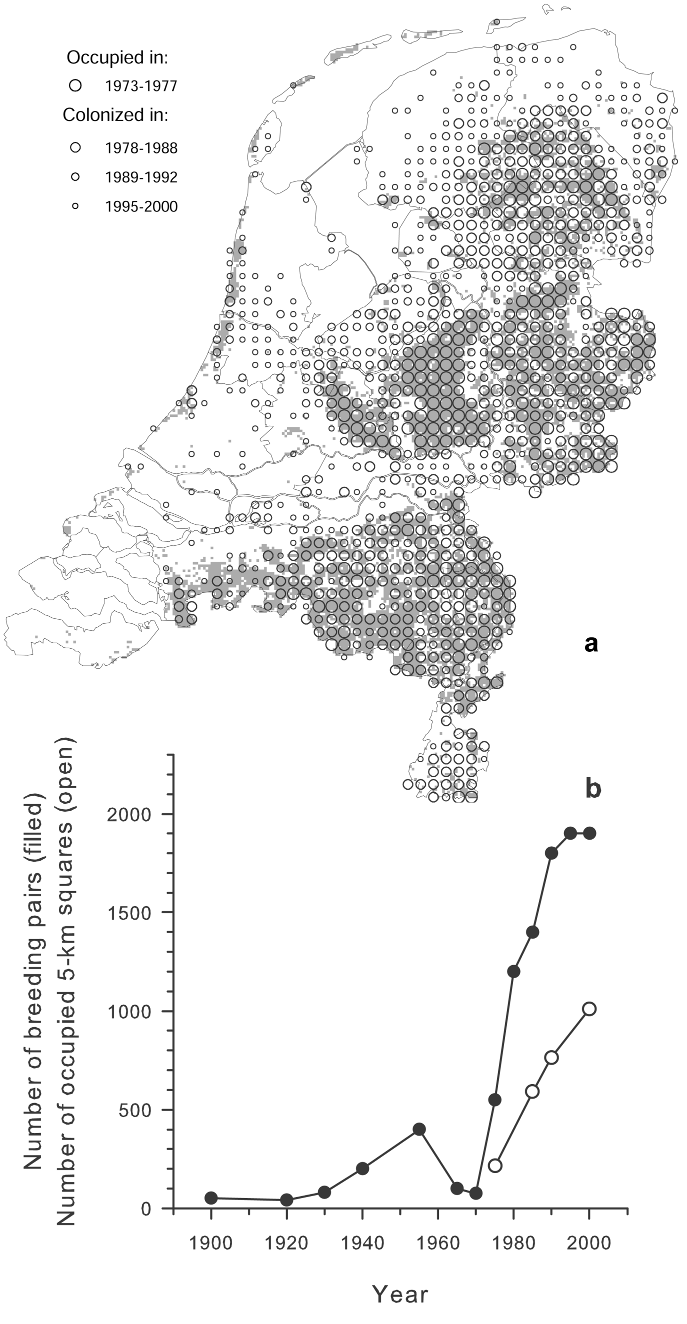

FIGURE 6. Population trend and breeding distribution of the goshawk in The Netherlands (a and b). In (a), distribution is shown as 5-km squares occupied in 1973–1977; smaller symbols show further colonization of 5-km squares in respectively 1978–1988, 1989–1992, and 1995–2000 (Bijlsma 1989, 1993; Bijlsma et al. 2001, Müskens 2002). The distribution of coniferous forest is shaded. Note the marked drop in breeding numbers in the late 1950s and 1960s in (b); the scale and timing of the decline and the subsequent recovery were consistent with an effect of pesticides, probably dieldrin and DDT. Whereas goshawks in the 1970s were largely confined to squares with a high proportion of coniferous forest, the west and northward spread in the 1980s and 1990s involved habitats never before occupied by this species in The Netherlands (a). For further details, see *Case study 1*.

TABLE 3. BREEDING SEASON DIET COMPOSITION OF THE GOSHAWK IN VARIOUS AREAS IN WESTERN, CENTRAL, AND SOUTHERN EUROPE.

Country	Area	Plot size (km²)	Forest area (%)	Study period	Prey items (N)	GD	Ra	Ow	Ga	RC	Wa	GT	PD	Wo	Th	Co	St	OP	Ma	Re	Sources
Portugal	Littoral center	220	70	2001	153	0.0	0.0	0.0	0.0	0.7	0.0	0.0	69.3	2.0	7.8	13.1	0.0	2.0	0.7	4.6	Petronilho and Vingada (2002).[a]
Poland	SW	600	23	1982–1994	1,167	0.6	1.1	2.4	4.6	0.5	0.2	0.2	50.8	4.7	12.0	10.3	3.8	5.0	3.3	0.2	Drazny and Adamski (1996).[a]
Poland	Central	?	71	1982–1993	803	(1.2)	2.0						(50.2)	6.1	7.1	8.9			(2.9)		Olech (1997).[c]
Britain	Kielder Forest	620	81	1973–1996	5,445		4.5		(11.4)				(49.8)			18.0			6.4		Petty et al. (2003a).[c]
Germany	City of Berlin, W	?	?	1982–1986	606	1.8	0.8	0.5	0.0	0.7	0.7	5.4	48.7	5.3	5.4	15.3	9.9	2.3	2.8	0.3	Jacob and Witt (1986).[a]
Germany	City of Hamburg	(3 pairs)	-	1997–1998	306	0.3	0.7	0.0	0.0	0.3	0.7	0.3	43.1	1.0	13.1	24.8	5.9	1.0	8.8	0.0	Rutz (2004).[a, d]
Netherlands	E (sand)	14,110	19	1997–2002	4,653	1.4	2.3	2.2	1.3	0.4	2.3	0.8	42.7	5.1	6.0	21.7	7.1	1.6	5.0	0.2	Bijlsma (1998–2003).[a]
Slovakia	Central	959	54	1991–1997	282	0.7	5.3	2.5	3.9	0.0	0.0	0.0	41.1	6.7	12.4	11.7	0.7	7.1	7.8	0.0	Šotnár (2000).[a]
Germany	City of Cologne	200	?	1989–1996	5,511								40.4		9.9	(26.3)	5.3		(11.4)		Würfels (1994, 1999).[c]
Denmark	Vendsyssel	2,417	8	1977–1997	19,670	0.8	1.3	0.9	(5.0)	0.5	1.5	5.0	(40.0)	0.9	14.0	19.0	3.3		4.0		Nielsen and Drachmann (1999b).[c]
Denmark	Sydjylland	10,700	?	1973–1981	4,472	0.6	1.7	1.7	4.9	1.3	3.1	3.4	37.2	0.8	17.6	13.9		12.6	1.0		Storgård and Birkholm-Clausen (1983).[c]
Poland	Central	110	21	1982–1985	1,054				5.4				(35.4)	(4.7)	(4.8)	7.4	1.9		8.8		Goszczyński and Piłatowski (1986).[b]
Germany	City of Berlin, E	?	?	1999–2001	2,083								34.1	(4.5)	(9.7)	(15.5)	15.9		2.8		Altenkamp and Herold (2001).[b]
Netherlands	N+W (peat, clay)	11,000	4	1997–2002	1,618	8.3	3.0	2.9	1.6	1.2	8.2	1.1	33.4	1.9	9.3	15.0	7.9	1.7	3.8	0.7	Bijlsma (1998–2003).[a]
Germany	N, two plots	-	-	1970–1975	2,845	0.6	2.2	4.4	4.7	0.6	5.7	1.5	32.3	1.1	18.6	9.7	4.9	3.5	3.1	7.1	Looft (1981).[a,e]
Wales		3,250	50	1991–1993	2,230	0.1	1.0	0.6	0.0	0.0	1.2	0.1	30.4	0.3	14.6	36.0	0.4	1.7	13.0	0.6	Toyne (1998).[a,f]
France	Alsace	(19 pairs)	?	1979-1998	727	1.5	2.2		4.5	1.0	0.4	0.4	28.1	4.3		23.0		3.6	12.6		Kayser (1993).[b]
Britain	several plots	-	-	1974–1980	848	0.9	0.8	0.1	33.1	0.4	1.4	0.5	26.3	0.2	5.0	5.8	1.3	0.8	22.8	0.6	Marquiss and Newton (1982).[a]
Austria	Alp foothills	250	?	1990–1998	712	(1.0)			(10.2)				25.7	(1.7)	(24.1)	(8.6)	5.8		(3.6)		Steiner (1998).[b]
Germany	Bayern	6,690	?	1969–1996	13,498	0.6	0.7	5.4	0.8	0.4	0.1	0.2	25.1	1.0	46.5	9.7	1.8	5.7	1.9	0.1	Bezzel et al. (1997b).[a,g]
Belarus	N	800	~35	1973–1994	639	3.9	1.4	1.1	17.4	(0.0)	2.7	(0.0)	23.2	1.8	1.9	31.7		2.3	4.0	8.6	Ivanovsky (1998).[a]
Estonia	mainly N, SE	?	?	1987–1992	988	2.5	1.6	1.1	9.9	0.0	5.0	0.0	19.4	2.1	16.8	27.2	2.7	8.1	2.9	0.7	Lõhmus (1993).[a]
Spain	Granada	(8 pairs)	?	1994	410		0.5	0.5	9.0				19.3	1.7	4.1	20.7			22.0		Padial et al. (1998).[a,h]
Poland	NE	96	63	1989–1997	1,539	0.6	0.6	0.4	4.8	0.1	1.3	1.5	17.5	6.0	10.4	23.7	0.9		5.7		Zawadzka and Zawadzki (1998).[a,i]
Spain	Catalonia	176	≤30	1985–1989	1,636				19.3				(12.8)			13.5			(19.4)		Mañosa (1994).[c]
Italy	Abbruzzi region	318	?	1984–1993	782			1.7					(8.5)	(2.2)	22.4	26.9	0.0		26.2		Penteriani (1997).[b,j]
France	Lorraine	148	35	1965–1966	233	1.7	6.0	0.9	0.9	1.7	0.4	0.4	7.3	6.9	22.7	12.4	26.6	7.7	1.7	2.6	Thiollay (1967).[a]

Notes: This is not an exhaustive list of goshawk diet studies from Europe. In cases where two or more studies described the diet of Goshawks in a certain area, the most recent or the one based on the largest sample size was included. The definition of breeding season varies slightly between studies, and the reader is referred to the original sources for further details. All studies estimated diet composition from pluckings, which had been collected at or near nest sites. Note that this method has been shown to underestimate the contribution of small (Ziesemer 1981) and large prey species (Rutz 2003a). Values in brackets are minimum estimates, as the original source gives only data for the most important species in the taxonomic group (e.g., Blackbird [*Turdus merula*] in case of thrushes), and other species may have been included in the other birds category. A missing entry means that the relevant information could not be extracted from the original source; it does not mean, however, that a certain prey group had zero contribution to total diet. Studies are arranged according to the dominance of pigeons and doves in the diet. Abbreviations for prey groups: GD = grebes, ducks and geese; Ra = raptors; Ow = owls; Ga = galliformes; RC = rails and coots; Wa = waders; GT = gulls and terns; PD = pigeons and doves; Wo = woodpeckers; Th = thrushes; Co = corvids; St = European Starling; OP = other passerines; Ma = mammals; Re = rest.

[a] Complete prey list given in original source.

[b] Only main prey species and groups listed (for details, see original source).

[c] Only major taxonomic groups listed.

TABLE 3. CONTINUED.

[d] A total of 18 unidentified prey items, which had been recorded by radio telemetry, were excluded.
[e] List contains 187 unidentified prey of various sizes.
[f] List contains 12 unidentified prey items.
[g] Sample size reported by authors (N = 13,342) is incorrect.
[h] List contains 52 unidentified birds of various sizes.
[i] List contains 358 unidentified birds of various sizes.
[j] List contains 61 unidentified birds of various sizes.

this resource had indeed been acting as a limiting factor. Because of the obvious practical difficulties, no such study has been carried out with goshawks. However, sometimes humans unwittingly provide goshawks with extra food in the form of managed game, domestic poultry, or racing pigeons. These cases are not properly controlled and replicated experiments, so care must be taken in interpreting any associated response in goshawk numbers (or the lack of it)—the increase in food supply may be coupled with an increase in killing of hawks by humans (Kenward 2000, Nielsen 2003).

If food supplies limit goshawk numbers we expect to find two major correlations: (1) at the regional scale, differences in goshawk density match differences in food supplies (spatial correlation), and (2) at the level of the local population, breeding numbers track changes in local food supplies over time (temporal correlation). Before investigating the published information for concordance with these predictions, however, we need to understand the general feeding ecology of the species.

The goshawk is a versatile predator, focusing on prey species which are abundant, profitable, and sufficiently vulnerable to an attack (Dietrich 1982, Kenward 1996, Tornberg 1997, Bijlsma 1998). There are marked regional differences in goshawk diet across Europe, as illustrated by the selection of studies presented in Table 3.

A significant functional response to temporal variation in prey abundance has been demonstrated for populations in Fennoscandia (Kenward 1977, 1986; Kenward et al. 1981a, Wikman and Lindén 1981, Lindén and Wikman 1983, Tornberg and Sulkava 1991, Selås and Steel 1998, Tornberg 2001, but see Widén et al. 1987), but comparable data for goshawks in western, central, and southern Europe are scarce (Mañosa 1994; Olech 1997; Rutz and Bijlsma, in press). However, in cases where dietary studies were either carried out for a long period of time (Bezzel et al. 1997b, Nielsen and Drachmann 1999b, Nielsen 2003) or replicated in the same area after several decades (Tinbergen 1936, Pielowski 1961, Opdam et al. 1977, Brüll 1984, Haerder in Holzapfel et al. 1984; Bijlsma 1993, 1998–2003; Olech 1997; C. Rutz et al., unpubl. data) the observed changes in goshawk diet composition correlated well with obvious changes in the availability of prey species in the environment.

The ability of the goshawk to adjust its feeding ecology in response to changes in the availability of different prey species is further illustrated by marked dietary shifts in the course of the breeding season (Opdam et al. 1977, Brüll 1984, Bijlsma 1993, Mañosa 1994, Toyne 1998). We note, however, that it remains to be established whether predation by goshawks is indeed opportunistic, according to the technical definition of optimal foraging theory (Stephens and Krebs 1986). First results (Dietrich and Ellenberg 1981, Dietrich 1982, Ziesemer 1983, Tornberg 1997) suggest that prey vulnerability is an important determinant of goshawk diet composition (*cf.* Götmark and Post 1996).

It is inherently difficult to test for a spatial correlation between goshawk density and food supplies, because local populations differ markedly in their feeding ecology, and data on prey abundance and/or proportional availability have rarely been collected in the course of goshawk diet studies. These problems can be circumvented by using diet composition as a proxy measure of environmental prey availability (Rutz 2005b), and a cross-study meta-analysis employing this approach has recently been conducted (Rutz 2005b, C. Rutz et al., unpubl. data). Here, we will focus on material from just two studies, which each related goshawk breeding density in several sub-populations to an index of local land productivity (Bühler and Oggier 1987, Weber 2001). We re-analyzed the data sets provided in the original publications by means of robust GLMs (normal error, identity link function, controlled for plot size and forest availability in plot) and found no significant relationship for the German sample (N = 18 local populations, analysis on square-root-transformed data: $F_{1,14} = 0.92$, $P = 0.355$), but a significant negative association for the Swiss sample (nine local populations, analysis on $\log_{10}$-transformed data: $F_{1,5} = 7.01$, $P = 0.046$). It is questionable, however, whether the two productivity indices used (yield of winter corn and subjective rank scale, respectively) described goshawk prey abundance adequately. Areas in Sweden and Germany with the most abundant free-living Ring-necked Pheasants (*Phasianus colchicus*) were most attractive to goshawks, leading to higher winter densities than in a control area (Kenward 1986, *cf.* Mrlík and Koubek 1992), but this did not subsequently translate into differences in goshawk breeding densities. However, abundance of European rabbits (*Oryctolagus cuniculus*) in one area reduced dispersal tendencies and was associated with increased breeding density (Kenward et al. 1993a).

Temporal correlations between goshawk density and prey abundance have rarely been studied. In a long-term study (25 yr) in Germany, population growth rate did not vary significantly with food supplies, but the authors admitted that the indices used to describe food abundance were crude and probably biased (Ziesemer 1983, Krüger and Lindström 2001). Krüger and Lindström (2001) did not test the interaction between food supply and population density in the previous year, because they excluded a priori the possibility of a numerical response. In fact, even in Fennoscandia, where hawks primarily prey upon several species of woodland grouse (Tornberg et al., *this volume*), which show cyclic fluctuations in numbers, goshawk densities have rarely been found to correlate with prey abundance (Selås 1997a, 1998a; but see Lindén and Wikman 1983, Tornberg 2001, Ranta et al. 2003). In Denmark, a strong increase in released Ring-necked Pheasants since the early 1990s was not correlated with local goshawk trends (Nielsen 2003), but a numerical response might have been masked by increased hunting pressure on hawks (Mikkelsen 1986). Using data presented in Goszczyński (1997, 2001), we did not find a correlation between average number of prey found in goshawk nests during control visits and the number of successful broods in the study area (N = 6 yr, Spearman rank correlation, $r_s = 0.41$, $P = 0.419$).

Goshawk breeding density can remain stable after a crash in prey populations, providing that alternative prey are available (Ziesemer 1983, Mañosa 1994, Olech 1997). If, however, populations of several or all important prey species crash simultaneously, goshawk breeding density may decline. This is illustrated by *Case study 2*, which is the first attempt to quantify the effect of temporal changes in food supply on breeding density and demographic key parameters in western European goshawks. Recent survey work shows that European farmland bird populations are in precipitous decline (Pain and Pienkowski 1997, Newton 1998, Krebs et al. 1999, Donald et al. 2001), but, at present no evidence suggests that this shortage of food supply affects goshawk numbers on a continental scale. This is not surprising as most of the affected farmland bird species are small-bodied passerines that play only a minor role in goshawk diets (Table 3); in fact, some favored goshawk prey species (Woodpigeons [*Columba palumbus*] and corvids) show increasing trends in farmland-dominated landscapes, at least in parts of Europe.

Apparently, goshawks easily switch to an alternative prey if one of their principal prey species becomes scarce. Hence, scope for density limitation seems limited. So far, however, we have only been concerned with breeding season food supply. The availability of food during the winter may also limit breeding numbers (Newton 1998), if it negatively affects the survival of potential breeders or their physiological condition. In farmland-dominated areas in western Europe, breeding season and winter diets show similar species composition (Opdam et al. 1977, Ziesemer 1983, Brüll 1984, Nielsen 2003), suggesting that winter food does not form a significant bottleneck for the populations concerned. In more natural areas in central and eastern Europe, however, the situation may be quite different. In east Poland, for example, goshawks mainly depend on thrushes, woodpeckers, and Jays (*Garrulus glandarius*) during the breeding season, and face rapid depletion of food supplies when thrushes emigrate in autumn (Jędrzejewska and Jędrzejewski 1998, van Manen 2004). Poor food supply during winter and the pre-laying stage probably causes low goshawk breeding densities in this region (van Manen 2004) despite high food abundance during summer (Wesołowski et al. 2003).

Finally, circumstantial evidence demonstrates that various aspects of goshawk biology vary with food supply in a way consistent with theoretical expectations. This is probably best illustrated by studies that compare urban and rural-breeding goshawk populations, which differ significantly in their access to food resources; we will describe these findings in detail later. Much of the other work has been conducted in Scandinavia, but in this case we consider it reasonable to generalize the conclusions to hawks, living in other parts of Europe: (1) home-range size is a decreasing function of food availability (Kenward 1982, 1996; Ziesemer 1983), (2) daily activity patterns are related to hunting success (Widén 1981, 1984), (3) juveniles, which have been raised under good food conditions, disperse later (Kenward et al. 1993a, b) and are more likely to return to the vicinity of their natal nest site (Byholm et al. 2003), (4) productivity increases in relation to food availability (Lindén and Wikman 1980, Tornberg 2001, Byholm et al. 2002b, Ranta et al. 2003), and (5) during winter, juvenile hawks congregate in areas of high food supply (Kenward et al. 1981a).

Case study 2: The Netherlands—the effect of food shortage

In *Case study 1*, we described changes in goshawk breeding numbers in The Netherlands during the 20th century. Despite a continuing increase in geographic range (Fig. 6a), numbers stabilized from about the early 1990s (Fig. 6b). For example, between 1990 and 2000 the number of occupied 5-km squares increased by 30%, but breeding numbers remained stable at 1,900–2,000 pairs. This discrepancy can partly be explained by a substantial reduction in number and availability of main prey species in core breeding areas of goshawks in the last two decades of the 20th century.

The impact of food supply on density and reproductive output has been investigated in the central Netherlands (Bijlsma 2003, unpubl. data). The 20 km² large plot of Planken Wambuis (52°03’N, 5°48’E) is typical of coniferous forests planted on poor soil in the eastern Netherlands in the late 19th and early 20th centuries. Every 5 yr, the breeding bird fauna has been surveyed, using a low-intensity variety of the combined mapping method (Tomiałojć 1980). The recorded densities in large sampling plots are a relative measure of abundance, and useful in assessing changes in breeding bird composition and numbers. Annually since 1973, all nests of raptors, including goshawks, have been located and checked to determine clutch and brood size, and weigh and measure nestlings; molted feathers, for individual recognition, and prey remains were also routinely collected.

Avian biomass in spring and early summer declined by 80% between 1975 and 2000, especially in the weight categories of 51–250 g (pigeons, doves, thrushes, corvids, European Starling [*Sturnus vulgaris*]) and 251–500 g (pigeons), i.e. the major prey base of goshawks (Fig. 7a). Racing pigeons, weighing 250–300 g and an important male goshawk prey during the breeding season, declined dramatically, as demonstrated by data from regular counts of homing pigeons. And finally, the rabbit population crashed by >95% between the mid-1970s and early 2000s as a result of severe winters, the outbreak of viral hemorrhagic disease in 1990–1991, and dominance of *Deschampsia flexuosa* in the undergrowth caused by increased nitrogen deposition (Fig. 7a; Heij and Schneider 1991, Bijlsma 2004a).

In the early 1970s, the local goshawk population steeply increased, a recovery from the pesticide-induced decline in the 1960s, reaching stable numbers (six–seven pairs) in 1976–1986, then declining to three–five pairs in the 1990s and early 2000s (Fig. 7b). Several lines of evidence suggested that, over the years, floaters also disappeared from the area. In recent years, lost breeders have not been replaced, and territories remain vacant.

The declines in numbers of breeding pairs and non-breeders as well as in reproductive output closely mirror the changes in prey availability. Although circumstantial, this suggests a limiting effect of food supply, while other extrinsic factors apparently remained unchanged. The overriding impact of food supply is also visible in changes in predatory behavior, with increasing goshawk predation on raptors, owls and corvids, resulting in the local demise of Eurasian Kestrel, Eurasian Hobby (*Falco subbuteo*), Eurasian Sparrowhawk, Long-eared Owl (*Asio otus*),

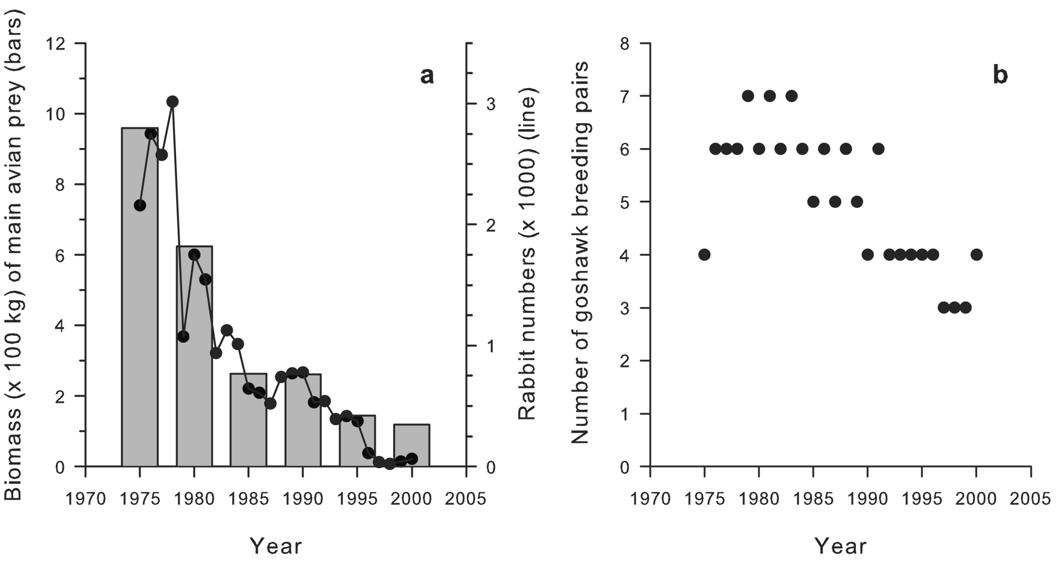

FIGURE 7. The effect of food shortage on goshawks at Planken Wambuis (20 km²), central Netherlands, 1975–2000. (a) Collapse of goshawk prey populations in the study area. Bars show estimated total biomass of birds in the body size category 51–500 g in 5-yr periods; figures were calculated on the basis of standardized breeding bird counts (combined mapping) and number of pairs in spring (×2 to include both pair members, but excluding young); line is local rabbit numbers. (b) Change in number of goshawk breeding pairs. For further details, see *Case study 2*.

and the increased frequency with which unprofitable prey—larks, tits, and finches—are captured. A full report of this study has been presented elsewhere (Rutz and Bijlsma, in press).

KILLING BY HUMANS

Because goshawks are predators of medium-sized mammals and birds, racing pigeons, and domestic poultry, they have a long history of being controlled. Moreover, their populations have also been harvested to provide captive birds for falconry—initially for food but subsequently for sport. The extensive literature describes past persecution and harvest but impact has rarely been quantified, mainly because goshawk populations were not monitored with precision during the periods when such activities were at their peak. Population monitoring is relatively recent, commencing broad scale from the 1970s following the large reduction in raptor populations in the 1950s and 1960s which was associated with widespread environmental pollution. Human persecution of raptors in Europe has been reviewed by Bijleveld (1974) and Newton (1979a, b). The case of the goshawk is probably best illustrated in a historical context, by comparing time periods with different levels of killing.

The killing of raptors was encouraged from the 16th century onward, with the payment of bounties to reduce predation of domestic stock. The numbers of goshawks killed must have been large, but there is no documented impact on wild populations, and breeding populations remained extant across Europe with no recorded national extinctions at that time. In the 19th century, game preservation became important as pheasant game shooting was enhanced with reared birds. Game preservers were employed to kill predators, including goshawks, which can be a problem particularly at pheasant release sites (Kenward 1977, Nielsen 2003). Moreover during the 19th century, raptors were commonly viewed as potential pests, so large numbers were killed (Braaksma et al. 1959, Richmond 1959, Bijleveld 1974), and it was not until some populations were clearly in decline, even to extinction in some places, that legal protection was initiated.

Goshawk populations were resilient where large areas of forest remained because game preservation was less intensive within forests and breeding production was sufficient to buffer the losses due to persecution. Recent work from Scandinavia shows that goshawk populations can, under some circumstances, withstand considerable levels of killing. For example, it was estimated from the recoveries of banded birds that 14% of the Fennoscandian goshawk population was killed annually by man (Haukioja and Haukioja 1970), with no apparent decline in the breeding population. Calculations by Kenward et al. (1991), based upon Swedish banding returns and supplemented by radio-telemetry data, suggest that a loss to persecution of up to 35% of young birds might be sustained without leading to population decline. Birds in their first year are more likely to be killed than are older birds, so persecution falls heaviest on non-breeders. We note, however, that the situation in Fennoscandia contrasts markedly with that in western and central Europe, where breeders and their broods have been the main targets. Such losses are likely to be additive to other sources of mortality, and hence have greater potential impact on breeding numbers than the destruction of non-breeders.

Irrespective of general population resilience, goshawks did decline at the end of the 19th century, mainly in countries with poor forest cover such as Denmark (Jørgensen 1989) and Britain (Marquiss and Newton 1982). Where forests are fragmented, goshawks are particularly vulnerable as few breeding pairs are remote from intensive human persecution. Goshawks can have large overlapping home ranges, both during and outside the breeding season (Kenward et al. 1981a, Kenward and Walls 1994); areas of food abundance, such as pheasant release pens, attract many individuals (Kenward et al. 1991, Nielsen 2003) so that a substantial proportion of the population can be at risk.

From the mid-20th century, at least partially in response to the pollutant-associated steep declines of the 1960s, goshawks became legally protected in many countries, and populations increased in a few areas. In conservation terms, the species is now considered secure though sufficiently vulnerable to be listed in the Bern Convention as a species requiring international coordination for its conservation (Tucker and Heath 1994). At present the goshawk has legal protection in the breeding season across Europe, though birds can be legally killed in some countries outside of the breeding season (Finland) or in special circumstances where they are considered damaging to game (Hungary, Czech Republic, some regions of Germany, and Sweden) or wildlife conservation interest (in several parts of Germany, after the re-introduction of Black Grouse [*Tetrao tetrix*]; Dobler and Siedle 1993, 1994; Busche and Looft 2003).

Despite protection, illegal killing continues throughout Europe, as documented by numerous anecdotal reports in the literature. We now focus on results from long-term studies that provide data sets sufficiently robust to assess the effects of past persecution on local populations. Human persecution has indeed been shown to negatively affect demographics and density of local breeding populations. Several studies demonstrated how persistent killing of adult birds at nests changed the age-composition of the breeding population (Link 1986, Bijlsma 1993, Bezzel et al. 1997a, Olech 1998, Rust and Mischler 2001), ultimately leading to reduced population productivity through age-dependent reproduction (Drachmann 2003, Risch et al. 2004). For populations in the northern Netherlands (Bijlsma 1993) and in Denmark (Drachmann and Nielsen 2002), it was possible to establish the complete causal chain where killing by humans (ultimate level) leads to demographic effects (proximate level) which in turn leads to changes in breeding density (*cf.* Rust and Mischler 2001). The aim of the Danish study was to identify the causes of a pronounced decline in breeding numbers between 1994–2000 in the Vendsyssel area (Drachmann and Nielsen 2002). In this period, illegal killing significantly reduced fecundity and survival of 1- and 2-yr-old females, which in turn appeared to reduce population growth rate (*cf.* Noer and Secher 1990). In a long-term study in northern Germany, a marked drop in breeding numbers coincided with a change in hunting law, legalizing the killing of goshawks; after legal protection was re-established, numbers increased again to their previous level (Looft 2000). Further examples of correlations between the intensity of hunting pressure and goshawk population trend are given in Bijlsma (1991a).

In conclusion, there is evidence that killing by humans can directly limit goshawk breeding density, but nowadays, it seems rarely substantial enough to cause widespread decline (Bijlsma 1991a). For any population, killing of adult territory holders during the breeding season has greater significance than the destruction of broods, or of immature birds during winter (Newton 1998). Even if direct effects seem generally negligible, moderate culling could have a substantial indirect impact by continuing to constrain goshawks in their choice of nesting sites. In many parts of Europe, remote habitats with low degrees of human activity are apparently preferred, such as in large mature forest—a limited resource in modern, human-altered landscapes. We explore this idea further in a later section.

Case study 3: Great Britain—the effect of killing by humans

In Britain, the goshawk population declined following reductions in forest, which fell to <5% of land cover by 1900 (Petty 1996a). Goshawks were widely persecuted for game preservation and were already rare by the early 19th century. Amongst the last records were nests robbed of eggs or young, and possibly the last breeding females were those killed in 1864 and 1893. There was sporadic breeding in southwest England from the 1920s but these birds were persecuted and did not persist (Meinertzhagen 1950).

During the 1960s and 1970s, goshawks started breeding in at least 13 widely separated regions of Britain, and five breeding populations subsequently established (Marquiss and Newton 1982). They probably all arose from birds imported from central Europe in the 1960s and from Finland in the 1970s, which had escaped from captivity or had been deliberately released. Kenward et al. (1981b) estimated that in the period 1970–1980, an average of 20 goshawks per year escaped from captivity, and a further 30–40 were released. These birds clearly had a major impact on the distribution of colonists and their establishment, because the number of new areas and the overall population trajectory were proportionately enhanced following years of high importation (Marquiss 1981).

By 1980, about 60 pairs probably existed but then importation was restricted and subsequent population growth varied according to annual productivity and deliberate killing (Marquiss et al. 2003). In some areas, breeding production was reduced by half due to the destruction of breeders or the removal of their eggs and young (Marquiss and Newton 1982). The impact of the illegal killing away from breeding sites was difficult to quantify but a potential effect was inferred from a comparison of population growth in two regions, Scottish borders where goshawks lived in a large area of state-owned forest remote from game interests, compared with northeast Scotland where many of the birds used privately owned woodlands close to pheasant rearing sites (Marquiss et al. 2003). In both areas, breeding performance was little affected by the killing, and production was similarly good at 2.45 young per breeding pair. However in the Northeast, goshawks were said to be a problem at pheasant release sites (Harradine et al. 1997) with ample evidence of birds shot and trapped.

The population growth in the Northeast was less than half of that in the Borders. Three types of evidence suggested that lack of potential recruits constrained the growth of the breeding population in the Northeast. Firstly, on average only 70% of breeding sites were occupied each year compared with virtually complete occupancy each year in the Borders. Secondly, breeding numbers increased or decreased from one year to the next correlated with the production of fledged young 2 yr earlier. Finally, the birds bred in the Northeast at a younger mean age. In the state forest of the Borders area, no birds were found breeding in their first year of life, whereas in the Northeast yearling birds comprised 13% of breeding females. The long-term consequence of poor population growth was pronounced. The two populations started simultaneously in the early 1970s, but by 1996, the Borders held 87 pairs compared with 17 in the Northeast.

The number of breeding pairs has increased slowly but steadily in Britain, and they are now widespread, though still absent from Ireland and the far North of Scotland (Marquiss 1993). By the mid-1990s, the population was possibly about 400 pairs (Petty 1996a), and has increased since then. Nevertheless, illegal killing is common and widespread, accounting for at least 42% of banded bird recoveries (Petty 2002). Some goshawks are poisoned or shot, and many are caught in cage traps set with live decoys for corvids. These traps are operated legally, providing that non-target species are released, but this does not always happen (Dick and Stronach 1999).

However, a substantial decline in the number of professional gamekeepers has occurred in Britain (Tapper 1992), and attitudes have changed at least in southern Britain (Kenward 2004). Thus, although some gamekeepers kill individual raptors that cause problems at pheasant pens, they no longer persecute them in the sense of seeking local eradication. The more enlightened approach has enabled rapid recolonization by Common Buzzards (*Buteo buteo*), but unfortunately, the much larger home ranges and greater predatory competence of goshawks makes them more vulnerable at pheasant pens (Kenward et al. 2000, 2001). However, secluded nesting habitat for goshawks has increased substantially as conifer plantations from the 1960s and 1970s have matured. State-owned forest, in particular, harbors relatively unmolested breeding goshawk populations, whose production fuels further increase despite killing by humans elsewhere.

ENVIRONMENTAL POLLUTION

The evidence for pollution effects on goshawks is largely indirect and circumstantial. They did not experience the sudden widespread regional extinction suffered by other bird-eating raptors (Hickey 1969), so investigative research was limited. In retrospect, had goshawks been severely affected in Europe, we would have expected four sorts of evidence (Newton 1979b): (1) a steep population decline in the 1960s, followed by slow increase as pesticide levels fell from the mid-1970s, (2) impaired breeding with many eggs broken, thin-shelled or failing to hatch, and small brood sizes in successful nests, (3) elevated levels of pesticide residues in unhatched eggs and in the tissues of full-grown birds, and (4) a spatial correspondence with these symptoms occurring in areas of greatest pesticide use.

Widespread population declines in goshawks happened in parts of Europe (Bijlsma 1991a), including a precipitous decline in The Netherlands (*Case study 1*). The scale and timing of that decline and subsequent recovery were consistent with an effect of pesticides, probably dieldrin and DDT (Thissen et al. 1981). Bijleveld (1974) reported cases of impaired breeding with failure of eggs to hatch in four of 20 clutches, but shell thinning was not pronounced. Samples from northwest Europe showed shells were 8% thinner than pre-pesticide levels (Anderson and Hickey 1974, Nygård 1991), which is insufficient to cause widespread egg breakage (Newton 1979a), and this apparently did not happen (G. Müskens, pers. comm.). In Germany, some shell thinning occurred and its extent was correlated with the concentrations of DDE in the egg contents (Conrad 1977, 1981). In Belgium, shells were at their thinnest (12.8% of pre-pesticide shell thickness) in the 1950s and less so (10%) in the 1960s (Joiris and Delbeke 1985).

In a few instances, the levels of pesticide residues in eggs and body tissues were sufficient to cause death (Koeman and van Genderen 1965), but median values in eggs from Germany, Britain, Norway, and Bohemia were usually much lower than in Eurasian Sparrowhawks from the same region (Bednarek et al. 1975, Conrad 1978, Marquiss and Newton 1982, Frøslie et al. 1986, Diviš 1990). The samples of goshawk material were small, pesticide levels often low, and the residues from DDT and DDE, the cyclodienes (HEOD), PCBs, and mercury were often correlated (Delbeke et al. 1984, Frøslie et al. 1986), so it was difficult to attribute effects to specific pollutants. However, the precipitous population decline in The Netherlands in the near-absence of egg breakage suggests the main causal factor was cyclodienes rather than DDT (Newton 1988b).

Lastly, the symptoms of pesticide poisoning were most apparent in regions of intense agriculture, such as The Netherlands, Belgium and Germany (Ellenberg 1981). However, because the monitoring of goshawk populations and breeding performance is so labor-intensive and goshawk populations are fairly tolerant of additive mortality (Kenward et al. 1991), it is likely that symptoms might have been overlooked elsewhere. Moreover, poor breeding success and some population decline can also be symptomatic of deliberate killing which occurred simultaneously with organochlorine use in some regions (Bednarek et al. 1975, Link 1981, Terrasse 1969, van Lent 2004).

Taken together, this evidence was sufficient to suggest that goshawks were affected by organochlorine pesticide pollution in Europe, though major population decline probably occurred only in regions of heavy application. Where affected, goshawks probably acquired most of their pollutant burden through their consumption of pigeons, a major food in agricultural landscapes (Table 3). Pigeons feed on newly-sown grain which, in the late 1950s and 1960s, was usually dressed with aldrin or dieldrin to protect it against insect attack. Populations remote from such regions seem to have been little affected, presumably because most goshawks, and much of their herbivorous prey (non-grain eating species accumulated only low levels of organochlorines) are relatively sedentary (Bühler and Oggier 1987, Mañosa et al. 2003). This, together with the fact that goshawks are widely distributed, means that they can be used as model bioindicator species (Ellenberg and Dietrich 1981). Such work continues with particular emphasis on PCBs (Herzke et al. 2002, Wiesmüller et al. 2002, Kenntner et al. 2003, Mañosa et al. 2003, Scharenberg and Looft 2004), although to date detrimental effects of these chemicals on goshawk populations are not established.

INTERSPECIFIC COMPETITION AND PREDATION

The goshawk is a powerful raptor, and throughout its European breeding range, it belongs to the upper segment of regional raptor guilds (Glutz von Blotzheim et al. 1971, Cramp and Simmons 1980). Goshawks seem unlikely to suffer much from interference competition, as most sympatric large raptors differ markedly in their habitat preferences and feeding ecology. The notable exception is the Eurasian Eagle-Owl.

Some competition for avian prey might be expected with the smaller Eurasian Sparrowhawk (van Beusekom 1972, Opdam 1975, Brüll 1984, Bijlsma 1993, Overskaug et al. 2000). Moreover, in large parts of Europe, goshawks share their preferred nesting habitat with four similar-sized species—Common Buzzard, European Honey-buzzard (*Pernis apivorus*), Red Kite (*Milvus milvus*), and Black Kite (*Milvus migrans*) (Kostrzewa 1987a, b; Gamauf 1988a; Dobler 1990; Kostrzewa 1996; Selås 1997b; Krüger 2002a, b; Weber 2001), and goshawks may compete with them for prime nesting territories. However, little doubt exists that competition within this species complex is highly asymmetric in favor of the goshawk. Goshawks have been shown to regularly kill adults as well as nestlings of the aforementioned species (Table 3; Uttendörfer 1952), take over their territories (Newton 1986, Kostrzewa 1991, Fischer 1995, Risch et al. 1996), and defend successfully their own nest sites against interspecific intruders (Kostrzewa 1991, Fischer 1995). Cases where goshawks fall victim to members of the other species are exceptional (Uttendörfer 1952, Krüger 2002b).

It is not surprising therefore that the few studies explicitly addressing the question of interspecific competition between goshawks and other raptor species, assumed a priori that the goshawk is dominant over its sympatric competitors (Kostrzewa 1991, Krüger 2002a; but see Dobler 1990). Indeed, goshawks were found to affect nest dispersion (Newton 1986, Kostrzewa 1987a, Gamauf 1988a, Toyne 1994) and density (Risch et al. 1996; but see Gedeon 1994) in various co-existing raptors, and to reduce their nest success and/or productivity (Kostrzewa 1991, Krüger 2002b, see also Petty et al. 2003a, Bijlsma 2004b). Only two studies took the opposite perspective and investigated whether goshawks themselves, despite their apparent dominance, suffer from the presence of another species. Dobler (1990) found no effect of the distance to the next Red Kite nest site on goshawk productivity (OFG). Likewise, Kostrzewa (1987b) observed no impact of Common Buzzards or Honey Buzzards on patterns of nest occupancy in goshawk. Stubbe (quoted in Gedeon 1994) found a significant increase in Red Kite density coincident with a drop in goshawk numbers, but this association on its own is insufficient evidence of interspecific competition.

In some parts of The Netherlands, goshawks have to compete for nests with the highly territorial Egyptian Goose (*Alopochen aegyptiacus*). Absent in the early 1970s, this species increased dramatically during the past two decades, reaching >5,000 pairs by 2000 (Lensink 2002). Egyptian Geese readily take over goshawk and Common Buzzard nests, whether unused or occupied. In an area of 45 km² in the northern Netherlands, all 24 nests of Egyptian Geese in 2002 were thus situated, and egg dumping took place in two of ten occupied goshawk nests in 2003 (R. G. Bijlsma, unpubl. data). So far, the geese have had no obvious impact on goshawk breeding numbers, but they presumably influence the raptor's nest-site choice in some regions.

Goshawks may also compete with mammalian predators where important food resources are shared. This is the case in southern Norway, where the red fox (*Vulpes vulpes*) seems to depress goshawk breeding numbers by limiting grouse abundance (Selås 1998a). Similar effects of resource exploitation could exist in western and central Europe, as suggested for the dunes in the western Netherlands (Koning and Baeyens 1990). Of course, extensive hunting of game by humans could act in the same way, depleting food supplies to a level where goshawks show a numerical response. This has not yet been investigated, probably because researchers have traditionally focused on the opposite effect, i.e., the potential impact of goshawks on game populations (REGHAB 2002).

The Eurasian Eagle-Owl is the largest owl species in the world with adult birds in western and northern Europe weighing about 2–3 kg (Mikkola 1983). Its breeding range in Europe largely overlaps with that of the goshawk (Cramp and Simmons 1980). Occasionally, eagle-owls kill other large raptors, including goshawks (Mikkola 1983, Brüll 1984, Tella and Mañosa 1993, Serrano 2000, Busche et al. 2004). Raptors typically make up about 5% of the diet of eagle-owls (Mikkola 1983, Penteriani 1996), but values as high as 21% have been recorded (Grünkorn 2000). For a goshawk study population in northeast Spain, Tella and Mañosa (1993) estimated that about 9% of all successful broods (N = 44) were affected by eagle-owl predation. However, predation on nestlings by eagle-owls has probably little effect on goshawk breeding numbers, because these losses are not necessarily additive to other sources of mortality. The same holds true for predation of nestlings or eggs by any other predator, e.g., pine marten (*Martes martes*; Sperber 1970, Möckel and Günther 1987). Losses of adult hawks are theoretically more relevant, but seem to occur too infrequently to have a significant impact on stable breeding populations at capacity level.

Of greater importance is the fact that eagle-owls compete with goshawks for nest sites in areas where suitable cliff ledges are scarce. In such habitats, eagle-owls may breed on the ground, but they seem to prefer tree nests built by diurnal raptor species, especially Common Buzzards and goshawks (Grünkorn 2000; C. Rutz et al., unpubl. data). In fact, evidence is accumulating that the large-scale reintroduction of the eagle-owl into parts of northern Germany, which is virtually cliff-free, had a substantial effect on the density and productivity of several local goshawk populations (Busche et al. 2004, C. Rutz et al., unpubl. data). Similar impacts of eagle-owls on Black Kites have been documented in the Italian Alps (Sergio et al. 2003). Following extensive conservation measures for about 20 yr, eagle-owls are thriving in Germany (Mädlow and Mayr 1996, Berndt et al. 2002, Dalbeck 2003) and elsewhere in Europe (Penteriani 1996, Mebs and Scherzinger 2000); some recovering populations have increased well beyond previous densities, and are now entering hitherto unoccupied areas (Doucet 1989a, Berndt et al. 2002, Wassink 2003). Competition with other diurnal raptors appears to have little effect on goshawk numbers, but as eagle-owls spread, they might well reduce sympatric goshawk populations.

WEATHER CONDITIONS

Potential weather effects on goshawk population dynamics were investigated by Krüger and Lindström (2001), using data from 25-yr population monitoring in eastern Westphalia, Germany. Per capita growth rate of their study population was best explained by a model including the variables annual mean habitat quality, weather during nestling rearing, autumn weather, and density which explained 63% of the variance. In particular, population growth was reduced in association with more rainfall during nestling rearing and in autumn, but increased with higher temperatures during these periods (especially in July and August). Although nest-site quality appeared to be the principal factor in shaping population dynamics, its effect was significantly modified by weather conditions. It is unclear whether this finding represents a direct influence of weather on goshawks or impacts of weather on the productivity of prey.

Being large, goshawks can withstand several days of fasting (Kenward et al. 1981a, Marcström and Kenward 1981a) which must help them survive through inclement weather that would kill smaller birds. In the harsh environment of Fennoscandia, however, severe weather conditions during winter have been shown to cause substantial losses among juvenile and adult goshawks (Sulkava 1964, Sunde 2002), probably through food shortage. To our knowledge, band recovery data from western and central Europe have not yet been examined for the potential effects of winter weather on adult mortality and subsequent breeding numbers. Pooling recovery data across years did not reveal a pronounced mortality peak during the winter months (Bijlsma 1993, Kostrzewa and Speer 2001).

Kostrzewa and Kostrzewa (1991) failed to find relationships between winter weather and breeding density or the proportion of pairs laying in the following season, but see Huhtala and Sulkava (1981). In The Netherlands, the severity of the preceding winter affected mean laying date, but had no obvious impact on clutch size or nest success (Bijlsma 1993). Goshawk mortality might be higher in particularly severe winters but it seems unlikely that winter weather is an annual bottleneck for populations in Europe's temperate regions. In contrast to their Scandinavian counterparts, goshawks in western and central Europe do not rely on the availability of a few prey species and can more easily switch to alternative prey as necessary. This fundamental difference in feeding ecology and hence, vulnerability to winter food shortage is reflected in differing migratory patterns—goshawks in Fennoscandia are partial migrants, whereas those in western and central Europe are sedentary (Glutz von Blotzheim et al. 1971, Cramp and Simmons 1980).

In a German area, heavy rainfall in the pre-laying period had no effect on the density of territorial pairs but appeared to influence the proportion of territorial pairs that laid eggs (Kostrzewa and Kostrzewa 1990 [MT]; see also Bezzel et al. 1997a). Favorable weather conditions in March are associated with early egg laying (Looft 1981, Bijlsma 1993, Drachmann and Nielsen 2002; V. Looft and M. Risch, unpubl. data), which in turn could positively affect productivity (Huhtala and Sulkava 1981, Bijlsma 1993, Penteriani 1997 [OFG], Drachmann and Nielsen 2002; V. Looft and M. Risch, unpubl. data; C. Rutz, unpubl. data), assuming a causal relationship between the two factors (Meijer 1988). In some cases, a direct correlation between rainfall and temperature in spring and reproductive performance of goshawk pairs has been found (Kostrzewa and Kostrzewa 1990 [OFG, MT], Bijlsma 1993, Penteriani 1997 [OFG, MT], Kostrzewa et al. 2000 [OFG, MT], Drachmann and Nielsen 2002; but see Goszczyński 2001, Altenkamp 2002). Dobler (1991) reported an effect of elevation on breeding density and laying date (OFG) and argued that elevation is most probably correlated with weather parameters, such as average temperature and precipitation (*cf.* Bühler and Oggier 1987).

Some anecdotal reports show that prolonged periods of rain or low temperatures can cause mortality among goshawk nestlings (Looft 1981, Link 1986, Anonymous 1990, Kostrzewa and Kostrzewa 1990), but the effects of such losses on population trends are likely to be small or non-existent.

The impact of a catastrophic weather event, a gale, on local goshawk populations was investigated in northeastern Switzerland and northern France (Schlosser 2000, Penteriani et al. 2002b). Despite the windstorm's devastating effect on forest-stand structure, no differences in subsequent breeding density, nest-stand choice, and productivity were found (Penteriani et al. 2002b [OFG]), suggesting a considerable tolerance of the species to sudden habitat changes caused by such drastic weather events—but see Kos (1980) and Bezzel et al. (1997a) for the possible impact of clear-felling of large forest tracts by humans.

It is difficult to interpret the available data on potential effects of weather factors on goshawk populations, because the topic does not lend itself to experimentation, and observational studies are often statistically compromised: some studies involved multiple-testing without correction of P-values, and most had insufficient data to control for confounding variables or for non-independence of data points. Weather conditions may account for some of the year-to-year variation in density (Newton 1986), probably acting through an effect on spring food supplies, but they do not generally seem to limit goshawk breeding numbers in temperate Europe.

PARASITES

To our knowledge, large-scale reductions in goshawk numbers due to epizootics have not been documented. Goshawks are hosts to a range of parasites, including various blood and other endo-parasites (Krone 1998, Krone et al. 2001). Lists of parasite species sampled from goshawks, however complete, tell us little about the potential impact of infections on goshawk populations. A crucial issue is whether parasites hold breeding numbers below the level that would otherwise occur, for example by causing substantial additive mortality among mature birds or by significantly reducing productivity (Newton 1998). We know of only three systematic studies that attempted to assess the potential importance of parasites for local goshawk populations in Europe.

Trichomonosis is an infectious disease in birds, which is caused by the protozoan flagellate *Trichomonas gallinae*. It is particularly common in the Columbiformes, which typically form a substantial part of the goshawk's breeding season diet (Table 3). This together with incidental cases of fatal trichomonosis infection in nestling goshawks, led several authors to hypothesize that the disease might be a significant mortality factor (Trommer 1964, Sperber 1970, Looft 1981, Link 1986, Cooper and Petty 1988). Recently, Krone et al. (2005, unpubl. data) investigated the prevalence of *T. gallinae* in an urban population of goshawks in the city of Berlin, Germany. In 80% of all investigated broods at least one nestling was infected (N = 90 broods, containing 269 nestlings, at 37 different territories). From necropsies of 46 adult hawks, 22% tested positive for *T. gallinae.* The authors conclude that trichomonosis is the most important infectious disease in their study population, but it remains to be established whether it acts as a population limiting factor. A similar result was obtained in a study in southwest Poland in which all surviving 35–40-d-old nestlings were found to be infected with *T. gallinae* (N = 11 broods, containing 28 nestlings; Wieliczko et al. 2003). In another study in Wales, Great Britain, the impact of the blood parasite *Leucozytozoon toddi* on nestling goshawks was investigated (Toyne and Ashford 1997). A total of 35% of 23 broods were infected, but the parasite had no detectable effects on nestling mass or mortality (*cf*. Wieliczko et al. 2003).

From this material, we cannot judge the impact of parasite infections on breeding numbers in goshawk, but, on basis of what is known from other bird species (Newton 1998), it is probably small or non-existent. Under extreme environmental conditions, such as food scarcity or in adverse weather, high parasite loads might contribute to the mortality of adult hawks, but this is not necessarily additive to other forms of mortality.

URBAN POPULATIONS AS NATURAL EXPERIMENTS

Most goshawks breed in natural or rural habitats with extensive patches of mature woodland and little human disturbance. However, during the last 30 yr, the species has colonized urban environments throughout Europe (Table 4). Now goshawks breed in metropolitan habitats, ranging from suburban districts to the centers of large cities with >9,000,000 inhabitants. Some urban populations have apparently already reached stable breeding numbers, whereas others are still expanding or have only a few pioneer pairs.

In the context of this review, these urban populations resemble natural experiments, offering valuable opportunities to assess our ideas on the dynamics of goshawk populations in semi-natural habitats or in rural areas. Regarding their biotic and abiotic properties, urbanized areas differ markedly from other environments generally inhabited by goshawks. In particular, cities are characterized by high levels of human activity, a comparatively small amount of woodland, and a high abundance of avian prey species.

MUCH HUMAN ACTIVITY BUT NO DELIBERATE KILLING

In most metropolitan environments, levels of human activity are high, but at the same time, deliberate killing of goshawks is virtually absent—a situation rarely encountered in other landscapes.

TABLE 4. URBAN BREEDING POPULATIONS OF GOSHAWK.

Country	City	Habitat type	Study area (km^2)	Remark	Year of first colonization	Pairs in [year][a]	Density (pairs/ 100 km^2)[a]	Trend[b]	Sources
Germany	Saarbrücken	suburban	315		unknown	≥14 bp (80)	≥4.4 bp	?	Dietrich (1982).
	Cologne	urban	200	western part of city	1988 (87?)	≥22 bp (98)	≥11.0 bp	0	Würfels (1994, 1999).
	Hamburg	urban	300	city north of river Elbe	1985	17 bp (00)	5.7 bp	0	Rutz (2001), and unpubl. data.
	Berlin	urban, suburban	701	eastern part of city + periphery	unknown[c]	42 terr. (01)	6.0 terr.	+	Altenkamp (2002).
		urban	486	western part of city	unknown[c]	35 terr. (97)	7.2 terr.	+	Altenkamp and Herold (2001).
Netherlands	Amsterdam	(sub-)urban	?[d]		probably 1990s	5 bp (03)	?	+	Zijlmans (1995), Müskens (2002), P. Marcus, pers. comm.
	Groningen	(sub-)urban	50	whole town	1996	6 bp (00)	12.0 bp	0	Dekker et al. (2004).
Russia	Moscow	urban	?[d]	whole city	end of 19th century	~35 bp (00)	?	+	Samoilov and Morozova (2001), I. Aparova, pers. comm.

Note: Anecdotal reports of goshawks breeding in or near cities; Germany—Münster, Billerbeck, Dülmen (Bednarek 1975), Wuppertal (Richter 1994), Leipzig, Coburg, Nürnberg (Fischer 1995), Kiel (Berndt et al. 2002), Leverkusen (P. Wegner, pers. comm.), Russia—Perm (Kazakov 2003), Ukrania—Kiev (Domashevskiy 2003), Latvia—Riga (U. Bergmanis, quoted in Altenkamp 2002), Czech Republic—Prague (Danko et al. 1994).

[a] bp = breeding pair; terr. = breeding territory.

[b] Use of symbols same as in Table 2.

[c] For a detailed discussion, see Altenkamp (2002).

[d] As yet, no systematic survey work.

The fact that goshawks successfully colonized large cities is an impressive demonstration that the mere presence of humans is not sufficiently disturbing for the species to prevent successful breeding. This finding contrasts strikingly with the conclusions reached by studies on nest-site characteristics of goshawks in semi-natural or rural landscapes, which we have reviewed above.

Urban-breeding goshawks are remarkably tolerant of human activity (Würfels 1994, 1999; Rutz 2001, 2003a, b, 2004; Altenkamp and Herold 2001, Altenkamp 2002, Aparova 2003, Kazakov 2003). In highly urbanized settings, the flushing distance for perched hawks is typically as low as 10–20 m (Würfels 1994, 1999; Rutz 2001, 2003b; R. Altenkamp, pers. comm.); birds can often be approached even closer, as long as the observer shows no particular interest in them and behaves like other nearby humans (Rutz 2001, 2003b, 2004). The degree of tolerance presented by breeding adults appears to increase with the average stress level they are exposed to at their nest sites (Altenkamp 2002; C. Rutz, pers. obs.). Deviating from footpaths in parks rarely provokes alarm calls from nesting hawks, and mobbing attacks during nestling banding are exceptional (Altenkamp 2002; C. Rutz, pers. obs.). Brooding females generally do not flush from the nest when approached even when the nest tree is struck with a stick (Altenkamp 2002, Aparova 2003; C. Rutz, pers. obs.). A similar degree of tolerance of human activity at nest sites has been described for breeders in rural areas, but only exceptionally.

Hawks regularly perch in single trees beside busy streets or in back yards in residential areas (Rutz 2001, 2003b, 2004). More surprisingly, this forest-dwelling raptor often sits completely exposed on anthropogenic structures, including roofs of buildings, television aerials, electricity pylons (Lessow 2001, Rutz 2004), and even parked cars (Wittenberg 1985) and garden furniture (P. Wegner, pers. comm.). In Hamburg, at least five male and two female territory holders regularly used prominent man-made structures to engage in peregrine-like perched hunting (Rutz 2001, 2004). In several cities, goshawks pluck prey on roofs, chimneys, and balconies (Tauchnitz 1991, Würfels 1994; Rutz 2001, 2003b, 2004). Three radio-tagged males used buildings and parked cars for cover while hunting in low-quartering flight (Rutz 2001, 2003b) and plucked their prey in back yards (Rutz 2001, 2004; C. Rutz et al., unpubl. data). Several foraging trips were recorded after sunset under artificial light conditions (Dietrich 1982).

Despite their extraordinary tameness, urban goshawks still present obvious stress responses in certain situations. They seem to become nervous when aware of being watched and fly off immediately when an observer raises a pair of binoculars (C. Rutz, pers. obs.). Urban-breeding goshawks appear to be unaffected by human activity but could pay a price for living in this novel environment if, for example, they had lowered reproductive performance due to high stress levels or increased mortality risk due to anthropogenic obstacles in their hunting habitat (Sweeney et al. 1997). Nothing indicates that this is the case; in fact, all closely monitored urban populations in Europe had higher productivity even after breeding numbers stabilized toward the end of the colonization process than did rural populations (Table 5), and the observed adult and juvenile mortality rates are low (C. Rutz, unpubl. data; but see Rutz et al. 2004). Detailed color-banding studies in Hamburg show that a considerable proportion of new recruits had fledged in the city (Rutz 2005b, unpubl. data).

Almost Complete Absence of Mature Woods

If, for this raptor, mature woodland per se were necessary for nesting, we would expect comparatively low breeding densities in highly urbanized areas. Quite the opposite is true: where detailed census data are available, densities in metropolitan habitats exceed those found in nearby rural areas with more woodland (Table 5). For example, Altenkamp and Herold (2001) reported a density of 6.0 territories/100 km^2 for a study plot in urban Berlin and a density of 3.8–4.1 territories/100 km^2 in surrounding rural areas of the federal state of Brandenburg. Likewise, the high density of 11.6 pairs/100 km^2 in urban Cologne (Würfels 1999) compares with only 4–5 territories/100 km^2 in a rural plot west of the city boundary (Kostrzewa et al. 2000). The same applies to Hamburg and its rural surroundings (C. Rutz et al., unpubl. data).

Urban goshawks use various types of green space for nesting. Some public parks, cemeteries and hospital grounds resemble non-urban nesting sites. Examples are large parks at the periphery of the cities of Cologne (Würfels 1994, 1999) and Moscow (Aparova 2003), inner-city park complexes with extensive patches of mature trees in Berlin (Altenkamp and Herold 2001, Altenkamp 2002), or a well-forested cemetery in the city of Hamburg (Rutz 2001). In the same cities, however, successful broods in private gardens and small parks (1–20 ha in size), which are completely surrounded by built-up habitat and present high levels of human activity compared with rural nest sites, are not unusual (Fig. 8; Zijlmans 1995, Würfels 1999, Rutz 2001, Altenkamp 2002). In Hamburg, one pair successfully fledged young from a nest in a solitary tree, situated in a residential area. Nests are often located close to or even above extensively used footpaths and in close proximity to buildings (Würfels 1994, 1999; Aparova 2003, R. Altenkamp, pers. comm.; C. Rutz, unpubl. data); in Hamburg, a successful nest was only 10 m from a five-story building (C. Rutz, unpubl. data).

Above we emphasized that woodland provides not only nest sites for goshawks, but also important food supplies. In fact, provisioning males in

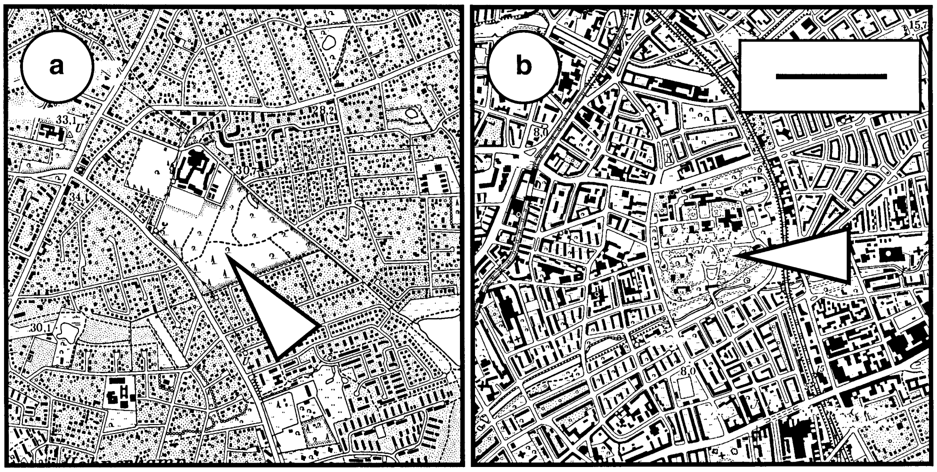

FIGURE 8. Examples of typical goshawk breeding sites (nest near arrow head) in a metropolitan setting (city of Hamburg, Germany; C. Rutz, unpubl. data). (a) Territory in small public park in residential area. (b) Territory in hospital park. Scale bar (for both maps) is 500 m.

TABLE 5. COMPARISON OF GOSHAWK KEY DEMOGRAPHICS BETWEEN EUROPE AND NORTH AMERICA.[a]

	Europe					North America				
	North	West	Central	South	(Sub-)Urban	North-west	West coast	West-central	North-central	East coast
Forest cover in study area (%)	53 (20–80) [9]	30 (4–82) [30]	44 (8–90) [11]	55 (30–83) [4]	5, 16, 40 [3]	50, 85 [2]	25, 86 [2]	95 [1]	62 [1]	48 [1]
Breeding density (pairs/100 km^2)	4.0 (1.4–5.6) [9]	4.8 (0.8–31.6) [39]	8.8 (1.9–20.0) [11]	5.0 (0.2–15.3) [5]	8.8 (5.9–12.0) [4]	4.0, 10.0 [2]	4.8 (1.0–8.2) [7]	4.8, 12.5 [2]	1.8 [1]	1.2 [1]
Nearest-neighbor distance (km)	3.4, 5.0, 6.3 [3]	2.6 (1.2–4.0) [8]	1.7, 3.7 [2]	3.4 (1.5–5.0) [4]	2.8 [1]	NA	3.3 [1]	3.9 [1]	NA	8.0 [1]
Nest success (%)	74 (57–86) [8]	77 (33–91) [44]	69 (63–100) [9]	72 (57–81) [4]	84 (69–93) [4]	75, 84, 95 [3]	83 (77–91) [4]	79 (47–91) [9]	70 (62–85) [5]	83, 85, 94 [3]
Brood size (juvs/succ. brood)	2.7 (2.2–3.1) [12]	2.5 (1.5–3.4) [50]	2.7 (1.8–3.0) [12]	2.5 (2.3–2.8) [4]	2.9 (2.0–3.1) [4]	2.0, 2.3, 2.9 [3]	1.9 (1.8–2.2) [4]	2.1 (1.7–2.6) [11]	1.8 (1.6–2.2) [5]	1.8, 2.1, 2.1 [3]
Productivity (juvs/started brood)	1.8 (1.3–2.5) [5]	1.8 (0.5–2.6) [41]	1.8 (1.1–3.0) [9]	1.4, 1.7, 1.8 [3]	1.7, 2.5, 2.9 [3]	1.8 (1.6–2.4) [4]	1.6 (1.4–1.9) [4]	1.6 (0.9–2.4) [13]	1.4 (1.1–2.2) [6]	1.5, 1.8, 2.0 [3]
Clutch size (eggs/clutch)	3.3 (2.8–3.6) [4]	3.4 (2.2–4.0) [14]	3.4 (2.9–3.6) [8]	3.2, 3.3, 3.4 [3]	3.4 [1]	NA	NA	NA	NA	2.8 [1]
Adult breeder mortality (%)	21, 37 [2]	29 (20–36) [4]	NA	NA	NA	36 (59) [2]	26 [1]	21 (14–29) [4]	20, 26 [2]	NA
Mammals in summer diet (%)	14 (1–18) [8]	5 (0–23) [23]	6 (3–10) [10]	20 (1–33) [8]	3 (0–11) [7]	65 (22–78) [5]	51 (8–79) [12]	67 (21–91) [9]	70 [1]	47 (30–73) [4]

Notes: This table is a raw summary of data from a detailed cross-continental meta-investigation of goshawk key demographics (C. Rutz et al., unpubl. data). Each cell gives median (for N >3), range of values (in brackets), and sample size (in square brackets) (NA = no data available). Note that studies vary considerably in methodology, e.g., climbing of nest trees *vs*. observation from the ground, size of the study plot, duration of study.

[a] *Sources*: The following are the sources used to compute summary statistics, organized by geographical region and country or state for Europe and North America, respectively (study plots that covered territory of two countries/states are listed only once—N = 5). Note that the number of sources does not necessarily match sample sizes given in table cells, as some papers reported data for several distinct study sites, whereas in a few other cases, data from several papers had to be combined to yield a single datapoint.

Europe—north: Estonia (Lelov 1991; Lõhmus 1993, 2004); Finland (Huhtala and Sulkava 1976, Wikman and Tarsa 1980, Huhtala and Sulkava 1981, Wikman and Lindén 1981, Tornberg and Sulkava 1991, Sulkava et al. 1994, Tornberg 2000, Tornberg and Colpaert 2001, Byholm et al. 2002a, Byholm 2003; Tornberg et al., *this volume*; R. Tornberg et al., unpubl. manuscript); Latvia (Weber 2001); Norway (Myrberget 1989, Selås 1997a, Grønnesby and Nygård 2000, Steen 2004); Sweden (Widén 1985b, 1987; Kenward et al. 1999, Ryttman 2001, R. E. Kenward et al., unpubl. data).

TABLE 5. CONTINUED.

Europe—west: Belgium (Draulans 1984, Doucet 1987, Draulans 1988, Doucet 1989b, De Fraine and Verboven 1997); Denmark (Storgård and Birkholm-Clausen 1983, Rassmussen and Storgård 1989; Nielsen and Drachmann 1999a, b); France (Nore 1979, Joubert and Margerit 1986, Kayser 1993, Joubert 1994, Penteriani et al. 2002b); Germany (Dietzen 1978, Hillerich 1978, Kos 1980, Knüwer 1981, Looft 1981, Oelke 1981, Gedeon 1984, Looft 1984, Heise 1986, Link 1986, Schneider et al. 1986, Möckel and Günther 1987, Staude 1987, Zang 1989, Dobler 1991, Schönbrodt and Tauchnitz 1991, Stubbe et al. 1991, Kehl and Zerning 1993, Albig and Schreiber 1996; Bezzel et al. 1997a, b; Hausch 1997, Raddatz 1997, Arntz 1998, Kostrzewa et al. 2000, Krüger and Stefener 2000, Altenkamp and Herold 2001, Weber 2001, Arbeitsgruppe Greifvögel NWO 2002, Ehring 2004); Switzerland (Bühler et al. 1987); The Netherlands (Thissen et al. 1981, Erkens and Hendrix 1984, Bijlsma 1989, Rosendaal 1990, Bijlsma 1993, Bakker 1996; Bijlsma 1998-2003; Woets 1998, Dekker et al. 2004); United Kingdom (Marquiss and Newton 1982, Anonymous 1990, Toyne and Ashford 1997, Toyne 1998, Marquiss et al. 2003, Petty et al. 2003a).

Europe—central: Austria (Steiner 1999, A. Gamauf, unpubl. data); Belarus (Ivanovsky 1998); Czech Republic (Diviš 2003); Hungary (Varga et al. 2000); Poland (Król 1985, Goszczyński and Piłatowski 1986, Czuchnowski 1993, Drazny and Adamski 1996, Pugacewicz 1996, Goszczyński 1997, Olech 1997, Jędrzejewska and Jędrzejewski 1998, Olech 1998, Zawadzka and Zawadzki 1998, Goszczyński 2001, Wieliczko et al. 2003, van Manen 2004); Romania (Kalabér 1984); Serbia/Macedonia (Grubač 1988); Slovakia (Šotnár 2000).

Europe—south: Italy (Perco and Benussi 1981, Penteriani 1997); Portugal (Petronilho and Vingada 2002); Spain (Morillo and Lalanda 1972, Veiga 1982, Mañosa et al. 1990; Mañosa 1991, 1994; Verdejo 1994, Padial et al. 1998).

Europe—(sub-)urban: Berlin (Deppe 1976, Jacob and Witt 1986, Altenkamp and Herold 2001, Altenkamp 2002); Cologne (Würfels 1994, 1999); Groningen (Dekker et al. 2004); Hamburg (C. Rutz, unpubl. data); Saarbrücken (Dietrich 1982).

Nearctic—north-west: Alaska (Zachel 1985, Titus et al. 1997, Flatten et al. 2001, Lewis 2001, Lewis et al. 2004); Alberta (Schaffer 1998); British Columbia (McClaren et al. 2002, Mahon et al. 2003); Yukon (Doyle and Smith 1994, Doyle 2000).

Nearctic—west coast: California (Bloom et al. 1986, Woodbridge et al. 1988, Austin 1993, Woodbridge and Detrich 1994, Keane 1999, McCoy 1999, Maurer 2000, Keane et al., *this volume*); Oregon (DeStefano et al. 1994b, Thrailkill et al. 2000); Washington (Watson et al. 1998, Bosakowski et al. 1999).

Nearctic—west-central: Arizona (Crocker-Bedford 1990, Zinn and Tibbitts 1990, Dargan 1991, Boal and Mannan 1994, Reynolds et al. 1994, Snyder 1995, Crocker-Bedford 1998, Reynolds and Joy 1998; Reynolds and Joy, *this volume*; Rogers et al., *this volume*); Idaho (Patla 1997, Hanauska-Brown et al. 2003; Bechard et al., *this volume*); Nevada (Oakleaf 1975, Herron et al. 1985, Younk and Bechard 1994a; Bechard, *this volume*); New Mexico (Kennedy 1991, 1997; McClaren et al. 2002); Utah (Lee 1981a, Kennedy 1997, Stephens 2001, McClaren et al. 2002); Wyoming (Good et al. 2001).

Nearctic—north-central: Michigan (La Sorte et al. 2004); Minnesota (Gullion 1981a, Smithers 2003; Boal et al., *this volume*); South Dakota (Bartelt 1977); Wisconsin (Rosenfield et al. 1996, Erdman et al. 1998).

Nearctic—east coast: Connecticut (Root and Root 1978, M. Root and P. DeSimone, unpubl. data; Becker et al., *this volume*); New York/New Jersey (Allen 1978, Bosakowski and Smith 1992, Speiser 1992; Bosakowski and Smith, *this volume*); Pennsylvania (J. T. Kimmel and R. H. Yahner, unpubl. data).

Hamburg spent 88% of daylight hours in forested patches (N = 3 radio-tagged birds; Rutz 2001). However, almost half of all 143 recorded kills were made during short hunting excursions into the matrix of built-up habitat, indicating that urbanized areas enabled more efficient hunting.

These examples demonstrate that the goshawk is much more flexible in its choice of nesting and foraging habitat than previously thought. Large stands of mature forest, usually considered to be of paramount importance for the species, are not obligate requirements for successful breeding, provided that food is readily available, some trees are present for nesting, environmental contaminants are not at poisonous levels, and there is little or no deliberate killing by humans. In most cities, the degree of nest-site competition with other raptor species is probably small, but in the presence of urban-living eagle-owls, intra-guild conflicts may arise. In Hamburg, for example, eagle-owls have recently started colonizing parts of the city, and have taken over traditional goshawk breeding territories in urban parks (C. Rutz, unpubl. data).

For two urban populations, well documented colonization histories are available with detailed information on all stages of the invasion process—first settlement, rapid expansion, and saturation (Fig. 9). Toward the end of the expansion processes, the number of successful breeding attempts stabilized, whereas new territories were still being established in the respective study plots, i.e., the cumulative number of territories increased further (Fig. 9). 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 settings are not generally limited by the availability of nest sites.

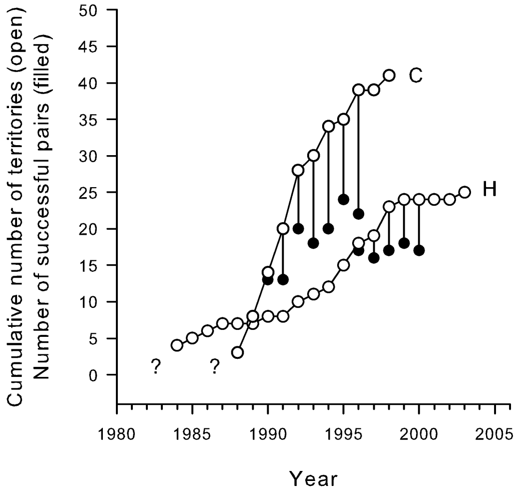

FIGURE 9. Expansion of two urban populations of goshawk in the cities of Hamburg (H) and Cologne (C), Germany. Cumulative number of established territories (open symbols) and number of successful pairs (filled) investigated in the course of monitoring studies are shown (Würfels 1999, C. Rutz, unpubl. data). The trajectory for Hamburg includes some pairs in the suburban periphery of the city; for a full description of the colonization process, see Rutz (2005b).

Abundant Food Supply

In many of the larger German cities, including Berlin, Cologne, and Hamburg, profitable goshawk prey (Table 3), such as feral pigeons, European Starlings, corvids, and thrushes are abundant. For example, 10,600 pairs of feral pigeons were counted in urban Hamburg (area = 747 km^2; Mitschke and Baumung 2001), which is more than twice the estimated number (4,300) for the whole federal state of Schleswig-Holstein north of the city (area = 15,763 km^2; Berndt et al. 2002). As detailed above, breeding densities of urban goshawk populations are comparatively high, associated with the rich food supply.

Consistent with the idea of favorable food conditions in cities, urban goshawks start egg laying about 10–14 d earlier, and have greater reproductive output, than their rural counterparts (Altenkamp 2002; C. Rutz, unpubl. data). In Berlin, nest success was 87.2% (N = 391 broods), and successful pairs fledged on average 2.85 juveniles (N = 302 broods; Altenkamp 2002). Breeding pairs in nearby rural areas showed lower productivity (Altenkamp and Herold 2001). The same holds true for a comparison of urban *vs*. rural pairs in the city of Hamburg and its exurban periphery (C. Rutz, unpubl. data). In fact, Altenkamp (2002) demonstrated that productivity of goshawk pairs was positively related to the degree of urbanization within individual territories, as measured by the proportion of built-up habitat around nests. Moreover, by comparing series of molted primaries found at nest sites, the longer time sequences for feathers from urban individuals suggested that the annual loss of breeders was lower for the Hamburg than for rural populations (C. Rutz, unpubl. data). When data on breeding performance and demographics are compared between an urban area and a rural control plot, both study populations should ideally be at capacity level to avoid artificial results (Newton 1998). In most studies, urban populations were still increasing during data collection, at least in the early years of the investigation. However, snapshot analyses in Hamburg, carried out several years after goshawk numbers had stabilized, indicated the generality of the above findings (C. Rutz, unpubl. data; Würfels 1999 and Altenkamp 2002 continued their studies well into the saturation phase).

Further, radio monitoring demonstrated (Rutz 2001) that, home-range size was smaller, time spent in active flight was shorter, and hunting success was higher for three urban-breeding males than for their rural counterparts (Hantge 1980, Kenward 1982, Ziesemer 1983, Widén 1981, 1984; Kennedy 1991). Taken together, these data provide compelling evidence that urban environments offer excellent foraging conditions for goshawks.

On basis of the available information, it is difficult to evaluate the relative importance of food and nest sites in limiting urban goshawk populations. Considering the extremely heterogenous spatial dispersion of resources in most metropolitan environments, it is possible that breeding numbers in different areas within the same city are ultimately checked by different extrinsic factors. In Hamburg, for example, breeding density is comparatively low in the western part of the city center despite high pigeon abundance, possibly because of a lack of suitable nest sites. On the other hand, in suburban parts in the northeast, parks suitable for nesting are still plentiful but food resources apparently are insufficient to permit settling of additional pairs.

COMPARISON WITH NORTH AMERICA

This section reviews evidence for differences in goshawk biology between Europe and North America. Whereas our focus remains on populations from western and central Europe as in previous sections of this paper, this part also considers all available studies from northern Europe (Tornberg et al., *this volume*). We look first at demographic parameters, then at densities and breeding habitats, and finally at movements and diets. We re-assess ideas from a preliminary comparison (Kenward 1996) that suggested goshawks in North America might be limited by intra-guild effects, primarily from Great Horned Owls (*Bubo virginianus*) and Red-tailed Hawks (*Buteo jamaicensis*), and/or by poor food supplies in winter. Our key findings are presented in Table 5.

DEMOGRAPHY

Variation in breeding performance parameters within and between regions of Europe and North America seem as great as between the continents (Table 5). Nevertheless, brood size and productivity seem generally larger in Europe than in North America. Nest success, on the other hand, is similar between continents with a tendency for low values in central and southern parts of Europe and northwestern North America. High variability within regions presumably reflects findings that clutch and brood sizes are influenced by food supply and the effects of weather conditions (Tornberg et al., *this volume*; Keane et al., *this volume*). Data on occupancy are not compared because this varies with length of study, declining initially as the infrequently used nesting places are discovered and then more gradually as tree stands change and new nesting sites become more attractive than some previous ones. Occupancy needs to be standardized with respect to search effort, and landscape change (Kennedy 1997; Reynolds and Joy, *this volume*).

Survival rates of adult goshawks have been estimated on both continents, using systematic banding of nestlings, mark-recapture of adult birds, cross comparison of molted feathers found at nests, and quantitative radio-tagging. Annual turnover rates for adults at nests in western central America are quite variable (14–29%; Table 5), but the median value of 21% is similar to the 20% and 23% of two studies in western Europe (Bühler et al. 1987, Drachman and Nielsen 2002; other estimates are probably inflated due to illegal killing), and 21% from 133 radio-tagged hawks on the Swedish island of Gotland (Kenward et al. 1999). The climate of this southern Baltic island is more typical of central Europe than the north, where adult mortality estimates of 37% for northern Finland (Tornberg et al., *this volume*) suggest higher mortality in the more extreme winters (Sulkava 1964, Sunde 2002). In Alaska, an adult mortality estimate was similar at 36% (Flatten et al. 2001); on basis of new data, adult male breeder mortality is as high as 59% (K. Titus et al., unpubl. data).

Data from banding tends to overestimate juvenile mortality of raptors (Kenward et al. 1999, 2000), and juvenile survival through the first year of life has been studied by radio tagging in only a few areas. In North America, three deaths were recorded when 39 young were tracked for 4–6 mo post-fledging during 2 yr in New Mexico (Ward and Kennedy 1996), giving a weighted annualized estimate of mortality of only 20%. In Utah, where a study did not extend beyond dispersal, only one death was recorded among 59 fledged hawks (Dewey and Kennedy 2001). Annualized estimates of 84% for 14 young hawks in Alaska (Titus et al. 1994) and 81% for eight in Finland (Tornberg and Colpaert 2001) were much higher which may reflect poor conditions in the north. Differences might be less if annualizing of mortality rates and analytic treatment through dispersal were comparable in all studies, but might well still indicate higher juvenile mortality at higher latitudes. The mortality rate was 42% for 185 radio-tagged juveniles tracked for 9–12 mo on Gotland (Kenward et al. 1999). Interestingly, life-table analyses for hawks banded as nestlings in The Netherlands similarly produced a first-year mortality estimate of only 41% (Bijlsma 1993), suggesting even better overall survival prospects in this more southerly country.

Although Goshawk mortality rates seem similar for Europe and North America, there may be differences in causes of death. Thus, natural predation accounted for five of nine deaths recorded for radio-tagged goshawks in Minnesota (Boal et al., *this volume*), compared with only two of 63 on Gotland, where other goshawks caused both deaths (Kenward et al. 1999). Analyses of extensive data sets of band recoveries also indicate that non-human predation accounts for only a small proportion of deaths in Europe (2.4%, Bijlsma 1993; 1.5%, Nielsen and Drachmann 1999c). Squires and Kennedy (*this volume*) speculate that Great Horned Owls are the dominant predator of goshawks due to their wide distribution, abundance, and capacity to prey on large raptors. Kenward (1996) noted that the Great Horned Owl is much smaller and nests more frequently in trees than the Eurasian Eagle-Owl, and hypothesized that goshawks in sub-boreal forests in North America may suffer from nest-site competition with the Red-tailed Hawk, a widely abundant North American Buteo (Crocker-Bedford 1990, La Sorte et al. 2004). Red-tailed Hawks are larger than their European counterpart, the Common Buzzard, and they tend to nest earlier in the season than goshawks (Craighead and Craighead 1956). Levels of intra-guild predation might increase in western European regions, as eagle-owl populations expand.

Nesting Densities and Habitats

Whereas many studies in Europe have searched systematically for nests in well-defined areas that do not focus on a particular habitat, North American researchers have mostly concentrated on large areas of forest. This complicates a landscape-based comparison of breeding densities between continents. Some researchers may also have selected areas perceived as good for the species and hence for obtaining large samples of nests.

A cross-regional median nest density for Europe of 5.0 pairs/100 km^2 (N = 5 regions; Table 5) compares with a median of 4.8 pairs/100 km^2 for North America (N = 7 values). A tendency for lower nearest-neighbor distances between nests in Europe (Table 5; Fig. 5) may reflect clumping in areas with more fragmented forest in Europe. We note that breeding densities in parts of western Europe, notably The Netherlands (Bijlsma 1993) and Germany (Mammen 1999), are generally higher than those found in northern and central areas of the European breeding range, and also clearly exceed those found in any part of North America. Study areas in Europe contained less woodland cover (median = 44%, N = 5 regions; Table 5) than those in North America (median = 62%, N = 7 studies; Rutz et al., unpubl. data).

Direct comparison of sites chosen for nesting is constrained by differences in the emphasis of studies in Europe as opposed to North America: European studies have tended to focus on fine details of predation and productivity, whereas North American studies have traditionally focused on habitat use (Kenward, *this volume*). Nevertheless, Penteriani (2002) has recently contrasted goshawk nesting habitat in 15 European studies with 28 in North America across three spatial scales: nest tree, nest stand, and landscape. The review failed to detect significant differences in goshawk habitat use between the two continents (Penteriani 2002 [MT]) Here, we briefly discuss the three most important nest-stand characteristics, updating and amending Siders and Kennedy (1994), and Penteriani (2002) (Table 6).

The range in diameter at breast height (dbh) of trees in nest stands from four western-European study areas (Anonymous 1989, Mañosa 1993, Penteriani and Faivre 1997, Penteriani et al. 2001) was 17–46 cm, similar to the 15–59 cm in North American studies. With nests in conifers, mixed, and deciduous woodland on both continents, and mature deciduous trees generally spaced more widely than conifers, tree density in nest stands is hard to compare. A highly variable stand density in five European studies, of 223, 300, 550, and 1,716 stems/ha, compared with a median of 757 stems/ha (range 387–1,345) in North America. Canopy closure is high in North American nest areas at a median 76% (31–95) in 26 studies of which only two were <60% (Hargis et al. 1994, Lang 1994). High canopy closure might indicate a tendency to hide from over-flying large raptors. Although only four European teams have measured this parameter, it is clear from use of trees in narrow rows or even standing alone in towns that goshawks in some parts of Europe can tolerate low canopy cover and tree density for nesting. To our knowledge, goshawks have not been found breeding in urbanized environments in their North American range.

TABLE 6. COMPARISON OF GOSHAWK NEST-STAND CHARACTERISTICS BETWEEN EUROPE AND NORTH AMERICA.[a]

Variable	Europe	North America	Mann-Whitney U-test
Diameter at breast height (cm)	26 (17–46) [4]	32 (15–59) [14]	U = 18.5 P = 0.327
Tree density (stems/ha)	550 (223–1,716) [5]	757 (387–1,345) [20]	U = 38.0 P = 0.447
Canopy closure (%)	84 (73–92) [4]	76 (31–95) [26]	U = 32.5 P = 0.245

Notes: Each cell gives median, range of values (in brackets), and sample size (in square brackets).

[a] *Sources*:

Diameter at breast height: Europe (Anonymous 1989, Mañosa 1993, Penteriani and Faivre 1997, Penteriani et al. 2002b); North America (Reynolds et al. 1982, Saunders 1982, Moore and Henny 1983, Hall 1984, Fischer 1986, Fleming 1987, Ingraldi and MacVean 1994, Siders and Kennedy 1994, Rosenfield et al. 1998, Finn et al. 2002b, McGrath et al. 2003, La Sorte et al. 2004; Becker et al., *this volume*; S. B. Lewis et al., unpubl. data).

Tree density: Europe (Gamauf 1988a, Anonymous 1989, Mañosa 1993, Penteriani and Faivre 1997, Selås 1997b); North America (Reynolds et al. 1982, Saunders 1982, Moore and Henny 1983, Hall 1984, Fischer 1986, Hayward and Escano 1989, Bosakowski et al. 1992, Ingraldi and MacVean 1994, Lang 1994, Siders and Kennedy 1994, Martell and Dick 1996, Squires and Ruggiero 1996, Patla 1997, Rosenfield et al. 1998, Bosakowski et al. 1999, Boal et al. 2001, Finn et al. 2002b, McGrath et al. 2003; Becker et al., *this volume*).

Canopy closure: Europe (Gamauf 1988a, Zanghellini and Fasola 1991, Penteriani and Faivre 1997, Penteriani et al. 2002b); North America (Reynolds et al. 1982, Saunders 1982, Moore and Henny 1983, Hall 1984, Fischer 1986, Crocker-Bedford and Chaney 1988, Hayward and Escano 1989, Joy 1990, Bosakowski et al. 1992, Bull and Hohmann 1994, Hargis et al. 1994, Ingraldi and MacVean 1994, Lang 1994, Siders and Kennedy 1994, Kimmel 1995, Squires and Ruggiero 1996, Titus et al. 1996, Patla 1997, Rosenfield et al. 1998, Bosakowski et al. 1999, Daw and DeStefano 2001, Finn et al. 2002b, McGrath et al. 2003, La Sorte et al. 2004; Becker et al., *this volume*).

Future comparisons of habitat characteristics between continents should make an attempt to include data from European studies that investigated goshawk populations in human-altered landscapes; these data are not yet available, but once they have been published their inclusion will probably reveal significant cross-continental differences in the above habitat measures.

MOVEMENTS AND DIET

Juvenile goshawks can disperse long distances in both Europe and North America, associated with food shortage (Byholm et al. 2003; Bechard et al., *this volume*; Sonsthagen et al., *this volume*; Tornberg et al., *this volume*; Underwood et al., *this volume*). However, throughout Europe south of Fennoscandia, dispersal distances are remarkably short—the majority of recoveries of banded hawks were typically made within 20 km of the nest (Unger 1971, Looft 1981, Link 1986, Bühler and Klaus 1987).

Goshawks in North America tend to favor woodland habitats for hunting, though some individuals use edge zones where woodland is fragmented (Boal et al., *this volume*; Sonsthagen et al., *this volume*; Squires and Kennedy, *this volume*). The same is true of northern Europe, though hunting in edge zones may prevail further south (Kenward and Widén 1989; C. Rutz et al., unpubl. data). The size of goshawk home ranges varies with habitat and food supply (Kenward 1982, 1996; Ziesemer 1983; C. Rutz et al., unpubl. data), so a standardization of recording and estimation techniques would be needed for rigorous comparison of resource use in Europe and North America.

The majority of diet studies are based on prey remains collected at nests, often late in the nestling period. The number of studies employing video-monitoring, caging of young in the nest, and stomach analysis (Rutz 2003a) is too small for systematic comparisons across regions. In most European goshawk populations, mammals form a relatively small proportion of items in the breeding season diet (Table 3). Cross-regional medians for Europe and North America are 6% (N = 5) and 65% (N = 5), respectively; the largest values reported for individual study populations in Europe are close to the lowest estimates from the Nearctic (Table 5). With lagomorphs being an important part of the mammalian prey in many areas, the difference in terms of prey biomass is even more dramatic. Breeding goshawks in North America are more dependent on mammals than in Europe.

Some of this difference may reflect availability of suitable prey. In North America, the lowest proportions of mammals were from the coast range of western Oregon (16%; Thrailkill et al. 2000) and Alaskan islands (22%; Lewis et al. 2004), while other values below the median were from coastal states of California, Connecticut, and New York or New Jersey (Table 5). In terms of distance from coasts with their more equitable climate and diversity of habitats for birds, most European study areas would qualify as coastal states in North America. European goshawks took most mammals in areas with abundant rabbits; the importance of this smallest European lagomorph for European goshawks is summarized elsewhere (Kenward 1996).

Differences in diet choice between continents seem more likely to be due to habitat, and/or prey availability rather than greater active selection of avian prey by goshawks in Europe as a result of either learning or being innately more prone to hunt birds. Several detailed radio-tracking studies militate against a greater innate tendency to hunt birds in Europe than in North America. They demonstrated that, at least in northern parts of Europe, winter diet contains more mammals than breeding season diet (71% *vs*. 20%, Tornberg 1997, Tornberg and Colpaert 2001; 82% *vs*. 14%, Widén 1987; 72% *vs*. 18%, R. E. Kenward et al., unpubl. data). Indeed, female European goshawks are adapted to subduing mammals by having relatively more powerful legs than males (Marcström and Kenward 1981), and in northern Europe they obtain more than half their biomass intake from mammals in winter (Kenward et al. 1981a; Tornberg et al., *this volume*). Tornberg et al. (1999) demonstrated that long-term changes in the foraging ecology, probably reflecting prey availability, of Finnish goshawks (1960s–1990s) were associated with significant morphological shifts—females increased in size with an increasing proportion of mountain hares in their diet. The proportion and biomass of mammals in the winter diet of European goshawks is smaller overall for males than for females, because females surpass males in being able to subdue full-grown lagomorphs; European red squirrels (*Sciurus vulgaris*) were killed by male goshawks at least as frequently as by females (Kenward et al. 1981a; Tornberg et al., *this volume*).

Noting that mass of snowshoe hares (*Lepus americanus*) makes them suitable for both male and female goshawks, Kenward (1996) speculated that the widespread nature of this prey may explain why male and female goshawks are less dimorphic in North America than in Europe. Further studies could show whether morphology of North American male goshawks is as adapted to subdue mammals as that of European females, or whether winter diet may give males mammal-hunting skills that influence diet at nests. In some areas, however, North American goshawks kill birds extensively (Table 5). It therefore seems most likely that, despite any possible adaptation for killing mammals among male goshawks in North America, greater tendency to kill mammals than in Europe reflects constrained availability of birds, perhaps reinforced by learning in winter.

In this context, it is interesting that productivity was lowest, and the proportion of mammalian prey highest, in the central North America region (Table 5). Perhaps it is only in regions with the most continental climate that goshawks may be constrained to large forests by persistence there of mammalian prey in winter. In this case, goshawks might be most likely to colonize woodland fragments in farmland of North America in mid-latitude coastal areas of the east, and that is where competitive or predatory constraints of Great Horned Owls and Red-tailed Hawks might best be sought.

CONCLUDING REMARKS

From preliminary screening of our databases and a raw summary of data presented in Table 5, it seems that goshawk ecology differs between North America and Europe in the use of some habitats, in diet, and in breeding density and productivity. Goshawks in North America apparently make little use of human-altered habitats for foraging and breeding. They live at lower densities than in Europe, and produce fewer young per pair. They also use mammalian foods more often than do hawks in Europe and, perhaps associated with this, North American goshawks exhibit less pronounced sexual-size dimorphism.

The differences in goshawk ecology between continents seem to be due to some underlying factor such as prey availability, rather than a discrete subspecific difference attributable to particular morphology or intrinsic behavior. Compared with Europe, in interior North America, fewer species of birds are resident—many more of them are summer breeding migrants (Newton 2003c). We do not know their relative abundances but it is possible that, compared with Europe, avian prey is less available in North America during the winter and spring. If this were true across a range of habitats in North America, it is one potential explanation for the greater use of mammalian prey, lower breeding densities, the lack of use of urban environments, and the overall lower breeding performance. Moreover, it could be argued that the greater use of mammalian prey is a sufficient explanation for reduced sexual-size dimorphism.

However, other major differences exist between the continents; two important confounding variables are the presence in North America of more predators such as Great Horned Owls and competitors such as Red-tailed Hawks and Cooper's Hawks (*Accipiter* *cooperii*). Both predation risk and competition might influence habitat use by goshawks, their diet, breeding density, and performance. On present evidence it is difficult to distinguish between the influences of food availability, predation and competition.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The goshawk is one of the best-studied raptor species in Europe. Much research remains to be done but taken together, the available information enables a qualitative assessment of the relative importance of various extrinsic factors in limiting breeding densities. Consistent with findings from other raptors, we identify nest-site availability and food supply as the two principal factors limiting goshawk populations. Importantly, given adequate food supply, nest-site availability appears to be heavily influenced by the level of killing by humans. The greater the killing, the more restricted is the range of nesting habitats acceptable to goshawks.

Currently, deliberate killing by humans only rarely has direct effects on goshawk population levels. However, even moderate levels of killing may have pronounced indirect consequences for both breeding density and breeding range. In some parts of Europe, goshawks nest in remote, mature forests, which are a limited resource in modern landscapes. In North America, such avoidance of human-altered habitats is even stronger, and may reflect more an avoidance of other raptors, notably Great Horned Owls and Red-tailed Hawks, than of humans. Natural selection among goshawks for avoidance of humans seems to be stronger in Europe than in North America, where researchers visiting goshawk nests routinely wear protective clothing because of attacks by hawks (Speiser and Bosakowski 1991). In Europe, goshawks typically hide or at least keep out of shotgun range, except for occasional attacks in the far north (T. Nygård, pers. comm.) and some western areas (M. Marquiss, pers. obs.; R. G. Bijlsma, pers. obs.).

Whether or not this avoidance of human-altered habitats is a response to past persecution or to other raptors, certain types of illegal killing may still critically affect goshawk populations by altering the species' tolerance of human activity and proximity, and hence, the suitability of habitat for nesting and foraging. For Europe, we deduced the above relationship mainly from the observation that, when deliberate killing ceased, goshawks in western Europe became highly tolerant of intense human activity. It would be wrong, however, to conclude that such an increase in stress tolerance is sufficient to trigger the invasion of urban habitats. A comparative analysis of all known urban goshawk populations (Table 4) shows that other factors often play a role, such as the availability of potential recruits from rural populations at capacity level (Rutz 2005b).

For populations that inhabit areas where nest sites are freely available and killing by humans is rare or absent, numbers are mainly limited by food resources. We have argued for the goshawk's strong dependence on forested habitat for nesting and hunting, but in the light of the above findings, it seems that the importance of certain nest-stand characteristics may be much overstated in the literature.

Case study 2 illustrates how goshawks can be affected by a shortage of food. Many farmland bird populations are in precipitous decline on a continental scale, but recent trend data give no evidence of widespread decline in European goshawk populations in agricultural areas. However, in order to efficiently evaluate the potential effects of changes in prey abundance on goshawks in the future, we need to learn more about how goshawks use prey resources: this involves careful monitoring of the avifauna in study plots and robust use-availability analyses (Tornberg 1997).

In some parts of Europe, goshawks appear to suffer from nest-site competition with re-introduced eagle-owls. At present, only a few local goshawk populations seem to be affected, but regional impact could accompany the current range expansion of eagle-owls. In Europe we are approaching the situation pertaining in North America, where lower levels of raptor persecution have permitted Great Horned Owls to remain common.

Other extrinsic factors appear to be of minor importance under most circumstances. Weather conditions may account for some of the year-to-year variation in nesting density, probably acting through an effect on spring food supplies, but they are not a principal limiting factor in temperate Europe. Circumstantial evidence suggests that pesticide use negatively affected European goshawk populations in the 1960s. Nowadays, however, levels of organochlorine pesticides and other environmental pollutants generally seem to be too low to have significant population-level consequences. The role of parasites and diseases in limiting goshawk breeding densities is unknown, but perhaps negligible by analogy with work on other species.

The insights produced by our review have implications for future conservation. A step toward conserving goshawk numbers in Europe would be to minimize activities (such as shooting) that enhance the avoidance of humans. If goshawk predation is to be managed for socio-economic or conservation reasons, this should be by live trapping, which enables release of non-target species and relocation of hawks. It is best done with traps set on fresh kills to selectively remove specific individuals (Kenward 2000). In contrast, illegal nest destruction should be discouraged because it has demographic impact on non-target individuals.

We predict that, once freed from selective or learned impacts of human antipathy, the species will begin to display its full behavioral plasticity, allowing it to use hitherto unexploited resources. Stress tolerance and relaxed nest-site preferences, as observed in The Netherlands and some European cities will no longer be the curious exception. Additionally, goshawk conservation should focus on important prey populations (Table 3) as well as breeding and hunting habitats. This will provide opportunity for cooperation for incentive-driven conservation with other stakeholders, including land-managers and hunters. Considering the good recovery of eagle-owl populations across Europe, we recommend that further releases of this top-predator be restricted until issues concerning their impact on raptor-guilds have been adequately addressed.

FUTURE RESEARCH

Most scientific research on goshawks in Europe involves the monitoring of local populations over long time periods. Such studies are extremely important, should be continued, and new ones will hopefully be launched in the future. Ideally, all population studies should simultaneously monitor a selection of extrinsic factors—use of habitat and food by goshawks can only be investigated appropriately if their availability in the environment has been quantified. It is evident from our review that a handful of long-term projects contributed disproportionately to our understanding of goshawk biology. We note, however, that most studies on the species, including those presenting large data sets, suffer from either or both of the following shortcomings—data are correlational and hence not ideal for establishing causal relationships, and/or they lack independent replication. We propose two standard approaches of scientific inference—controlled experiments to establish cause-and-effect relationships, and meta-analyses to indicate generality (Rutz 2005b).

Carefully designed field experiments are particularly needed in goshawk research; pioneering attempts in this direction have recently been undertaken (Kenward et al. 1993a, Dewey and Kennedy 2001, Krüger 2002b, Kennedy and Ward 2003). Such work benefits from being strictly hypothesis driven, but inevitably requires innovative approaches to overcome apparent practical constraints. We believe, however, that efforts will pay off by producing robust biological insight. For some aspects of goshawk biology, enough data have been gathered to conduct meta-analyses (Kennedy 1997, Rutz 2005b). We encourage researchers to embark on joint collaborative projects, as such large-scale work will give insight that cannot come from single-site studies.

New material needs to be gathered on: (1) the biology and dynamics of the non-breeding segment of goshawk populations, (2) year-round habitat use using radio telemetry, (3) the role of winter food and/or weather conditions for limiting local goshawk populations, (4) the effect of declining farmland bird populations and habitat fragmentation on rural-breeding goshawks, (5) the effect of humans and other predators on urban and rural-breeding goshawks, (6) nest spacing in relation to forest availability at various spatial scales, (7) goshawk prey choice in relation to prey availability, and, perhaps most importantly, (8) the direct and indirect influences of food availability on population dynamics and other aspects of goshawk biology. In addition, basic monitoring data are needed for some geographic regions, as illustrated by Table 5; the main gaps that need filling are: breeder mortality estimates for parts of Europe, and clutch-size data for the entire American breeding range. Our Table 5 may indeed serve as a good orientation to guide future research efforts at a regional and/or geographic scale, and, in 10–20 yr, a substantial update may enable an even better understanding of goshawk biology.

Finally, we suggest that goshawk researchers further standardize their field methodology—delineation of study areas, measurement of nesting habitat parameters, estimation of occupancy and productivity, description of ranging behavior, and resource use—and adopt a standard format for reporting key features of their study area and population, including information on the size of the study plot, its percentage woodland cover, breeding density (mean and maximum), and mean NND in continuously suitable woodland habitat. At present, cross-continental comparisons are hampered by substantial technique variations between areas (C. Rutz et al., unpubl. data). Bijlsma (1997) produced a manual describing field methods for raptor research, which succeeded in standardizing the work of Dutch field workers, yielding large, comparable data sets. It would be desirable if a similar manual could be compiled for international use. Taken together, these measures will ensure that data collected with much fieldwork effort can be efficiently used in collaborative analyses.

ACKNOWLEDGMENTS

We are most grateful for the invitation to contribute to this goshawk monograph. We thank A. Kacelnik and I. Newton for stimulating discussions of ideas presented in this paper; and I. Newton, V. Penteriani, W. van Manen, and F. Ziesemer for their in-depth review of the manuscript and many helpful comments. Thanks to C. Marti for his editing work, and for being so patient during the final stages of manuscript preparation. The following colleagues kindly communicated unpublished manuscripts and/or data: D. E. Andersen, I. Aparova, A. Dekker, A. Gamauf, E. Guthmann, S. Kluth, O. Krone, W. van Manen, P. Marcus, T. Mebs, A. Mitschke, J. T. Nielsen, V. Penteriani, M. Risch, W. Scharenberg, H. Sevink, H. Steiner, M. Weber, and H. Wirth. Our cross-continental comparison of goshawk demographics greatly benefited from having access to draft manuscripts of other articles in this volume. Dirk Zoetebier (SOVON Vogelonderzoek Nederland) prepared Fig. 6a, and the map shown in Fig. 1 was reproduced with permission from Oxford University Press. During the preparation of this review, CR was holding a Rhodes Scholarship and a Senior Scholarship of St. Catherine's College, Oxford.